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An eco-hydrologic model of malaria outbreaks

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Abstract

Malaria is a geographically widespread infectious disease that is well known to be affected by climate variability at both seasonal and interannual timescales. In an effort to identify climatic factors that impact malaria dynamics, there has been considerable research focused on the development of appropriate disease models for malaria transmission and their consideration alongside climatic datasets. These analyses have focused largely on variation in temperature and rainfall as direct climatic drivers of malaria dynamics. Here, we further these efforts by considering additionally the role that soil water content may play in driving malaria incidence. Specifically, we hypothesize that hydro-climatic variability should be an important factor in controlling the availability of mosquito habitats, thereby governing mosquito growth rates. To test this hypothesis, we reduce a nonlinear eco-hydrologic model to a simple linear model through a series of consecutive assumptions and apply this model to malaria incidence data from three South African provinces. Despite the assumptions made in the reduction of the model, we show that soil water content can account for a significant portion of malaria's case variability beyond its seasonal patterns, whereas neither temperature nor rainfall alone can do so. Future work should therefore consider soil water content as a simple and computable variable for incorporation into climate-driven disease models of malaria and other vector-borne infectious diseases.

1 Introduction

The World Health Organization estimates that 250 million clinical episodes of malaria occur annually, resulting in at least one million disease-associated deaths (World Health Organization, 2008). Malaria incidence is especially high in developing countries, where it is a leading cause of morbidity and mortality, in particular among children and pregnant women. Since the pioneering work by Ross (1910) and MacDonald (1957), progress in understanding malaria dynamics has been made through the development

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of mathematical models and their statistical inference with incidence data (e.g. Bailey, 1982; Hay et al., 2002; Depinay et al., 2004; Zhou et al., 2004; Pascual et al., 2008; Chaves et al., 2012; Bhadra, 2011; Laneri et al., 2010, among others). A subset of these models has considered the role that external forcing plays in generating patterns of seasonal and interannual case variability. Despite these advances, early-warning systems of malaria outbreaks still only have limited predictability (and thereby efficacy), and the factors contributing to malaria case variability still require more thorough investigation (Pascual et al., 2008; Craig et al., 2004a,b).

Two climatic variables that have long been known to influence malaria's seasonal and interannual dynamics are temperature and rainfall. Temperature is known to affect the development time of mosquito larvae, the probability of mosquito survival, and the development time of the malaria parasite *Plasmodium falciparum* in infected mosquitoes (Bayoh and Lindsay, 2003; Hoshen and Morse, 2004). Rainfall is hypothesized to affect malaria incidence through the creation of high-quality mosquito breeding sites during wet periods and the reduction of their availability during droughts (Patz et al., 1998). Although a moderate level of rainfall appears to have a positive effect on mosquito recruitment, intense rainfall events may destroy mosquito habitats and thereby reduce malaria incidence shortly following their occurrence (Briet et al., 2008).

Due to the multiple effects of temperature and rainfall on the malaria parasite and its mosquito vector, previous work linking malaria incidence to climate forcing has frequently focused on the direct impacts of temperature and rainfall on the risk of malaria (Craig et al., 1999; Lindasy et al., 2000). Several studies have found a correlation between malaria incidence and either minimum, mean or maximum temperatures (Hay et al., 2002; Zhou et al., 2004; Devi and Jauhar, 2007; Gomez-Elipe et al., 2007), while others have instead considered the effects of diurnal temperature fluctuations (Paaijmans et al., 2009) and sea-surface temperatures (Jury and Kanemba, 2007) on the disease. At regional spatial scales, malaria incidence has been correlated with rainfall amounts (Pascual et al., 2008; Craig et al., 2004a; Hay et al., 2001), interestingly with time lags of several months. These latter findings hint at the fundamental role that soil water content dynamics may play for malaria dynamics. Recent work has moved in this direction, with the role of surface hydrology being more fully recognized and explicitly included in mechanistic models. Some of these models have focused on water level fluctuations in small reservoirs and the effect of these fluctuations on malaria prevalence (Porphyre et al., 2005; Shaman et al., 2002). In an effort to predict the magnitude of malaria cases, several statistical models have also considered vegetation density (which depends on soil water availability) and distances between water bodies and humans populations (Gomez-Elipe et al., 2007; Kleinschmidt et al., 2001). Finally, detailed models linking hydrology with entomology have recently been proposed and tested for a semi-arid region (Bomblies et al., 2008; Yamana et al., 2011). The role of hydrologic processes in the dynamics of other vector-borne infectious diseases is also starting to become more fully recognized (Bertuzzo et al., 2008).

