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Seasonality of *Plasmodium falciparum* transmission: a systematic review

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Abstract

Although *Plasmodium falciparum* transmission frequently exhibits seasonal patterns, the role and drivers of malaria seasonality are unclear. Given the massive variation in the landscape upon which transmission acts, intra-annual fluctuations are likely influenced by different factors in different settings. Further, the presence of potentially substantial inter-annual variation can mask the seasonal patterns; it may be that a location has “strongly seasonal” transmission and yet no single season ever matches the mean, or synoptic, curve. Accurate accounting of the extrinsic factors of malaria transmission for a given location can inform efficient control and treatment strategies. In spite of the demonstrable importance of accurately capturing the seasonality of malaria, as well as the strength of the seasonal pattern, data required to describe these patterns is not universally accessible and as such localized and regional efforts at quantifying malaria seasonality are disjointed and not easily generalized. The purpose of this review is to audit the extant literature on seasonality of *P. falciparum* and quantitatively summarize the collective findings. The contradicting results of studies using similar but not identical data and modeling approaches from similar but not identical locations as well as the confounding nature of climatological covariates underlines the importance of a multi-faceted modeling approach that attempts to capture seasonal patterns at both small and large spatial scales - 215 words (needs to be 200).

Index terms— keyword, keyword

*These authors contributed equally to this work.

1 Introduction

2 Like many infectious diseases, malaria incidence often displays seasonal variation. The nature
3 and extent of the seasonality varies enormously from place-to-place and from year-to-year. Tem-
4 poral variation in malaria transmission is, along with its spatial distribution, among the most
5 basic aspects of its epidemiology. Knowledge of the main drivers of seasonality, their timing,
6 and interaction with malaria transmission in a given location can facilitate effective planning
7 and implementation of routine control and treatment activities. Some interventions can be more
8 effective if deployed at seasonally optimal times. Seasonal malaria chemoprevention, for ex-
9 ample, which involves the preventative administration of antimalarial drugs to young children
10 [Organization, 2013], is optimally targeted at regions with a short, intense, malaria transmission
11 season, and requires accurate timing within that season [Cairns et al., 2012]. An understanding
12 of seasonality is also important when measuring and describing geographical patterns of malaria
13 risk [Gething et al., 2011]: observations made at different months in the year are difficult to
14 compare without reference to a known underlying seasonal signal. Similarly, seasonality affects
15 interpretation between different types of malaria data: the overall and age-specific relationships
16 between vector population density, the entomological inoculation rate (EIR), the force of in-
17 fection, infection prevalence or parasite rate (PR), disease incidence and mortality all differ in
18 non-linear ways in areas of differing seasonality [Carneiro et al., 2010, Roca-Feltrer et al., 2010].

19
20 Despite the clear importance of quantifying the seasonality of malaria, data describing it
21 are not widely available. While those involved in day-to-day disease control and treatment may
22 harbor detailed knowledge of local seasonal patterns, there remains no single resource provid-
23 ing consistent and comparable data on the extent, timing, and determinants of seasonality at
24 regional to global scales. The first challenge is one of definition. In a malaria context, the term
25 seasonality encapsulates a complex and multi-faceted phenomenon which remains inconsistently

26 defined, described, and interpreted. A basic description of seasonality in a location would in-
27 clude the relative magnitude, timing of onset, and duration of different seasons. These attributes
28 must be characterized separately for each malaria metric of interest. Crucially, characterization
29 of the “typical” seasonal pattern is likely to differ from that observed in any single year, since
30 inter-annual variation is often substantial. Malaria seasons often start earlier or end later, last
31 for a longer or shorter duration, or are more or less pronounced from one year to the next, and
32 so this year-to-year variation around an average pattern must be captured and described.

33

34 A second challenge, leading directly from the first, is the availability of standardized and
35 geolocated data describing patterns of seasonality that can be compared across a wide set of
36 locations. While there is a degree of consensus on the broad global patterns of seasonality, this
37 falls considerably short of a geographically detailed, quantitatively rich characterization that
38 could support in-depth control planning. Our understanding of the geographical distribution
39 of malaria has benefited enormously from the proliferation of standardized [Hou, 2013], often
40 nationally representative [DHS, , MIS,] cross-sectional parasite rate surveys, and their assimi-
41 lation into geospatial models [Gething et al., 2011, Gething et al., 2012], but such data are not
42 well suited to capturing seasonal variation. Conversely, longitudinal or other time-series data
43 that are ideal for analysing temporal patterns are less commonly obtained, address a disparate
44 set of malaria metrics, tend to be unevenly distributed geographically [Gething et al., 2014] and
45 can be prone to biases and missing data [Rowe et al., 2009].

