Dear Recommender,

Thank you for taking the time to assess our manuscript "Physiological and behavioural resistance of malaria vectors in rural West-Africa : a data mining study to address their fine-scale spatiotemporal heterogeneity, drivers, and predictability". We would also like to thank the two reviewers for their time, their positive assessment of the work, and their thoughtful feedbacks. The reviewer's comments have helped us to further improve and sharpen the manuscript.

Below we provide the point-by-point responses to the reviewer's comments. When changes made in the manuscript are described, the words in green are those that were added in the revised version ; while the words with ~~strikethrough~~ are those that were removed in the revised version. Please note the line numbers refer to the lines in the revised manuscript.

Sincerely,
Authors

Reviewed by anonymous reviewer, 11 Nov 2023 16:11

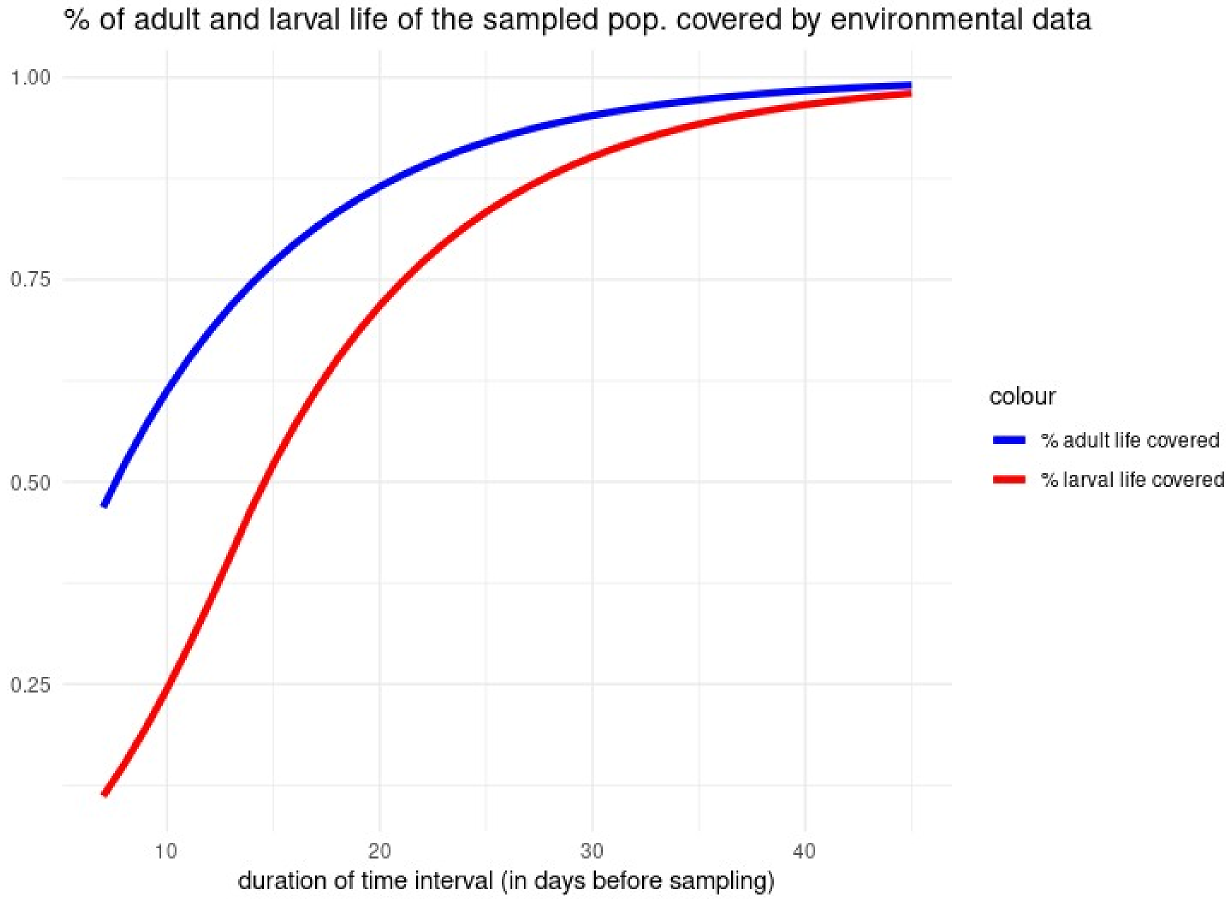
This is a very nice piece of work that demonstrate the intensity and spatio-temporal heterogeneity of physiological and behavioural resistance in malaria vectors, at the scale of a rural health district over the study period.

However, there are few things to clarify for guiding the readers. These are as follow:

1) What motivated the use of weather data collected "a month" preceding mosquito collection as we know mosquito takes ~14 days between eggs to adults?

Thank you for your comment. The choice of one month was made because we wanted to encompass largely the whole duration of the Anopheles life cycle in the field (including aquatic and aerial stages).

Considering a maximum daily survival rate of 0.9 (Soma et al. 2020) for adult anopheles in our study area and a larval stage duration dependant on temperature (Bayoh et al. 2003), we expect that a 1-month interval allow to cover 95 % of both adult and larval life of the sampled population as shown in the figure below. The code used to produce this figure was made available in the Data and code used for this article (Taconet et al., 2023a).



To generate the variables of weather conditions during the month preceding collection, we first collected meteorological satellite-based data distributed at a daily temporal resolution over one month (i.e. 30 days) preceding each collection. We then averaged these data to get one single value representing average of respectively diurnal temperature, nocturnal temperature, and rainfall, over the month preceding collection.

To be clearer in the manuscript, we have rephrased the section where we present the collection of weather data in the revised version of the manuscript (l xx) :

"Meteorological conditions on the day of collection and ~~during the~~ over one month preceding collection were extracted from satellite imagery. Namely, rainfall estimates were extracted from the GPM - IMERG daily Final products (Center, 2019). Diurnal and nocturnal temperatures were derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) daily Land Surface Temperature (LST) Terra and Aqua products (Wan et al., 2015a,b). These data ~~Rainfall and temperatures~~ were then cropped and averaged in 2-km buffer zones around each HLC collection point. ~~to create meteorological variables on both the day of collection~~ From this, variables representing meteorological conditions on the day of collection and over one month preceding collection were constructed (for the latter, by averaging the 30-day time series). Detailed descriptions of the methods used to collect and process these data are provided in Taconet, Porciani, et al. (2021)."

2) As you explored the association between the weather data (within a 2 km buffer) and the mosquito exophagic behaviour, how far were the indoor and outdoor position to each other?