Motivated by these previous efforts, here we test the hypothesis that soil water content is an important driver of malaria dynamics, with an application of an eco-hydrologic model to malaria incidence data from three South African provinces (Fig. 1). Although the eco-hydrologic model we derive makes a series of simplifying assumptions, our results show that variability in soil water content is significantly correlated with variability in malaria incidence, whereas neither rainfall nor temperature alone show this correlation (beyond their seasonal associations). Future work should therefore focus on soil water content as a simple and computable environmental variable that can be incorporated into more mechanistic models of malaria transmission that include internal feedbacks.

2 Materials and methods

2.1 Malaria data

Monthly malaria incidence data over the period July 1996–March 2007 were obtained from the South African Department of Health (http://www.health-e.org.za/resources/

statistics.php, last access: February 2012) for three South African provinces: Limpopo, Mpumalanga and KwaZulu-Natal (Fig. 2). Implementation of malaria control strategies, mainly due to the Lumbobo Spatial Development Initiative, resulted in a steady decrease in the number of reported malaria cases in the provinces of Mpumalanga and Limpopo starting in 2005 and in the province of KwaZulu-Natal starting in 2002. To neglect this transient and consider a time series driven only by climate variability, we therefore limited our analysis to incidence data before June 2005 for Mpumalanga and Limpopo and before July 2001 for KwaZulu-Natal (Fig. 2).

2.2 Climate data

The meteorological data consisted of daily rainfall and daily minimum and maximum temperature records collected from weather stations managed by the South African Weather Service. We restricted our analysis to datasets with less than 20 % missing meteorological data that were obtained from stations in areas with high population densities and intermediate to high malaria risk (Fig. 1). For each province for which we had malaria data, spatially-integrated daily time series were first obtained by averaging across the selected weather stations. Finally, to have the same temporal resolution for the malaria and climate datasets, we estimated monthly meteorological data from these spatially-integrated daily time series (Fig. 2). A preliminary inspection of monthly malaria data alongside the meteorological data highlighted different responses to temperature and rainfall. We observed that daily maximum temperatures above 39 °C tended to be followed by a decrease in the number of malaria cases, most likely resulting from the effect of heat-stress on mosquitoes (Craig et al., 1999). Periods of moderate to high precipitation had a positive and delayed effect on malaria incidence, presumably because of the increased availability of mosquito breeding sites (Wyse et al., 2007). The few instances of anomalously high precipitation were followed by a rapid decrease in malaria incidence, presumably a result of habitat destruction for mosquito vectors (Briet et al., 2008).

2.3 Model description

We assessed the association between climatic drivers and malaria cases in three ways: (i) standard linear regression between climate anomalies and malaria case anomalies, at time lags of zero and one month; (ii) an eco-hydrologic model of malaria dynamics; and (iii) a transfer function model accounting for delayed climate effects on malaria dynamics. The first approach (i) provided a baseline to quantify the improvement of models (ii) and (iii). We choose not to consider the maximum temperature data in depth as an explanatory variable for malaria cases, as it did not have significant explanatory power in preliminary analysis. Instead, we focused our analysis on minimum temperature and precipitation anomalies.

The full eco-hydrologic model explicitly coupled a model of malaria transmission dynamics with a hydrologic model of soil water content. Through a series of assumptions, detailed below, this full eco-hydrologic model was reduced to a minimal, linear model that describes the expected relationship between precipitation levels in previous months and current malaria incidence.

The full model of malaria transmission is given by the following equations, where M is the population size of the *Anopheles* mosquito vector, M_I is the population size of infected mosquitoes, H_S is the population size of susceptible individuals, and H_I is the population size of infected individuals (Ross, 1910; Porphyre et al., 2005; Kermack and McKendrick, 1927; Smith and McKenzie, 2004; McCallum et al., 2001):

$$\frac{dM(t)}{\mathrm{d}t} = \Psi_0[w(t),T(t)]M(t-\tau_M) - \delta M(t) \tag{1}$$

$$\frac{dM_\mathrm{I}(t)}{\mathrm{d}t} = \alpha H_\mathrm{I}(t-\tau_\mathrm{I})M(t-\tau_\mathrm{I}) - \delta M_\mathrm{I}(t) \tag{2}$$

$$\begin{aligned}\frac{dH_\mathrm{S}(t)}{\mathrm{d}t} &= \mu H_\mathrm{TOT} + \gamma[H_\mathrm{TOT} - H_\mathrm{S}(t) - H_\mathrm{I}(t)] + \\ &- \eta_0 M_\mathrm{I}(t)\frac{H_\mathrm{S}(t)}{H_\mathrm{TOT}} - \mu H_\mathrm{S}(t)\end{aligned} \tag{3}$$

$$\frac{dH_\mathrm{I}(t)}{\mathrm{d}t} = \eta_0 M_\mathrm{I}(t)\frac{H_\mathrm{S}(t)}{H_\mathrm{TOT}} - (\upsilon + \mu)H_\mathrm{I}(t) \tag{4}$$

The number of individuals recovered and immune to malaria infection at time t is not explicitly modeled, but given by $H_\mathrm{TOT} - H_\mathrm{S} - H_\mathrm{I}$ where H_TOT is the constant total host population size.