46

47 This scarcity of robust and comparable data means the empirical evidence base on patterns
48 of seasonality remains unconsolidated. The purpose of this review is to audit the extant litera-
49 ture on seasonality of *Plasmodium falciparum*, and to provide a quantitative summary in terms
50 of: (i) the geographical regions represented; (ii) the type of malaria metrics measured; (iii) the
51 climatic drivers identified; and (iv) the analytical approach taken to explore seasonal dynamics,

52 which include a broad class of both statistical and mechanistic modeling approaches.

53

54 **2 Methods**

55 **2.1 Constructing a Systematic Bibliographic Database**

56 The intended scope of this review was all studies in the scientific literature that have either
57 explicitly or implicitly observed, described, or modeled malaria seasonality and its drivers. Hun-
58 dreds of such studies exist from sites around the world, fostered in part by the increasing diversity
59 and availability of environmental and climatic covariates arising from both satellite imagery and
60 improved on-the-ground data collection techniques. Six search terms were selected to system-
61 atically compile a list of papers relevant to the seasonality of *P. falciparum* transmission. These
62 terms were then entered into the academic search engine Web of Knowledge [WoK,] and new
63 papers from each search term added to the list each time (Table 1). These search terms were
64 deliberately broader than the scope of this review to capture as many potentially relevant papers
65 as possible, with the large set of returned studies then successively screened for inclusion accord-
66 ing to a set of criteria described below. First, the abstract and titles of each paper were checked
67 to identify papers with a focal subject that was not malaria seasonality. These papers were re-
68 moved from consideration at this stage (471 papers). To systematically quantify the remaining
69 broad assembly of literature, we designed and implemented a classification questionnaire that
70 we applied to every publication. The 'questionnaire' was structured as follows:

71

- 72 i) Does the paper try to understand malaria seasonality or produce a model of the relationship
73 between malaria and environmental variables?
- 74 ii) Does the paper include environmental or climatic variables and, if so, which variables are
75 considered?

- 76 iii) Are the data used by the authors new and if so what type of data is used to represent
77 malaria?
- 78 iv) In which locations is the study based?
- 79 v) What time periods does the paper cover?
- 80 vi) Is the analysis primarily mechanistic or statistical in nature and what are the main methods?
- 81 vii) What aspects of seasonality does the paper consider (e.g. timing of malaria peaks, difference
82 between minimum and maximum, environmental drivers)?
- 83 viii) Is the paper primarily concerned with climate change?
- 84 ix) Is the method of particular interest because of its novelty or because it creates a solution
85 to a particular problem?
- 86 x) Does the paper call for work on this issue?

87 The answers to these questions were recorded systematically to produce a reference for the
88 comparison of approaches to investigating malaria seasonality as well as the global coverage of
89 these attempts.

90 **3 Results**

91 Classifying each manuscript using the above questionnaire generated a considerable amount of
92 detailed information. For brevity, we summarize this information in general terms below. To
93 provide readers with increasing levels of detail, we include 6 supplemental tables in the SI, and
94 finally provide the raw database as an additional supplemental file.

95 **3.1 Regions**

96 In total, we identified 159 manuscripts that satisfied our criteria for inclusion (Flowchart 1).
97 Across these papers, the vast majority (74.2%, 118/159) concerned the effects of climate and

98 seasonality on malaria in Africa (see Figure 1). 5 studies covered all of Africa, while 9 focused on
99 regions of Africa (Table S1). Excluding these regional and continent-wide studies, there were 104
100 studies of 26 African countries. Outside Africa, there were 28 studies within Asia, with China
101 (8) and India (4) being the two most studied countries (Figure 1). Beyond these locations, there
102 were 11 studies in South and Central America, 2 studies in Iran and 2 studies in Europe (1
103 each in Portugal and Poland). Some studies attempted to analyze single locations within the
104 countries of interest, while others utilized data from numerous locations within the country. For
105 complete classification of the frequency of location utilization, see Table S1.

106 **3.2 Malaria Metrics**

107 Malaria transmission has historically been evaluated using various metrics. Abundances or fre-
108 quency of blood feeding by *anophele* mosquitoes, the vectors of malaria, have been used as a
109 proxy for transmission, and a measure of transmission potential . EIR, which is the product of
110 the number of vectors attempting to feed and the percent of mosquitoes actively infective, gives
111 quantitative estimates of the number of infective bites per person per unit time. Prevalence of
112 infections or incidence of clinical cases, detected actively in the community or passively at health
113 facilities provide direct measures of the current level of transmission and disease within human
114 hosts. Different metrics of malaria are representative of different aggregated temporal windows
115 of transmission, which complicates attempts to link the environmental drivers and malarimetric
116 outcomes of seasonal transmission.