The distance between indoor and outdoor collection points was at least 10 meters to minimize competition between mosquito collectors (Coffinet et al. 2009). To make it clearer, we have added the following sentence in the methods section (l. xx) :

« The distance between indoor and outdoor collection points was at least 10 meters to minimize competition between mosquito collectors (Coffinet et al., 2009).»

3) How reliable are you on your human behavioural data? Have you considered that may be possible biases in these behavioural data because the head of the house will not stay/sleeping in the same house as the >18 years olds people, and will not know when that person is sleeping or not under bed-nets. Additionally, the time given will be approx.

Thanks for your comment on the quality of the human behavioural data. We fully agree that it is only declarative data, with all the limits associated with such kind of data. Unfortunately, although it has been acknowledge that human behavioural data are fundamental to understand residual malaria transmission, there is no standard way to collect them (Monroe et al.. 2019). The review by Monroe et al. identifies the studies that have collected these kind of data in sub-saharian countries. According to this review, the method that we used in our study was also used in other studies (Moiroux et al. 2014, Cooke et al. 2015, and Kamau et al., 2017), providing, if not a validation, at least some kind of confidence in the methodology. However, we acknowledge that these data may contain biases, and that, as stated by Monroe et at., a standardized and validated approach to collect these data is urgently needed.

Nevertheless, to limit the biases as much as possible, in our study we have made an important sampling representing more than a third of the total population of the villages (Soma et al., 2021). In addition, we have excluded from further analyses answers to the survey that were given with a precision lower than the nearest hour. See Soma et al., 2021 for more details on these human behavioural data and Moiroux et al. 2014 for the questionnaire and data collection methodology.

4) Since you consider the rainfall during collection as binomial (presence/absence). Was there any collection when it was raining? Please advise how this was done - in the manuscript.

Yes, collections (outdoor) and rotations of collectors may have been interrupted when it was raining (even though we tried to ensure that outdoor collections took place under cover). This variable was used to take into account these possible interruptions, which were not necessarily indicated in the entomological data. To get the information on whether it was raining or not during the night of collection, we have collected satellite data from the Global Precipitation Measurement (GPM) mission that are made available at an half-hourly temporal scale, as described in l. xx of the manuscript. We have collected these data on the dates and places of collection, from 17:00 to 09:00, and then summed-up the rainfall values for each hour of collection. If the sum was > 0, we have considered rainfall during the hour of collection as ‘present’, else ‘absent’. According to this method, the data shows ‘presence of rainfall’ for, in total, 17% of the hours of collections.

To explain in the manuscript how this was done, we have revised the « methods » section. We have added the following sentence l. xx :

« For example, we constructed a binary variable "Rainfall during collection" (presence/absence of rainfall during the hour of collection) by summing the source data available at a 30-minutes temporal resolution and then applying a threshold (> 0 mm of rainfall = presence, otherwise absence) ».

5) Authors should revise the line 359, as “R2 Î{0.02, 0.13}” is considered twice but first “very weak” and then “weak”. Should also revise the closing brackets on lines 359 - 360 then 366 – 367

Thank you for pointing out these inconsistency. We have now revised the manuscript as suggested : removing one of the two occurrences of “R2 Î{0.02, 0.13} and closed the brackets on lines xx and xx.

6) Revise line 377 to remove the second “were” after “used”. Then, on page 15, second line, make space between the dote and “For” then on the third line should the “th” be “the” instead?

Thank you for pointing out these inconsistencies as well. We appreciate your attention to detail. We have now revised the manuscript as suggested.

7) In addition, it increased when luminosity got relatively higher indoors compared to outdoors.” Is that correct? If yes, how do you explain the fact that luminosity get higher indoor than outdoor while outdoor you have the sunlight?

Yes, the sentence is correct. Mosquito data collection occurred between 17:00 pm and 09:00 am (see l. xx of the revised version), hence mostly during night time (but also at dusk and dawn). During the night hours, the luminosity outdoor was almost null, while indoors, lights might be used by the population : this is the reason why luminosity can be higher indoor than outdoor.

8) Should remove the closing bracket on line 571 and please revise the line 576, word may be missing “… in fine …”

Thank you for pointing out this inconsistency. For the closing bracket , we appreciate your careful observation. We have revised the manuscript as suggested. For line 576, in response to question n°16 from Reviewer 2, we have removed the whole sentence that contained the words “… in fine …”.

9) Should consider revising the sentence from line 609 to 612; “Second, the exophily were substantially higher than those, overall, historically ...” and subsequently your discussion on the following lines as checking on some of your references - the (Sanou et al., 2021) - you cited indicates outdoor biting of 54% which is > 41% you found here.

Thanks for this comment, which led us to moderate our comparison with historical data. In fact, some of the references that we initially cited reported mixed exophagy rates compared to ours (some were in fact higher, but others were more or less equal, or slightly lower). We have hence modified the pointed sentence, by both developing and moderating our demonstration. Here is the revised text :

“Indeed, the exophagy rates measured here tended to be higher than those historically reported for these species. For example, a recent review of *An. gambiae s.l.* biting behaviour from a range of African countries between 2000 and 2018 concluded that during this time period, ~ 80% of the vectors bite occured indoor (all countries included) and in particular ~ 75% in Burkina Faso

(Sherrard-smith et al., 2019) (hence respectively ~ 20% and 25 % outdoor). Here we measured substantially higher levels of exophagy : 44% (range ~ 18-56%) in the Diébougou (BF) area and 56% (44–60%) in the Korhogo (IC) area. Other recent studies, contemporaneous to ours, have found relatively high levels of exophagy for *An. gambiae s.l.* in rural areas, e.g. 54% in southwestern Burkina Faso (Sanou et al., 2021) or 55% in Ivory Coast (Assouho et al., 2020). Such high levels of outdoor biting, in comparison with past levels, suggest that behavioural adaptations may be ongoing in the study areas, most probably in response to the widespread and prolonged use of insecticide-based vector control tools."

NB : Reviewer 2 made a similar question (see questions n°23 and n°24 of Reviewer 2)

10) Authors should also bear in mind when interpreting the results that human behaviour is somehow affected by the weather condition too. Thus, the time spend indoor is probably higher when temperature is cooler outside houses thus affecting the perceptions on exophagic behaviour at that time of collection. Thinking about, An. funestus biting outdoor for example. In addition, did you check for correlation between % indoor temperature and human behaviour that may affect mosquito behaviour as well? Please provide some insight on that.

Thank you for this interesting and very relevant comment. In fact, as suggested, it has been shown that weather conditions can be associated with shifts in human behaviours, e.g. time spent indoor or LLIN use. For instance (among other studies), Moiroux et al., 2012a found that low nocturnal temperature and high biting nuisance were good predictors of LLIN use > 60% in Bénin. Fombang & Moungbakou, 2022 showed that the very high temperatures discourage the use of mosquito nets in Cameroon.