The dynamics of the mosquito population, given by Eq. (1), are modeled by a delay differential equation where Ψ_0 is the mosquito growth rate (a function of soil moisture, w, and temperature, T), $\frac{1}{\delta}$ (∼10 days) is the average lifespan of a mosquito, and τ_M (∼10 days) is the time delay between oviposition and mosquito emergence (Chitnis et al., 2008). The number of infected mosquitoes, governed by the dynamics given in Eq. (2), increases through feeding on infected hosts at a rate α, with τ_I being a time delay representing the incubation period for malaria parasites, and decrease with background mortality at a rate δ. The number of susceptible hosts increases with births (μH_TOT) and loss of immunity ($\gamma(H_\mathrm{TOT} - H_\mathrm{S} - H_\mathrm{I})$) and decreases with background mortality (μH_S) and malaria transmission via infected mosquitoes ($\frac{\eta_0 M_\mathrm{I} H_\mathrm{S}}{H_\mathrm{TOT}}$, Eq. 3). Finally, the number of infected hosts increases with transmission and decreases with background mortality and recovery from infection (υH_I).

Soil water content, w, is described by a soil-moisture and surface-water balance equation (Wyse et al., 2007; Porporato et al., 2004):

$$\frac{dw(t)}{\mathrm{d}t} = P(t) - mw(t) \tag{5}$$

where $P(t)$ is rainfall at time t, and $mw(t)$ is a linearized soil water loss function accounting for plant transpiration, surface evaporation, and deep infiltration. The use of this function is justified by the large spatial scale (Fig. 1) and relatively low temporal resolution (∼1 month) we are considering. In contrast to classical models of soil water content, we chose a form for Eq. (5) that does not saturate, so as to account for both soil and surface water storage.

- Assumption 1: as a first approximation, we assume that the fraction of the host population that is susceptible to infection, $\frac{H_S}{H_{TOT}}$, is relatively stable (i.e. $H_I << H_{TOT}$). With this assumption, the dynamics in the number of infected individuals are simplified to:

  $$\frac{dH_I(t)}{dt} = \eta M_I(t) - (\upsilon + \mu)H_I(t), \tag{6}$$

  where $\eta = \eta_0 \frac{H_S}{H_{TOT}}$.

- Assumption 2: because our datasets are resolved only at the monthly time scale, we assume that both the time delay between mosquito oviposition and emergence, and the incubation period, can be neglected. These assumptions yield:

  $$\frac{dM(t)}{dt} = \Psi_0[w(t),T(t)]M(t) - \delta M(t), \tag{7}$$

  $$\frac{dM_I(t)}{dt} = \alpha H_I(t)M(t) - \delta M_I(t). \tag{8}$$

- Assumption 3a: in the case that climate is the only limiting factor to mosquito emergence, we can re-write Eq. (7) as:

  $$\frac{dM(t)}{dt} = \Psi[w(t),T(t)] - \delta M(t). \tag{9}$$

- Assumption 3b: alternatively, in the case that the mosquito population exhibits logistic growth, with climate determining its carrying capacity, we can re-write Eq. (7) as:

  $$\frac{dM(t)}{dt} = r\left[1 - \frac{M(t)}{K[w(t),T(t)]}\right]M(t). \tag{10}$$

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- Assumption 4: we assume that the total mosquito density is approximately in equilibrium at the monthly time scale, on the ground that both the soil water content (with a mean transit time of 1–3 months) and the size of the infected population (transit time ~10 months) fluctuate at longer time scales than mosquito density (transit time ≪1 month) (Chitnis et al., 2008). With Assumption 3a in place, this yields:

  $$\widehat{M}(t) = \frac{\Psi[w(t), T(t)]}{\delta}. \tag{11}$$

  Alternatively, with Assumption 3b in place, this yields:

  $$\widehat{M}(t) = K[w(t), T(t)]. \tag{12}$$

- Assumption 5: since we are considering a large geographic area where spatial heterogeneity likely weakens the nonlinear nature of the interaction between infected humans and mosquitoes (as shown for other systems, see e.g. Katul et al., 2007b), we also assume that the density of infected mosquitoes is proportional to the total mosquito density: $\widehat{M_\mathrm{I}}(t) \cong \gamma \widehat{M}(t)$. With these assumptions, $\widehat{M_\mathrm{I}}(t)$ is given by:

  $$\widehat{M_\mathrm{I}}(t) = \gamma \frac{\Psi[w(t), T(t)]}{\delta}, \tag{13}$$

  and

  $$\widehat{M_\mathrm{I}}(t) = \gamma K[w(t), T(t)] \tag{14}$$

  from Eqs. (11) and (12), respectively. Equations (13) and (14), together with Eq. (5) and (6) lead to a system of two coupled linear equations driven by rainfall