117

118 Across the 159 manuscripts, 21 used mosquito abundance as a malaria metric (Fig. S1 a).
119 The majority of these studies concerned regions of Africa. Incidence of clinical disease was the
120 most frequently investigated malaria metric (62 papers), and most of the regions of the globe
121 with malaria were represented by studies using this metric (Fig. S1 b). EIR and infection
122 prevalence were only investigated in regions of Africa (Fig. S1 b, c respectively). As with

123 mosquito abundance, EIR and prevalence were far less frequently studied relative to incidence
124 (6 and 18 studies respectively).

125 **3.3 Climatic Drivers**

126 The most commonly reported aspect of malaria seasonality was observed temporal relationships
127 between a given malaria metric and a given putative environmental or climatic driver of that
128 seasonality. The most direct method of obtaining data in specific locations is to take on-site
129 measurements of variables of interest or to use local weather stations. However, accurate and
130 complete records of all variables of interest across space and time may be lacking, particularly
131 in many of the resource-poor locations of interest for malaria transmission. Over wider areas
132 the use of nationally collected data from weather station networks may be more appropriate
133 (e.g. National Meteorological Services Agency in Ethiopia, Islamic Republic of Iran Meteorological
134 Organisation, and China Meteorological Administration). A common source of global
135 climatic data is WORLDCLIM which, by interpolating data to cover areas away from initial
136 weather station locations, has made available fine resolution interpolated surfaces from several
137 trusted weather databases over a 50 year time period [Hijmans et al., 2005]. An alternative to
138 terrestrial weather and climate data is provided by satellite sensor such as Moderate-resolution
139 Imaging Spectroradiometer (MODIS) on the Terra and Aqua satellites; [King et al., 2003]. Un-
140 like data from weather stations which can be patchy in their coverage, satellite sensors can
141 achieve complete global coverage, and data from satellite mounted sensors such as the Advanced
142 Very High Resolution Radiometer can be used to infer variables such as sea surface temper-
143 ature [McClain, 1983], water vapour levels [King et al., 2003], atmospheric gas concentrations
144 [Thies & Bendix, 2011] and precipitation [Kidd & Levizzani, 2011] as well as compute vegeta-
145 tion indices such as the normalised difference vegetation index (NDVI) which measures the
146 “greenness” of vegetation based on its reflectance. The choice of data source on climatic drivers
147 of malaria metrics will depend on various factors such as the spatial and temporal resolutions,

148 time period and location of the study in question.

149

150 The majority of papers analyzed the relationship between malaria metrics and temperature
151 or rainfall (40.3%, 64/159 and 34%, 54/159, respectively; Figure 2 a,b). Satellite-derived indices
152 quantifying vegetation coverage were also frequently investigated (11.3%, 18/159; Figure 2c),
153 often in conjunction with temperature and/or rainfall. All other potential drivers (e.g., relative
154 humidity, wind speed and direction, sunspots) were either used rarely (2.5%, 4/159; Figure 2d)
155 or in conjunction with a subset of the three main drivers (12.6%, 20/159). Here we summarize
156 findings from those studies that used statistical methods to investigate seasonal drivers.

157 **3.3.1 Temperature**

158 Temperature covariates were found to be a significant driver of malaria seasonality in statistical
159 models more frequently than any other climatological drivers (64). Amongst temperature-based
160 variables, minimum monthly temperature was most frequently found to have a significantly
161 relationship with temporal malaria metrics (24 analyses), followed by maximum monthly tem-
162 perature (19 analyses) and mean monthly temperature (12 analyses). The range of significant
163 time lags between monthly temperature and malaria metrics varied by both region and, as
164 expected, malaria metric. As with all analyses, the dominance of malaria incidence-based in-
165 vestigations within the literature was again evident. However, as is evident by the history of
166 lab and field-based experiments correlating temperature with mosquito population dynamics
167 [Craig et al., 1999], it is not surprising that 14 papers found a significant relationship between
168 some measure of monthly temperature and vector abundance (Fig. S2). All but one of these was
169 a zero-month lag, with a single study lagging temperature by two months and all but one of the
170 studies concerned regions in Africa (one was in Portugal). Incidence was the most frequently in-
171 vestigated malaria metric, and of the 62 statistical analyses that correlated climatological drivers
172 with incidence, 28 found a significant relationship between monthly temperature and incidence.

173 Temperature was a significant driver in incidence studies throughout the Old World, with lags
174 ranging from 0 to 9 months (Fig. 3). EIR, the other direct measure of current transmission
175 activity within a region, was found to be significantly related to temperature in 4 studies, at
176 lags from 0 to 5 month, all within Africa (Fig. S3). Finally, across the 4 papers that found sig-
177 nificant relationships between monthly temperature and prevalence, all again occurred in Africa
178 and most found a maximum lag of 2 months significant (Fig. S4c). A more detailed break-down
179 of the number of times a specific temperature variable was found to be a significant driver of a
180 specific malaria metric in a specific region can be found in the SI.