In our study, as explained in the mat&met section, we first excluded the independent variables that were poorly associated with the dependent variable and then filtered-out the remaining variables that were collinear, based on empirical knowledge (i.e. keeping only 1 variable out of the 2 that were collinear, where applicable). Hence, all the variables that were retained as input of the multivariate models were both highly associated with the dependent variable and not correlated with one other. When variables encoding for both human behaviour and weather conditions were retained in the multivariate models, this meant that they were not correlated (Pearson correlation coefficient < 0.7).

11) Please revise the lines 683 - 684 where the word "data" may be missing after "… resistance..."

Thank you for pointing out this inconsistency. We have revised the manuscript as suggested, by adding the word « data » after « resistance » as recommended.

12) The first sentence of the conclusion is confusing, as in the paragraph (lines 482 - 4885) it is stated that exophagic behaviour was not associated with the time since LLIN distribution within the time frame of the current study. Please revise accordingly.

Thank you for pointing out this confusing sentence. We have deleted it from the manuscript and rearranged the text in the conclusion, so as to first present the main results of the study and then open the discussion. The new version of the conclusion is as follow :

«~~Less than a decade after the first universal LLIN distribution, malaria vectors in two areas of rural West-Africa seem to be growingly adapting to avoid or circumvent the lethal effects of insecticides used in control interventions.~~ In an attempt to better understand the drivers of the intensity and spatio-temporal heterogeneity of physiological (genotypes) and behavioural (phenotypes) resistance in malaria vectors, at the scale of a rural health district over a period of 1.5 years, we have mainly (i) shown that resistance (both physiological and behavioural) was quite homogeneous across the villages and seasons at theses scales, and (ii) hypothesized that at these spatiotemporal scales, vector resistance seemed to be only marginally driven by environmental factors other than those linked to insecticide use in current vector control. Following the distribution of LLINs, the rapid widespread of physiological resistance occurring in tandem with probable lower acting behavioral adaptations, are very likely contributing to the erosion of insecticide efficacy on malaria vectors. We believe that without waiting to understand precisely the underlying drivers, mechanisms, and rates of selection of resistances, the malaria control community needs to think very strategically about the use and usefulness of current and novel insecticide-based control interventions. »

Reviewed by Haoues Alout, 03 Nov 2023 16:54

In the manuscript entitled "Physiological and behavioural resistance of malaria vectors in rural West-Africa : a data mining study to adress their fine-scale spatiotemporal heterogeneity, drivers, and predictability" presents a modeling work taking advantage of a very large dataset to identify environmental drivers of insecticide resistance in malaria vectors. Among the insecticide resistance traits investigated, they are mutations in kdr and ace-1 loci and also behavioural resistance phenotypes. As detailed in the ms, genetic basis of behavioural phenotypes are not characterized and the apparent resistant phenotypes have not been related to molecular mechanism. Due to the absence of evidence of inheritance of such behavioural phenotypes, we cannot clearly qualify these as resistance. Therefore the discussion related to this should be more developed.

Thank you for reminding that in our study, it is unknown whether changes in the prevalence of studied mosquito behaviours are the result of constitutive resistances (i.e. inherited traits selected by the insecticide pressure) or of inducible resistance that rely on phenotypic plasticity. It is true that the latter (inducible resistance) does not fit an accepted definition of insecticide resistance that rely on the heritability property (Zalucki & furlong 2017), as highlighted by the reviewer. However, it is common to characterize phenotypes as resistant (« phenotypic resistance » or « non-inherited resistance ») when (i) genetic basis are unknown, (ii) genetic doesn't explain all the variability, or (iii) phenotypic plasticity is involved, both for the particular case of insecticide resistance and for other fields such as antibiotic/drug resistance. Nevertheless, we agree that we should still be more prudent with the terminology used in general in the manuscript regarding this important point. Towards this aim, we have modified the text and the figures to use, when relevant, the terminology 'behavioural resistance phenotypes' instead of 'behavioural resistance'.

We have also rephrased the warning in the methods sections:

"Here, it is unknown whether changes in prevalence of studied mosquito behaviours are the result of constitutive resistances (i.e. inherited traits selected by the insecticide pressure) or of inducible resistance (that rely on phenotypic plasticity). The latter do not fit an accepted definition of insecticide resistance that rely on the inheritance property (Zalucki 2017). Therefore in the remainder of this manuscript, we will qualify the three studied phenotypes, possibly constitutive or inducible, as 'behavioural resistance phenotypes'."

Overall the ms is well written and provide clear explanations to understand their complex models so that their work is quite accessible to a large audience.

Here are some comments to help improve the ms.

1) The use of the term "development" for an adaptive traits in the field of ecology and evolution is misleading. Indeed, development is a very complex process more often used at the individual level that does not describe an adaptative process that occurs at the population level. The term selection is more appropriate and should be used along the manuscript (for instance but not limited to selection "of physiological mechanism of resistance", l72; selection "of resistant phenotypes", l77; "of physiological and behavioral resistances", l125; "of the kdr-e mutation", l559; "of resistances", l737)

Thank you for pointing out this subtle yet important difference, with which we agree. As proposed, we have replaced the term « development » by « selection » when relevant, including but not limited to the lines indicated by the reviewer.

2) L190: It is not clearly specified in this section whether mosquitoes from IC were genotyped for kdr-w and -e and ace1 G119S. Authors should add this information with some brief justification here.

Thank you for pointing out this lack of information. In the IC area, contrary to the BF area, individuals belonging to the *Anopheles gambiae s.l.* complex were not systematically genotyped for kdr-w and -e and ace1, due to the very large number of individual captured. The sampling methodology is detailed in the data paper describing the entomological collections (Taconet et al., 2023b), whose reference is provided at the end of the section « Anopheles collections » in the mat&met section of the manuscript. Here is a reminder :

In the CI area, for the first four entomological surveys : Due to the vast numbers of vectors collected, a subsample of Anopheles vectors from six villages randomly chosen out of the 28 included in the study were further analyzed: […] for one individual of the *A. gambiae* complex randomly selected per hour per collection site (indoors/outdoors) during each survey in these six villages: species were identified by PCR; *P. falciparum* infection was detected by qPCR; L1014F (kdr-w) and G119S (ace-1) mutations were detected by qPCR.

In the CI area, for the last four entomological surveys : for a subsample representing 25% of the captured *A. gambiae* : species were identified by PCR; *P. falciparum* infection was detected by qPCR; L1014F (kdr-w) and G119S (ace-1) mutations were detected by qPCR.

In our study, we decided to exclude the IC data from the modeling of the physiological resistances because data were available only for 6 villages in half of the entomologial surveys.