181 **3.3.2 Rainfall**

182 54 papers across the globe have found rainfall to be a significant predictor of malaria seasonality.
183 Ten papers found a significant relationship between mean monthly rainfall and malaria metrics.
184 Presumably driven by the non-linear relationship between rainfall and malaria, many investi-
185 gators assessed specific statistics of rainfall other than mean monthly amount, such as seasonal
186 rainfall [Mabaso et al., 2007], total rainfall during a set period (e.g., [Small et al., 2003]), and
187 various other indices of variation. 2 papers (both based in Africa) found a significant relation-
188 ship between rainfall and vector abundance (Fig. S5) with lagged relationships between 0 and
189 2 months. For both incidence and EIR, lags ranged from 0 to 4 months (33 papers, Fig. 4; 2
190 papers, Fig. S6 respectively). Across the 3 papers that found significant relationships between
191 monthly rainfall and prevalence, all found a 0 month lag to be statistically significant (Fig. S7a).
192 A more detailed regional break-down of the number of times a specific rainfall variable was found
193 to be a significant driver of a specific malaria metric can be found in the SI.

194 **3.3.3 Vegetation Indices**

195 18 papers found a satellite-derived vegetation index to be a significant driver of malaria metrics;
196 all but three used NDVI. Across various monthly vegetation indices, 4 papers found a significant
197 correlations to vector abundance (Fig. S8). All of these were 0 month lags and located in

198 either Africa or Asia. Significant relationships between vegetation indices and incidence were
199 found across the globe at 0 to 3 month lags (9 papers, Fig. S9). 2 papers found significant
200 concurrent relationships between vegetation indices and EIR in Africa (Fig. S10) and across the
201 3 papers that found significant relationships between monthly vegetation indices and prevalence,
202 also all in Africa, lags of 0.5 and 1 month were identified. (Fig. S11a). Again, more detailed
203 break-downs of these results are provided in the SI.

204 **3.4 Approaches - Statistical Methods**

205 The database of seasonality studies included a wide range of different statistical modeling ap-
206 proaches to investigate empirical associations between malaria metrics an environmental drivers
207 (116 papers). These ranged from descriptive approaches to fuzzy logic models and complex
208 spatio-temporal methods. Thirteen studies used methods classified by the authors as 'simple.'
209 This included descriptive methods and purely correlative approaches with no model fitting. The
210 largest number of papers, 38, used classes of regression methods including both parametric and
211 non-parametric. Some included residual error structures such as autoregressive terms. Logistic
212 and Poisson regression were common approaches within this group along with several multivari-
213 ate methods and mixed models. A further six studies used spatial methods, including spatial
214 regression and spatial autocorrelation terms, along with geostatistical and niche modelling meth-
215 ods, and two additional studies used explicitly spatio-temporal methods. Ten of the papers using
216 statistical methods used Bayesian approaches. Of these, two were spatial models and one used
217 spatio-temporal methods.

218

219 The overall number of papers published per year increased towards the present (Fig. S12),
220 although a clear trend of increasing modeling sophistication was evident, with a proportional
221 decline in studies using simple statistical methods and non-spatial regression approaches whilst
222 spatial and Bayesian approaches increased. Almost all of the descriptive papers concentrated on

223 Asia and Africa and were largely concerned with malaria cases or incidence. Rainfall and temper-
224 ature predictors were commonly used within this group of papers. Among the models using re-
225 gression methods the most common malaria metrics investigated were again number of cases and
226 incidence. However, within this group the diversity of malaria metrics investigated was greater
227 than for other approaches. The majority of papers using regression methods dealt with Africa but
228 there were also examples in Asia, the Americas and Europe. Regression methods, perhaps due to
229 the breadth of studies using these approaches, used the most diverse range of predictor variables.
230 Malaria cases and prevalence were again well represented by studies using Bayesian methods.
231 However, the two studies using spatio-temporal Bayesian models investigated environmental
232 drivers of malaria prevalence [Gemperli et al., 2006] and vector abundance [Sogoba et al., 2007].
233 Similarly the spatio-temporal regression models were concerned with EIR, vector abundance
234 and PR rather than number of cases and incidence [Amek et al., 2012, Mirghani et al., 2010].
235 Bayesian modelling approaches were most commonly associated with temperature as a predictor
236 along with rainfall in many cases and were mostly focused on Africa.

237 **3.5 Approaches - Mechanistic Models**

238 31 publications investigated the possibility of incorporating seasonality, or seasonal drivers, into
239 mechanistic models of malaria response variables. The majority of these studied malaria in
240 Africa, but there have also been several investigations in Asia and South America (Fig. S13).
241 From the initial models of Ross and then Macdonald [Smith et al., 2012], mechanistic models of
242 malaria have, in general, not greatly deviated from the original framework [Reiner et al., 2013].
243 There have been a few exceptions to this general observation, and some of the most complex
244 mechanistic modeling approaches have also been adapted to incorporate seasonal differences in
245 malaria. As with the statistical models, there are stark differences in the modeling approach
246 between models that attempt to model monthly malaria incidence data or parasite rate surveys
247 and models that attempt to model mosquito abundance. However, as was true for the statistical

248 approaches, local rainfall and temperature were the most frequently used climatological covari-
249 ates used to drive temporal variation in malaria.

250

251 3.5.1 Mosquito abundance

252 *Anopheles* abundance is known to have a non-linear relationship with temperature [Craig et al., 1999].
253 If the ambient temperature is too cold or too hot, vectors of malaria have a diminished prob-
254 ability of survival. Thus, considerable effort has gone into identifying the optimal temperature
255 window for *Anopheles*. Incorporating temperature into an understanding of the suitable range of
256 mosquitoes (and then further a suitable range of malaria) has resulted in global maps of malaria
257 potential [Gething et al., 2011]. Additionally, the potential that the regions of the globe that are
258 within the optimal temperature window for *Anopholes* may shift or expand with global climate
259 change has resulted in numerous investigations and publications [e.g., [Mordecai et al., 2013]].
260 Although much of the work has concerned defining the spatial distribution of temperature that
261 is ever in the suitable range for malaria, several efforts have further investigated the seasonality
262 of mosquito abundance and climatic drivers' effect on abundance.

263

264 Martens, in 1999, modeled the death rate of mosquitoes as a function of temperature in
265 Celsius, $g(T)$, as:

$$g(T) = \frac{1}{-4.4 + 1.31T - 0.3T^2} \quad (1)$$

266 From basic maps of climate suitability [Craig et al., 1999] to being used as an integral
267 part of complex malaria models [Parham & Michael, 2010, Ermert et al., 2011a], this equa-
268 tion/functional form, or an approximation of it, has been used extensively. Other incorpo-
269 rations of temperature to identify climate suitability have either taken a simple approach of
270 directly defining a window outside of which a mosquito population could not be sustained

271 [Goswami et al., 2012] or using a similar but mathematically different functional form such as
272 the logistic equation used by Lourenço et al [Lourenço et al., 2011]. In addition to temperature,
273 functional forms have been used to incorporate other climatological covariates such as rainfall
274 and temperature into estimates of climate suitability for *Anopohles*. As with statistical models
275 of mosquito abundance, there was no estimated lag between the climatological covariates and
276 mosquito abundance.

277

278 Complex agent-based models whose primary focus is based on mosquito abundance that in-
279 corporate mosquito population ecology and impacts of multiple simultaneous interventions have
280 also been built to accommodate multiple climatological drivers as well as some of their inter-
281 actions. Eckhoff [Eckhoff, 2011] explicitly tracks cohorts of eggs through their life cycle using
282 mechanistic relationships implemented on the individual level. Modelling local population dy-
283 namics (as opposed to well-mixed patches common to mechanistic models defined by differential
284 equations) may allow for locally optimized control strategies once parameterized for a specific
285 location.

286 **3.5.2 Malaria incidence**

287 Several mechanistic models included within our review primarily concern the mathematical prop-
288 erties of models that permit intra-annual variation. Recent work by Chitnis et al [Chitnis et al., 2012]
289 and Dembele et al [Dembele et al., 2009] have both analyzed periodically fluctuating parameters
290 within a larger system of differential or difference equations. Chitnis et al incorporated consid-
291 erable complexity, especially with respect to the life cycle of *Anopholes*, and both analyze the
292 asymptotic stability of their system as well as investigate the effects of various control efforts.
293 Although these models are not directly applied to data, they provide a rigorous framework within
294 which seasonally fluctuating variables, driven by climate or otherwise, can be incorporated. As
295 noted in a recent review of mechanistic models of mosquito-borne pathogens [Reiner et al., 2013],

296 the complexity of a mechanistic model is typically determined by the exact purpose of the re-
297 search.

298

299 A variety of compartmental models of malaria have incorporated temperature and rainfall
300 to different ends. For example, Massad et al [Massad2009] incorporated both a seasonal sinu-
301 soidal driver of mosquito abundance and a second host population into their compartmental
302 modeling approach to assess the risk of travelers to a region with endemic malaria but in doing
303 so they ignored the incubation period for both host and mosquito. Conversely, Laneri et al
304 [Laneri et al., 2010] used a single host population, but incorporated rainfall, incubation periods
305 and secondary infection stages to separate the roles of external forcing and internal feedbacks
306 in inter-annual cycles of transmission.