To clarify these information in the manuscript, we added the following sentence, l xx :

« In IC, also due to the large numbers of individuals collected, a subsample only of the *An. gambiae s.l.* were genotyped for the L1014F and G119S mutations. Due to the significant risk of bias associated with the sub-sampling strategy (not all villages were sampled in all surveys), we excluded these data from the analysis. »

3) L254: Streams are used as proxy of breeding sites but several stream characteristics (such as the width and the inter connections) are important factors for mosquito oviposition and

density. Authors should give more information on the streams in the studied area and provide evidence or reference that such streams are primary breeding sites for Anopheles gambiae?

Thanks for the suggestion. In fact, we have references showing that streams are breeding sites for Anopheles in our study areas (although they are not the only ones, i.e. rice paddies, dams, and puddles are also important habitats for Anopheles spp. larvae) :

- In the Korhogo area (CI), a field study aiming at identifying the Anopheles spp. breeding habitats was specifically performed by our team (Zogo et al., 2019) and concluded that in the rainy season, edges of rivers and streams were the second most abundant habitats for Anopheles spp. larvae (after being rice paddies) ;
- in the Diébougou area (BF), a modeling study using the anopheles data and satellite-derived environmental variables hypothesized that streams and marshlands (which are spatially interrelated) may be potential breeding sites for *An. gambiae s.s.* and *An. coluzzii* (Taconet et al., 2021).

It should be noted as well that in our study areas, streams are spatially interrelated with other potential breeding sites, e.g. riparian forests (i.e. streams flow under riparian forests) or flooded crops which depend on the streams (e.g. rice), as can be seen from the very high spatial resolution land-use-land-cover data that were produced in both areas and published in an open data repository (Taconet et al., 2023c, Taconet et al., 2023d).

To moderate our statement and provide more information about the breeding sites in the manuscript, we have slightly modified the text (l xx) and added the references : « […] distance to the nearest stream (as a proxy for the distance to ~~the~~ potential breeding sites, as shown in other studies conducted in these areas (Zogo et al. 2019, Taconet et al., 2021)»

NB : we have, as well, included the references to the raw land-use-land-cover data in the Methods section (l xx). These data were not published at the date the article was submitted.

4) L297: I wonder how relevant/important is to model separately for each site; authors should provide a clearer justification for this strategy. One can question the generalization of their results to other similar sites which could decrease the relevance for the scientific community.

Thanks for this interesting comment. As explained in the manuscript l xx : « Each indicator was modeled separately for each main species in each study area, as determinants of resistance might be species- or site-specific (i.e. mosquitoes might respond differently to environmental variations depending on the species and study area, due to potential local chromosomal forms, adaptation, etc.) (Durnez and Coosemans, 2013; Riveron et al., 2018). » Importantly, we allowed ourselves to do so because the number of mosquitoes collected at each site and for each species was, overall, sufficiently high to obtain statistically significant correlations - where applicable. In the results, we see that the independent variables retained by the variable selection process are not necessarily identical between the two areas (for one given resistance indicator and species), and that the shape of the relationship, for identical variables retained in both areas, may differ. In some way, this supports the hypothesis that mosquitoes might respond differently to environmental variations due to local settings.

5) L321: Authors should provide examples of empirically known collinear variables.

Thank you for your suggestion. In the revised version of the manuscript, we provided two example of collinear variables found in the data, according to our criteria (Pearson correlation coefficient > 0.7) (l xx) :

« Next, we calculated the Pearson correlation coefficient among the retained variables and filtered-out collinear variables (~~Pearson~~ correlation coefficient > 0.7) based on empirical knowledge (for instance, diurnal and nocturnal temperature over the month preceding collection were often correlated and in such case we retained nocturnal temperatures ; % of the population indoor and under an LLIN in the village on the hour of collection were often correlated and in such case we retained % of the population under an LLIN). »

6) L397: Authors presented a detailed results of mosquito collections in both sites. However, overall percentage of mosquito species did not reach 100%: 98% in Ivory Coast and 86% in Burkina Faso. What other vectors were found?

Thank you for your careful observation. In fact, among all the *Anopheles* mosquitoes collected, respectively 98 % and 86 % in Ivory Coast and Burkina Faso were *An. gambiae s.l* or *An. funestus*. Other Anopheles species were found, but they were not included in the study due to their low frequency. In Ivory Coast, they included : *An. nili, An. pharoensis, An. ziemanni, An. coustani* and in Burkina Faso : *An. nili, An. pharoensis, An. rufipes, An. squamosus.* For additional details, see source data (Soma et al., 2023) as well as publications related to these data : Zogo et al. , 2019, Soma et al., 2020 , Taconet et al., 2023b . Although subtle, the fact that other species were found is traduced by the word « main » in the sentences (l xx and xx) : « The **main** species/complex found were ... ».

7) Table 2: To what part of the table this computation refers to? Description of the computation of standard deviation may be more relevant in the mat & met section.

Thank you for noting that it is unclear what the « computation of standard deviations » refers to in the caption of Table 2. It actually refers to the columns 'Temporal confidence interval and range' and 'Spatial confidence interval and range'. We actually preferred to put the description of this calculation in the caption of the table rather than in the mat&met section because in the mat&met we wanted to stay focus on the modeling workflow (which is already a quite important piece of work). Placing this calculation harmoniously in the materials and methods section is not trivial to us.

However, to clarify what the « computation of standard deviations » refers to, we have modified the caption in the manuscript, by harmonizing the terms used between the columns of the table and its caption : '[…] *Format of these columns: ~~standard deviation~~ confidence interval (minimum – maximum). Computation of ~~standard deviations~~ confidence intervals (columns 'Temporal confidence interval and range' and 'Spatial confidence interval and range') : to take into account the uneven sample size between entomological surveys (resp. villages) (i.e. to avoid excessive consideration of small / very small sample size), ~~standard deviations~~ confidence intervals for temporal (resp. spatial) variability were extracted by first calculating the resistance indicator for each entomologial survey (resp. village) and then computing the standard deviation weighted by the number of mosquitoes collected in each entomologial survey (resp. village).*'

8) L440: An explanation/justification should be provided on the removing of dependent variable with low number of resistant (i.e. “small size of their resistant class”). I would understand that when sample size is very small but having few or no resistant mosquito in a village is still informative and should be considered.