307

308 In general, the vast majority of mechanistic models of malaria incidence that incorporate
309 seasonality or climate are bespoke to address a specific concern. There are, however, several
310 important exceptions. Several research groups have spent the last decade (or more) developing
311 extremely complex and detailed models of malaria. Combining statistical approaches, mechanis-
312 tic models and in some cases fuzzy logic, these models attempt to recreate transmission patterns
313 at large scales. Amongst these approaches, the utilization of climate and climatic drivers differs.
314 Researchers from Imperial College and the London School of Hygiene & Tropical Medicine built
315 an agent-based simulation model of malaria transmission fitted to 34 transmission settings across
316 Africa [Griffin et al., 2010]. Using seasonal profiles of EIR fit to different regions they categorize
317 transmission settings into different intensities and identify those locations where reasonable con-
318 trol efforts would have the largest impact. The Liverpool Malaria Model [Hoshen & Morse, 2004]
319 models both malaria and the climatic drivers themselves and incorporates rainfall and temper-
320 ature to drive the vector population. This complex model has been updated to incorporate
321 further complexities [Ermert et al., 2011a] and then calibrated and validated on data from West

322 Africa [Ermert et al., 2011b]. Quantities such as the “start” and “end” of the malaria season were
323 simulated and compared well with observed values where applicable. This model, as noted in
324 [Ermert et al., 2011b], does not incorporate fine-scale hydrologic variability (since there is not
325 extensive data to support its inclusion). This has been proposed as an explanation as to why
326 year-to-year comparisons between simulations and observations at single locations are generally
327 only weekly correlated.

328

329 Bomblies and colleagues [Bomblies et al., 2008] have introduced a modelling approach that
330 explicitly incorporates hydrologic variability into vector abundance and then malaria incidence.
331 In direct response to the typical mismatch of scales between the resolution of climatic drivers
332 and the scale of vector population dynamics, the Hydrology, Entomology and Malaria Trans-
333 mission Simulator (HYDREMATS) uses soil moisture and local hydrology to calibrate a model
334 that captures mosquito abundance at a scale much closer to what is seen in the field, and
335 has been used in several small scale validation and calibration studies [Bomblies et al., 2009,
336 Yamana & Eltahir, 2011]. The inclusion of hydrology implicitly incorporates a lag between
337 rainfall and malaria that is non-linearly determined based on ground cover, control practices
338 and size of natural pools within the community. This level of high-resolution hydrological detail
339 is difficult to obtain, or accurately simulate for entire regions or countries.

340 **4 Discussion/Conclusion**

341 Following an exhaustive literature search, we categorized 159 studies that either explicitly or
342 implicitly addressed the seasonality of malaria. The vast majority of these efforts did not in
343 fact attempt to quantify or describe the patterns of seasonality per se, but instead associated
344 malaria data with climatic data. However, because the climatological covariates themselves fol-
345 low seasonal patterns (some more strongly than others), linking climate with malaria, even at a
346 lag, indicates the potential presence of seasonality. The two clearest aspects of these studies that

347 partitioned the existing literature, somewhat predictably, were the types of data (both explana-
348 tory and response) and the types of analyses (generally speaking, statistical versus mechanistic).
349 In every combination, although the limitations of available data soften the conclusions, the pres-
350 ence of variation in ‘seasonality’ seems to be both conditioned and driven by location and climate.

351

352 As discussed above, the increase in resolution (both spatially and temporally) of satellite-
353 based climatological covariates has greatly contributed to the analyses performed and, in many
354 cases, the amount of the variation in malaria explained. Additionally, improved data collection
355 and data maintenance from existing weather stations, has provided ground reference data with
356 which the satellite sensor data can be validated. Due to the necessary transmission steps that
357 occur within the mosquito, it is not surprising that climatological covariates that are most clearly
358 associated with mosquito ecology have been linked to malaria metrics. Rainfall and temperature,
359 measured in a variety of ways, have been found to be significant drivers of malaria considerably
360 more than any other covariate (34%, 54/159 and 40.3%, 64/159, respectively). Although there
361 is an increase in the spatial and temporal resolution of explanatory covariates, as noted previ-
362 ously, existing data are often inadequate to predict mosquito abundance at the fine spatial scale
363 upon which mosquito population dynamics occur [Ref]. For example, measured either at a local
364 weather station or through satellite derived metrics, it is unclear how to translate a single ‘rain-
365 fall’ data location to predict the presence and quantity of larval breeding sites. Satellite-derived
366 vegetation indices, such as NDVI, have been demonstrated to be useful to measure landscape
367 suitability for mosquitoes (19%, 4/21) but they have only been shown in the literature to cor-
368 relate concurrently to abundance (or at most lagged one month). In general, remotely sensed
369 climate data provide an opportunity for increased understanding, but their utility (and accu-
370 racy) must be tempered by complex confounding variables such as land-type. For example, high
371 NDVI values can indicate very different climates depending if the region measured has irrigation,
372 is heavily forested or is on the desert fringe. Likewise, due to small-scale variation in land-type,

373 the same amount of rainfall can have a very different impact on mosquito larval sites depending
374 on where it is measured.