We have indeed made the choice to exclude some of the dependent variables because they had a combination of a very low number and percentage of resistant mosquito (the criteria for the exclusion of dependent variables, as indicated in the mat&met section, was : ‘resistant’ class ≤ 50 observations & ≤ 3% of the total observations.). As can be seen in Table 2, the dependent variables that were excluded with respect to these criteria had the following sample sizes:

- BF, early biting of An. gambiae s.s. : 19 ‘resistant’ mosquito out of a total of 616 collected
- BF, early biting of An. coluzzii : 28 ‘resistant’ mosquito out of a total of 1321 collected
- BF, early biting of An. funestus : 9 ‘resistant’ mosquito out of a total of 708 collected
- BF, late biting of An. gambiae s.s. : 8 ‘resistant’ mosquito out of a total of 616 collected
- BF, late biting of An. coluzzii : 46 ‘resistant’ mosquito out of a total of 1321 collected
- IC, late biting of An. funestus : 4 ‘resistant’ mosquito out of a total of 714 collected
- BF, ace-1 for An. coluzzii : 2 % out of a total of 1321 collected

When we started modeling the data, we made some preliminary attempts to model these dependent variables and extract relevant information, but they resulted inconclusive (e.g. no statistically significant associations despite the amont of independent variables, or spurious coefficients, etc.), most probably because, at the same time, these data (i) have very few samples from the class of interest, and (ii) are that very imbalanced (i.e. number of samples from one class >> number of samples from the other class).

However, we do agree that this is not presented in a clear manner in the manuscript. In order to be more precise, we have modified the text in the mat&met section (l xx) :

« ~~Before modeling, we excluded the dependent variables that had too few ‘resistant’ observations, according to the following criteria : ‘resistant’ class ≤ 50 observations & ≤ 3% of the total observations.~~ First, we excluded from the modeling process those dependent variables that could hardly be modelled due to the combination of very few ‘resistant’ observations and extreme class imbalance (number of samples from the ‘resistant’ class << number of samples from the ‘sensible’ class). The following criteria were used for exclusion : ‘resistant’ class ≤ 50 observations & ≤ 3% of the total observations. »

9) Figure 3: The presentation of the effect of other variables should be better organized, probably splitting the insecticide effect and the environmental in two separate panels.

Thank you for the suggestion. Although we do agree that the presentation of the effects of other variables could be better organized, we have not find a simple and convincing way to reorganize the plot (mainly due to plot size constraints). However, to mark the distinction between insecticide-related and environmental variables, we modified the title of the panel located on the left-hand size of the plot : « Effect of ~~other~~ LLIN use and environmental variables ». For consistency, we made the same modification in Figure 4.

10) Figure 3: Attention should be paid to the square indicators that are not clearly presented in the figure caption. There are two types of squares in the figures that should be both presented.

Thank you for this precision. We have modified the captions of Figure 3 and 4 to clearly present the two kind of squares and differentiate between them, as following :

« The coloured squared at the bottom-right represents the ‘family’ the variable belongs to (one color for each family, see legend inside the light green frame placed on the left hand side of the plot) . The grey squares distributed along the x-axis at the top and bottom of each plot represent the measured values available in the data »

11) Figure 3: In the result section, the influence of kdr-w genotypes on the probability of collecting a resistant mosquitoes shown by orange squares in figure 3 is not presented clearly.

Thanks for pointing this lack, we added the following paragraph in the results sections :

"Association with variables encoding genotype for other insecticide resistance target-site mutations: The likelihood of collecting a host-seeking An. gambiae s.s. or An. coluzzii carrying a resistant kdr-e allele was negatively associated with the number of mutated kdr-w alleles in the collected mosquito. Conversely, the likelihood of collecting a host-seeking An. gambiae s.s. carrying a resistant Ace-1 allele was higher in individuals also carrying kdr-w mutated alleles."

And the following was added to the discussion section (l xx):

"We also found interactions between some target-site mutations. Indeed, as the kdr-e and kdr-w are mutations of the same base pair, the allelic frequency of the kdr-e mutation was negatively correlated with the allelic frequency of the kdr-w mutation in both An. gambiae s.s. and An. coluzzii. We also found a positive relationship between the allelic frequencies of the Ace-1 and kdr-w mutations in An. gambiae s.s.. This is consistent with laboratory observations in Culex Quinquefasciatus and An. gambiae s.s. showing that the cost of the Ace-1 mutation is reduced in presence of the kdr mutation (Berticat et al., 2008, Assogba et al., 2014, Medjigbodo et al., 2021)"

12) Related to figure 4, the difference between the inference made from glmm (explanatory) and RF (predictive) should be made clearer by providing more detailed explanation or by providing examples. To illustrate this point, the explanatory power for exophagy in An. gambiae from IC is very low, suggesting that none of the tested variables can explain exophagy variation or that these variables captured very little of this variation. Thus how could they explain (or predict) well exophagy ?
Generally, it should be clearly stated that non-significant variables are not presented.

Thank you for this relevant comment. In the statistics scientific community, a distinction is made between explanatory and predictive modeling : explanatory modeling refers to « *the application of statistical models to data for testing causal hypotheses about theoretical constructs* », while predictive modeling is « *the process of applying a statistical model or data mining algorithm aimed at making empirical predictions, and then assessing its predictive power.* » (Shmueli, 2010a). This fundamental difference implies that choices made throughout the whole modeling process (choices of variables, of model types, model evaluation, etc.) will differ depending on whether the goal is explanation or prediction (see e.g. Schmueli 2010a). For example, the choice of the model : by definition, explanatory modeling needs, transparent, interpretable models (hence the choice of GLMM for example) while predictive modeling needs models that are able to capture at best complex, potentially unhypothesized, associations between variables. Another example of difference between explanatory and predictive modeling is the selection of the method used to evaluate the performance of the model : explanatory power should be measured from the in-sample data while predictive power should be measured from out-of-sample data or using cross-validation. This is because explanatory power evaluates the strenght of the relationship between the dependant and independent variables, while predictive power evaluates the ability of the model to generate accurate predictions of new observations. It is important to note that aside from their practical usefulness, predictive models play an important role in theory building, theory testing, and relevance assessment. (Schmueli, 2010b). For instance, by evaluating the predictibility of a phenomenon using data, we can test theories: if the predictive power is high, then we can hypothesize that the phenomenon is well apprehended ; and conversely, if the predictive power is low, it probably means that many variables are missing.

In our study, as explained in the Box 1 (l xx), we used both explanatory and predictive modeling to get the best of both worlds :

- we used explanatory modeling, with transparent and directly interpretable models (i.e. GLMMs), to test whether vector control significantly increases vector resistance (as could be expected) + possibly find environmental factors that impact vector resistance and, if so, measure their effect, statistical significance. Even if the explanatory power of the model is low, associations that are statistically significant are worth discussing, because they can be used to infer the functioning of the complex system under study. This is, actually, what we mainly do in the discussion when we translates the statistical associations catured by the GLMM in terms of mosquito bio-ecology ;

- we used predictive modeling, with RF able to capture complex associations, to assess the distance between theory (potential / identified determinants of vector resistance) and practice (are they enough to predict resistance on unseen mosquitoes ? If not, why ?). In the results section, we have reported that both the explanatory and predictive powers of our models were overall weak for the behavioural resistance models, especially for exophagy (see section «Explanatory and predictive power of the statistical models » starting from l. xx). In the discussion, a paragraph (starting from l xx) makes use of these information to infer, for example, that mosquito foraging behaviour was probably only marginally driven by environmental variation (since most of the independent variables were environmental).

Nevertheless, we do agree that the manuscript lacks explanations regarding the conceptual differences between explanatory modeling and predictive modeling and how we used them in our study for inference. To clarify our point, we have modified the first paragraph in the « Box 1 » by taking an 'explanatory vs. predictive modeling' point of entry instead of a 'logistic regression vs. random forest models' one. The modified text is as following :

« Box 1 : *What is the difference between explanatory and predictive models, and how were they used for inference in this study ?

Explanatory and predictive models serve distinct but complementary functions in the production of scientific knowledge. In statistics, explanatory modeling refers to « the application of statistical models to data for testing causal hypotheses about theoretical constructs » (Shmueli, 2010). Explanatory modeling, commonly used for inference in many scientific disciplines such as biology or epidemiology, is useful to test existing theories and to reach to "statistical" conclusions about causal relationships that exist at the theoretical level, e.g. : vector control significantly impacts vector resistance (or not). Explanatory modeling needs transparent and interpretable models, such as linear of logistic regression, to extract statistical information about the associations contained in the data (e.g. effect size and statistical significance) and further discuss them. On its side, predictive modeling is « the process of applying a statistical model or data mining algorithm aimed at making empirical predictions, and then assessing its predictive power. » (Shmueli, 2010). Predictive modeling requires models capable of capturing complex patterns in the data, including interactions and non-linear associations, such as *machine learning* models like random forests or support vector machines. Predictive analytics is typically recognised for its usefulness in practical applications, such as predicting the incidence of diseases. However, it can also play a crucial role in scientific knowledge production. For instance, predictive models can help generate new theories by capturing and revealing potentially complex, unanticipated patterns within the data. They can as well be used to evaluate the overall relevance of a theory, through the interpretation of the predictive power of the models (Schmueli and Koppius, 2010). In a "big data" context like that of this study, with large datasets containing numerous observations and variables, predictive analytics is increasingly used to support scientific theory development (Breiman (2001b), Karpatne et al. (2017), Shmueli and Koppius (2010)).

In our study, we use explanatory modeling with GLMMs to i) test whether vector control significantly increases vector resistance, as could be expected, and ii) infer the potential determinants of vector resistance along with the size of their effect . We use predictive modeling with RFs to i) account for potential unhypothesized, complex associations between independent and dependent variables, and ii) infer the overall contribution of the independent variables to the prevalence of vector resistance, allowing at the same time to formulate hypotheses on other potential determinants. »

Lastly, as suggested, we have added in the captions of Figures 3 and 4 that non-significant variables are not presented in the plots.

13) L553: in the title, probably replace and by of

Thank you for the suggestion. However, we are not sure which «and » you propose to replace by « of » in the title. The title in its current form suggests that we study, at fine spatio-temporal scales, i) the heterogeneity, ii) the drivers, and iii) the predictability, of physiological and behavioural resistance of malaria vectors in rural West-Africa.

14) L554: One interesting result is the increase of kdr-e associated with the time of LLIN distribution. However, it is not challenged enough against the literature. Several reports showed that ageing of LLIN reduce their efficacy thus the insecticide selective pressure is reduced. So how do authors discuss that kdr-e increases if the selective pressure decreases?

Thank you for your interesting remark. In our context, in the BF area, a mass distribution of LLINs (PermaNet 2.0) was carried out by the National Malaria Control Program in July 2016 (i.e. 6 months before our first entomological survey), as indicated in the mat&met methods ; and the duration of our study was 15 months. Hence, the last entomologial survey was 21 months after the last distribution of new LLINs.

Long-term efficacy studies of PermaNet 2.0 LLINs conducted in the field seem to have produced results that, while sometimes contradictory, suggest that the efficacy of the LLINs was satisfactory within the time frame of our study (21 months) – or at least for the first 12 months : For example :

- Kilian et al., 2008 found that the PermaNet 2.0 caused 80% mortality of *Anopheles gambiae* after 36 months of follow up.
- Kayedi et al. 2017 found that *Anopheles stephensi* mortality rate was not less than 85% after 5 years of use of the LLIN.
- Tan et al, 2016 found a high efficacy 1 year after distribution (89 % mortality at 24 h of exposure) and quite low (32%) 2 years after distribution.
- Djènontin et al., 2023 found that *An. gambiae s.l.* mortality rate was still above 90% after 2 years of use of the LLIN.

Hence, we can probably consider that the selective pressure on the malaria vectors remained high, at least for the first half of the study, resulting in an increase of kdr-e. It is interesting to note that the random forest model (which is inherently able to capture non-linear associations, unlike the GLMM) for the kdr-e mutation seem to indicate that the probability of collecting a host-seeking mosquito carrying the kdr-e mutation increases up to 12 months after LLIN distribution, but then stabilises for the next 10 months. This may indeed be due to a reduced efficacy of the LLIN after 1 year, resulting in a lowered selective pressure.

To discuss this point in the manuscript, we have added the following lines :

- l xx (results) : «However, the likelihood of collecting a host-seeking *An. gambiae s.s.* or *An. coluzzii* carrying a resistant kdr-e allele increased with the time since LLIN distribution, and as well with the % of users of LLINs in the village population. Noteworthy, for both species the random forest models predicted a significant linear increase in the 12 first months after the distribution, and a slowdown in the increase from the 12th to the 21th month after LLIN distribution. »

- l xx (discussion) : «In this study, we found that the probability of collecting a host-seeking *An. gambiae s.s.* or *An. coluzzii* in the Diébougou area carrying a kdr-e resistant allele significantly increased with both the time since LLIN distribution (up to 12 months after distribution) and the % of LLIN users in the village population. PermaNet 2.0 LLINs have been shown to retain their insecticidal efficacy under field conditions for at least one year after distribution (Kilian et al., 2008, Kayedi et al. 2017, Tan et al, 2016, Djènontin et al., 2023), exerting high selective pressure on vectors over this period at least. In contrast, there was no significant association between any of the target-site mutations and any of the crop-related variable. Altogether, this could indicate that within the spatiotemporal frame of our study, the development of the kdr-e mutation in the vector population was more likely due to insecticides used in public health than pesticides used in agriculture.»