375

376 There are (at least) three different time-scales of malaria metrics, as described below. As the
377 time-scale of the metric increases, and the lag between occurrence of a driver of transmission and
378 the time its effect is felt upon the given metric increases, the complexity of the relationship like-
379 wise increases. First, mosquito population dynamics are essentially instantaneously responsive
380 to climatological forcing. In addition to a non-linear relationship to temperature, the necessity of
381 rainfall for larval sites combined with the hazard of flushing of these sites by flooding associated
382 with heavy rainfall introduces a second non-linear relationship between climate and ‘malaria’
383 vis-à-vis mosquito density. Translating the climatic effects through mosquito density, two blood
384 meals (one infecting the mosquito and a second infecting a susceptible host) and the IIP clearly
385 temporally separates human incidence and climate drivers. Adding to this complexity, climatic
386 drivers such as temperature have been shown to influence incubation periods. Thus, the second
387 scale of drivers is based on malaria data associated with incidence (e.g. case data, death, etc).
388 The longest scales of metrics are associated with prevalence. Integrating the amount of incidence
389 across an entire transmission season, and then incorporating the waning of immunity that will
390 slowly decrease the contribution of early infections to later prevalence surveys, these malaria
391 variables are the least immediately influenced by season. Beyond the expectation of three dif-
392 ferent temporal scales of climate influence on malaria, different challenges are involved with
393 measuring each of these malaria metrics. Those most likely to be greatly influenced by climate
394 (e.g., mosquito abundance) are also the most stochastic and require the most serial samples to
395 accurately account for measurement noise.

396

397 Perhaps due to the relative simplicity of the corresponding data analysis, or perhaps due to
398 the noise reduction that occurs when taking means, synoptic data have been used extensively

399 to assess both seasonal patterns of malaria as well as the effects of climatological covariates on
400 malaria data. In a sense, the synoptic curve of incidence in a location is a close proxy to the
401 seasonal pattern of malaria within the region. Were there to exist no inter-annual variation in
402 incidence (or drivers) these two quantities would be comparable. As such, to infer a basic level
403 of understanding of seasonal patterns, synoptic data can be a useful tool. However, in reality the
404 previous premise is demonstrably false. Natural, intrinsic periodicity in malaria transmission
405 suggests that averaging over years to produce a single value for expected incidence on a given
406 day (or, more commonly, in a given month) obfuscates the truth and may bias inference [Ref].
407 Further, if climate is closely linked to incidence, averaging incidence across years with vastly dif-
408 ferent rainfall or temperature may result in producing seasonal signatures that in practice never
409 occur themselves. Finally, global climatological drivers of climate like ENSO have multi-year
410 cycles and synoptic data implicitly ignore any potential impact of these sorts of covariates.

411

412 The analysis conducted by a paper is typically strongly driven by the question the study is
413 designed to address. Because most of the studies included in this review were not focused on
414 assessing the strength and signal of seasonality, it is not surprising that the types of analyses
415 were not appropriate for those questions. The vast majority of statistical approaches were a
416 variation of regression. The most frequent purpose of a study was to link climatological co-
417 variates to temporal variation. This variation was acknowledged to occur at both intra- and
418 inter-annual scales, but beyond fine-scale temporal variation, the papers most frequently fo-
419 cused on inter-annual scales. For the mechanistic approaches, except for a few that investigated
420 the intrinsic periodic properties of their system, seasonality was incorporated by including re-
421 lationships between parameters and climatological and temporal covariates. The most frequent
422 driver of temporal variation in these studies concerned the daily survival rate of the mosquito. A
423 non-linear relationship [Martens] has been identified in lab and field studies, where mosquitoes
424 are more likely to die at both extremely cold and extremely hot temperatures.

425

426 The scope of this review concerns the current seasonal patterns of malaria across the globe.
427 Although it is, thus, outside the purview of this review, the growing literature assessing the po-
428 tential changes in the range and incidence of malaria in the face of potential changes in local and
429 global climate must be noted. Within our review, 51 publications were excluded from further
430 analysis because they were identified as being solely concerned with assessing some aspect of the
431 impact of climate change on malaria. Many of these works have combined the predicted climate
432 maps produced by WorldClim or ClimMond with the mosquito daily survival rates identified
433 by Martens and others to predict either changes in range of climate suitability (which does not
434 always imply ‘increases’ in range) or changes in incidence vis-à-vis changes in the length of the
435 year for which transmission is possible. Given the extremely complex interplay between the nat-
436 ural transmission dynamics of malaria and the impact that humans and economic development
437 exert on the system (either positively or negatively), understanding the consequences of a 5° C
438 increase in local temperature on malaria remains a pertinent, but poorly understood problem.