- l xx (discussion) : « Noteworthy, the fact that there was no increase in the probability of collecting an An. gambiae s.l. carrying a kdr-e resistant allele 12 months post-LLIN distribution, as indicated by the RF model, could be attributed to a potential decrease in LLIN insecticidal efficacy after this period (Tan et al., 2016), resulting in lower selection pressure. »

15) L571: remove the bracket

Thank you for the suggestion. We removed the bracket.

16) L575: "As stated previously, weather may impact the fitness or the activity of mosquitoes carrying resistant genotypes; and may therefore in fine impact the probability of collecting a physiologically resistant mosquito". As exactly stated, this is repetitive and it may not be necessary for clarity unless it is discussed with different angle.

Thank you for the proposition, which we agree with. We have removed this sentence from the manuscript, as suggested.

17) L577: Authors did discuss weather impacting fitness but only as a cost. Could the associations captured would possibly traduce an advantage of resistant individuals? (for instance rainfall) or is this related only to the current analysis? in such case more detailed information should be provided.

We agree with the reviewer. There is some evidence in the literature for fitness advantages associated with the kdr mutation in *An. gambiae* under laboratory conditions. Consequently, changes in frequency due to weather could also be interpreted as a result of fitness advantage and not only as a cost.

To include this point in the manuscript, we modified the sentence as follow:

“Here, the associations that were captured could hence traduce biological costs/advantages associated with target-site mutations, both in terms of fitness and activity [...]”

and we added the following (l. xx) :

“Noteworthy, our results could also be interpreted in terms of fitness advantages instead of fitness costs : for instance, some studies have highlighted fitness advantages (e.g. for longevity) of the kdr-w mutation in An. gambiae s.l. in laboratory conditions (Alout et al., 2016, Medjigbodo et al., 2021).”

18) L581: Decrease of mutated allele is discussed as associated with hot season. Seasonality is different from hot (or hotter) vs cold (less hotter) season. Thus authors should define better the hot season in the context of west Africa.

Thank you for your proposition to better the define what we call here « hot season ». It is named this way, in fact, in contrast with the less hot season. We rephrased the sentence in the revised version of the manuscript to make it clearer (l xx) :

« Regarding fitness, we found that the likelihood of collecting a host-seeking mosquito (*An. gambiae s.s.* or *An. coluzzii*) carrying a mutated allele, overall, decreased (to varying extents depending on the species and mutation) ~~in the hot seasons (i.e.~~when diurnal or noctural temperatures during the month preceding collection got higher), i.e. in the hottest periods of the year (corresponding to ~ the months of March-April). »

19) L582: “Carrying a kdr mutation might be associated with a reduced ability to seek out optimal temperatures”. Authors should rephrase this sentence to make it clearer.

Thank you for the suggestion. We rephrased the sentence in the revised version of the manuscript to make it clearer (l xx) :

« Carrying a kdr mutation might be associated with ~~a reduced ability to seek out optimal temperatures~~ a decreased propensity to locate optimal temperatures, potentially resulting in a decreased longevity, fecundity, or ovarian development rates »

20) L595: “The relative seasonal ...” Authors should rephrase this sentence to make it clearer.

Thank you for the suggestion. We rephrased the sentence in the revised version of the manuscript to make it clearer (l xx) :

« ~~The relative seasonal homogeneity might traduce that fitness costs, despite their existence, might be limited within the range of meteorological conditions in our area.~~ The quite stable rates of physiological resistance throughout the seasons might traduce the fact that the possible fitness costs/ advantages are likely rather limited, within the range of meteorological conditions in our area. »

21) L607: “to” should be replaced by “of”

Thank you for the suggestion. We have revised the manuscript as suggested.

22) L609: While genetic basis of behavioural phenotypes may be indeed found, it is difficult to understand how larval stage may support this. Maternal/paternal effect should better support a genetic basis of behavioural phenotypes and their associated adaptative changes

(i.e. resistance) due to the inheritance of alleles to the next generation. This part of the discussion needs more arguments/clarifications.

We agree with the reviewer that this is over-interpretation. We therefore only focused this part of the discussion on comparison of exophagic rates with that of previous studies, and modified the paragraph as follow (l xx):

"Nonetheless, comparison of the exophagic phenotype rates with that of previous studies in the same countries, suggest that there may still be a genetic component in mosquito foraging behaviour. Indeed, the exophagy rates of the main malaria vectors in both areas [...]"

We then discuss the associations between phenotype prevalence and meteorological condition during the month preceding the collection later in the same paragraph, trying to not over-interpret these results (l xx):

"[…] most probably in response to the widespread and prolonged use of insecticide-based vector control tools. We also found many statistically significant associations between the likelihood of collecting a behaviourally resistant phenotype and the meteorological conditions during the month preceding collection. This might indicate that these phenotypes could be induced by past environmental conditions, acting at the adult or larval stage, or through paternal/maternal effect. Relationships between environmental condition at the larval stage and adult behaviour have been observed in other insects (Müller et al 2016, and ref cited in)."

Nevertheless, under the hypothesis that the resistant phenotypes have genetic basis, if past environmental conditions (during the month preceding the collection) had an effect on the prevalence of behavioural phenotypes, this might indicate that the densities for one phenotype (e.g. the resistant one) increased relatively to the other one. As discussed in the response to 1st comment of reviewer 1, given the mean life span and larval development duration of the Anopheles species collected in our area, weather during a month before collection was expected to influence both the larval and adult lifetime of collected mosquitoes. Therefore, a change in the prevalence of a resistant phenotype in relation to past environmental conditions is expected to be caused by differential effect (for opposite phenotypes) on survival (at adult or larval stages).
According to this, we continue the discussion as follow (l xx):

"The hypothesis of a hereditary component in the behavior of malaria vectors (at least for the biting hour) is supported by a recent study which has observed, for Anopheles arabiensis in Tanzania, that F2 from early-biting F0 (grandmothers) were - to some extent - more likely to bite early than F2 from mid or late-biting F0 (Govella et al., 2023). Under this hypothesis, the relationship between the prevalence of behaviourally resistant phenotypes and the meteorological conditions during the month preceding collection could indicates a cost/advantage, at the adult, larval or both stages, of their associated genotypes."

23) L610: Authors should provide the ranges or confidence intervals with the average exophagy rates.

Thank you for this suggestion. We have modified the sentence by detailing the average exophagy rates and ranges for *An. gambiae s.l.* for each area. More widely, the paragraph including this sentence has been rephrased in response to a comment from Reviewer 1 (see answer to question 9 of Reviewer 1).

24) L613: Authors should provide estimates of the outdoor biting levels from their analysis and the literature ("past levels")

As presented in response to the previous comment and question 9 of Reviewer 1, we have modified the manuscript to provide estimates of the outdoor biting levels from our analysis and the literature.

25) L622-625: Authors discuss the association between time and behavioral resistance with two opposite examples in the literature. They should provide details on the difference and similarities between these two studies and particularly vector species and insecticide resistance.

Thank you for the suggestion. These examples were used mainly to illustrate the previous sentence, i.e. the fact that mosquito behaviours are likely complex multigenic traits that might respond slowly to selection, and that for this reason our 2-years long study, as well as that of Sanou et al. 2021 might be too short too capture any change in mosquito behaviour.

To clarify our point, we modified the manuscript as follow (l xx) :

"In our study, the absence of significant association between the probability of behavioural resistances and insecticide-related variables might be due to the relatively short length of the study (2 years). In a similar study conducted in another region of Burkina Faso over a two-year period as well, researchers recorded, as we have, no changes in the biting behaviour of Anopheles gambiae s.l., including early biting, exophagy, and exophily, throughout the duration of the study (Sanou et al., 2021). Although resistance phenotypes can emerge in this time frame (Moiroux et al., 2012), a recent (almost) 4-years-study in Tanzania (Kreppel et al., 2020) detected shifts in vector behaviour (i.e. increased rate of exophily for An. arabiensis and An. funestus) that could be obscured in shorter-term surveys, in agreement with the hypothesis that mosquito behaviours are likely complex multigenic traits (Main et al., 2016) and might therefore respond slowly to selection (at least, slower than target-site mutations, which are linked to single genes and may hence respond rapidly and efficiently to selection). Anyhow, the results of these various longitudinal studies suggest that long-term monitoring of vector behaviour (> 2 years), particularly in areas with a long history of use of insecticides in public health, is critical to better understand the biological mechanisms underlying behavioural resistances, to potentially assess their development rate, and more broadly to assess residual malaria transmission risk (Sanou et al., 2021; Kreppel et al., 2020; Durnez and Coosemans, 2013)."

26) L632: Authors should explain what is the "activity" of the phenotypes.

Thank you for pointing this. We were talking about foraging activity of the vector populations, not the studied phenotype (that was a non sense). The sentence was therefore rephrased as follow (l xx) :

« Weather can impact the fitness of possible genotypes associated with resistant behavioural resistant phenotypes, but may also directly influence the time and location of foraging activity (see Introduction for more details).»

27) L697: This study suggested more a correlative relation between LLIN and the rise of insecticide resistance than evidence.

Thank you for pointing out that we maybe jumped to conclusions too quickly. To moderate our statements, we have modified the manuscript as following (l xx) :

« ~~Despite these successes, our study adds to the growing body of evidence that the insecticides they are impregnated with are responsible for the rise of physiological resistances in the malaria vectors populations~~ However, despite these successes, many studies strongly suggest that the insecticides they are impregnated with are responsible for the rise of physiological resistances in the malaria vectors susceptible populations (see Introduction). In our study, the positive and significant associations found between the probability to collect a physiologically resistant mosquito and LLIN-related variables (time since LLIN distribution, LLIN use rate) supports these findings.

28) L700: Authors should provide or recall the data to support the growing of resistance in a susceptible population.

Thank you for the suggestion. As suggested, we recalled the references to support the growing of resistance in a susceptible population (Labbé et al., 2017; Riveron et al. 2018), but we did it two sentences before the one that you pointed out, as it seems to make more sense in the text here (l xx) :

« […] many studies strongly suggest that the insecticides they are impregnated with are responsible for the rise of physiological resistances in the malaria vectors susceptible populations (Labbé et al., 2017; Riveron et al. 2018) (see Introduction) »

In the specific sentence that you pointed out, we wish to draw attention to the rapid increase of physiological resistance in the population.

29) L715: Clarifications are needed to better understand how managing vector control would be beneficial. For instance, why different strategy? why at small scale only?

Thank you asking some clarifications. Perhaps the sentence isn’t clear enough or isn't worded properly. Our only intention here was to highlight that since biting rates vary greatly across villages and seasons, while resistances do not, interventions targeted at reducing human-vector contact and reducing resistance selection (both essential) should be managed distinctly in the field :he former should be highly locally tailored (i.e. specific to each village and season), while the latter, due to its stability across villages and seasons, would not benefit significantly from being customized at these spatio-temporal scales.

To make our point more clear, we have hence rephrased the sentence in the manuscript as following, hoping it is clearer now :

« Here, we observed that both behavioural and physiological resistances of mosquitoes were quite stable across the villages and seasons within the spatiotemporal frame of the study. This contrasts with their biting rates, which was found, in another study (Taconet, Porciani, et al., 2021), highly variable across the villages, seasons, and amongst the species.~~At small spatiotemporal scales, this calls for different strategies for respectively vector control (interventions aiming at reducing the human-vector contact) and resistance management (interventions aiming at reducing the development of physiological or behavioural resistance) at such spatiotemporal scales. While vector control plans should be very locally-tailored (species-, season-, and village-specific) (Taconet, Porciani, et al., 2021), resistance management strategies would probably not gain much in being adapted to the season or village within our areas.~~ This calls for distinct spatio-temporal management of interventions targeted at reducing human-vector contact and reducing resistance selection (both essential) in the field. While the former should be highly locally tailored (i.e. specific to each village and season) (Taconet, Porciani, et al., 2021), the latter, due to its stability across villages and seasons, would probably not benefit significantly from being customized at these spatio-temporal scales in our areas. In other words, while resistance management plans are undoubtedly urgently needed, there is no compelling evidence – in the current state of the knowledge - that they should be tailored at very fine scales (village, season). »

30) L718: Authors should remove "such spatiotemporal scales" that is repeated at the beginning of the sentence.

Thank you for pointing out this inconsistency. We appreciate your careful observation. We have revised the manuscript as suggested.

31) L723: It would be important to explain why sampling occurred during the dry season when mosquito density is low.

Actually, mosquito sampling did occurr both during the dry and rainy season but for the latter, only at its begining and end (not at the peak) (see additional figure 1F). These mosquito collection were part of a randomized controlled trial aiming at the evaluation of vector control tools complementary to LLIN. Timing of entomological surveys was therefore defined with the gaol to evaluate these interventions. Unfortunately, the deployement of the complementary intervention to be evaluated was delayed later than expected in the rainy season. For this reason, we were not able to carry out entomological survey at the peak of the rainy season (and therfore probably at the peak of abundance).

To be more precise, we have made the following replacements in the manuscript :

« ~~Noteworthy, no entomological survey was performed during the high rainy season (July to September), at the known mosquito abundance and malaria transmission peaks.~~ Noteworthy, mosquitoes were collected during the dry season and at the beginning and end of the rainy season, but, for logistical reasons, not at the peak of the rainy season (and therefore not at the likely peak of mosquito abundance)."

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