439

440 It is important to note that several previous studies have paved the way for this comprehen-
441 sive review and have, themselves, begun the effort in earnest to quantify seasonal patterns either
442 on small scales or in large regions across the globe. Mabaso et al [Mabaso et al., 2005] applied
443 Markham’s concentration index [Markham, 1970] to data from Zimbabwe. They identified signif-
444 icant effects of both temperature and rainfall in determining the strength and timing of seasonal
445 outbreaks. Roca-Feltrer et al [Roca-Feltrer et al., 2010] conducted a systematic literature review
446 of studies concerning the age of paediatric hospital admissions with severe malaria syndromes.
447 This was followed by estimations of the potential impact of seasonal malaria chemoprevention
448 on children across Africa [Cairns et al., 2012], work which suggested that seasonal prevention
449 strategies could avert millions of malaria cases and tens of thousand childhood deaths every
450 year. Ermert et al [Ermert et al., 2011b] utilized the Liverpool model [Ermert et al., 2011a] to

451 approximate seasonality by identifying when the estimated EIR in a location first exceeded 0.1.
452 They also were able to reliably recreate seasonal quantities such as the beginning and end of the
453 ‘season’ with their model when applied to West Africa. Gemperli et al [Gemperli et al., 2006]
454 used a seasonality map derived from climatological covariates (rainfall, temperature and NDVI,
455 Ref) within a mechanistic modeling framework to estimate the length of the malaria season.
456 Each of these studies, as well as several others, has indicated that there appears to be some level
457 of predictability of malaria seasonality in endemic settings.

458

459 While these and other studies have investigated aspects of seasonality, either synoptically at
460 a large spatial scale or in depth at a small spatial scale, the drivers and patterns of seasonality
461 at the global level remain poorly understood. Malaria seasonality, though difficult itself to
462 fully describe quantitatively, is not measurable from a single years’ transmission patterns. The
463 confounding and driving nature of climatological covariates requires a multi-faceted modeling
464 approach. Both statistically and mechanistically, parsing the relative contribution of climate and
465 an underlying seasonal pattern to observed data requires acquiring data with a minimal amount
466 of measurement error or in sufficient quantities to reduce prediction error. Further, linking the
467 patterns observed or identified in one specific location to the surrounding area and understanding
468 the uncertainty in the extrapolated patterns of seasonality in the locations where data are scarce
469 is critical. Both statistical and mechanistic approaches provide useful (and different) information
470 and, thus, both should be used in concert to most adequately exploit the available data. We
471 believe that only by modeling seasonal patterns at both small and large spatial scales while
472 incorporating the inter-annual variability introduced by capricious climatological drivers can a
473 clear picture of malaria seasonality be understood.

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605 Figure Captions

606

607 **Figure 1: Global distribution of malaria seasonality papers.** The frequency various coun-
608 tries across the globe are the focus of malaria seasonality papers is plotted with an exponential
609 color scale. Studies that considered individual locations are indicated by grey points on the map.

610

611 **Figure 2: Distribution of malaria seasonality papers by climatological driver.** The
612 frequency that climatological covariates are identified as significant drivers of malarial metrics is
613 plotted for rainfall (panel A), temperature (panel B), vegetation indices (panel C) and all other
614 covariates (panel D). Studies that considered individual locations are indicated by grey points
615 on the maps.

616

617 **Figure 3: Reported relationships between temperature and malaria incidence.** In
618 panel A, the distribution of significant temperature lags to incidence is plotted. Different ap-
619 proaches used different forms of monthly temperature in their model. In panels B, C, and D,
620 the maximum significant temperature lag is plotted by country in South America, Africa and
621 Asia respectively.

622

623 **Figure 4: Reported relationships between rainfall and malaria incidence.** In panel A,
624 the distribution of significant rainfall lags to incidence is plotted. Different approaches used dif-
625 ferent forms of monthly rainfall in their model. In panels B, C, and D, the maximum significant
626 rainfall lag is plotted by country in South America, Africa and Asia respectively.

627

Search Term	Hits	Cumulative total papers
Malaria & Seasonality & Model	74	74
Malaria & Seasonality & Mathematical	47	100
Malaria & Season & Mathematical	121	207
Malaria & Season & Model	181	325
Malaria & Climate & Model	376	640
Malaria & Climate & Mathematical	116	653

Table 1: **Summary of systematic search.** Number of papers returned by each of the six search terms selected to systematically compile a list of papers, from the academic search engine Web of Knowledge, relevant to the seasonality of *Plasmodium falciparum* transmission.