P, water content w, and temperature T:

$$\frac{dw(t)}{dt} = P(t) - mw(t) \tag{15}$$

$$\frac{dH_{\mathrm{I}}(t)}{dt} = \eta\gamma\varepsilon[w(t),T(t)] - (\nu+\mu)H_{\mathrm{I}}(t) \tag{16}$$

where $\varepsilon[w(t),T(t)]$ is given by either $\Psi[w(t),T(t)]$ or $K[w(t),T(t)]$. Equation (16) predicts a rapid growth in the number of infected individuals when climate is favorable for mosquito emergence (large ε) or exponential decay in the number of infected individuals when climate is unfavorable ($\varepsilon \approx 0$). At the time scale of a month, malaria incidence A is just the first term of Eq. (16), $A(t) = \eta\gamma\varepsilon[w(t),T(t)]$.

- Assumption 6: if we assume that the effect of the soil water content and temperature on mosquito growth rate is linear, we have $A(t) = a + bw(t) + cT(t)$.

Under these assumptions, the minimalist model given by Eqs. (15) and (16) is linear in both the state variables and the climatic factors, allowing us to remove the seasonal component of these dynamics, leaving the dynamics themselves in terms of anomalies from the seasonal averages. This solution is appropriate because the disease and climate time series are both strongly seasonal, therefore hindering the identification of how climate variability drives disease dynamics on an interannual time scale (Hay et al., 2000; Briet et al., 2008). Seasonal averages for malaria case incidence and for precipitation levels are shown in the insets of (Fig. 2) for each of the three provinces.

Indicating the monthly anomalies with prime signs and the seasonal monthly averages with an overbar, we have $P(t) = \overline{P} + P'(t)$, $A(t) = \overline{A} + A'(t)$ and $H(t) = \overline{H} + H'(t)$. Because the monthly temperature anomalies are negligible in comparison to the anomalies in the hydrologic variables (the maximum standard deviation of the anomalies of temperature is 0.84, recorded for the province of Limpopo, and the maximum standard deviation of the temperature seasonal average is 4.19 in the province of KwaZulu-Natal), Eqs. (15) and (16) can be re-written:

$$\frac{dw'(t)}{\mathrm{d}t} = P'(t) - mw'(t) \tag{17}$$

$$\frac{dH_{\mathrm{l}}'(t)}{\mathrm{d}t} = A'(t) - (\nu + \mu)H_{\mathrm{l}}'(t) \tag{18}$$

with

$$A'(t) = bw'(t) \tag{19}$$

Given monthly malaria case incidence anomalies A' and monthly precipitation anomalies P', we sought to fit parameters m and b. To this end, Eq. (17) was integrated numerically with a given value of m through a finite difference approach to yield soil water content levels over time, $w'(t)$, and parameter b was then estimated through linear regression (Eq. 19). Calibration was performed by using the differential evolution adaptive Metropolis (DREAM) algorithm (Vrugt et al., 2008), yielding best fit values for parameters b and m along with their posterior probability density functions. Our expectation is that b is positive (anomalously high water soil content should have a positive effect on mosquito growth rate) and that the rate of soil water loss m is on the order of 0.3–0.5 months^{-1} (Katul et al., 2007a). To yield predictions of monthly malaria cases (Fig. 3), malaria case anomalies A' were first estimated (given the best fit parameter values b and m) and then added to the seasonal averages in malaria case numbers $\overline{A}$.

The third way we assessed the association between climatic drivers and malaria cases built on a stochastic model to reduce the uncertainty in model fitting through statistical efficiency. Specifically, we used a transfer function model, i.e. a linear filter of the climatic variables to predict malaria cases. The model was conceived by mimicking the relationship suggested by the eco-hydrologic model (Eqs. 17 and 19 above).

Given that the time series of monthly malaria cases A and monthly rainfall levels P both showed a seasonal pattern in their standard deviations, making the time series heteroscedastic and limiting robust parameter estimation, we adopt a transfer function model of the form:

$$w''_{i+1} = P''_\text{I} + n w''_\text{I} \tag{20}$$

$$A''_\text{I} = d\, w''_\text{I} \tag{21}$$

where double prime signs indicate that the variables are normalized with respect to their seasonal standard deviation. Equation (20) describes soil moisture anomaly at month i as rainfall anomaly plus a portion of the previous month anomaly, while Eq. (21) is analogous to Eq. (19). Parameters d and n are conceptually similar to b and m, and are estimated with the same genetic optimization algorithm as detailed above. Again, we expect that d is positive. To yield predictions of monthly malaria cases using this transfer function model (Fig. 3), malaria case anomalies A'' were estimated (this time given the best fit parameter values d, and n), denormalized with respect to standard deviations and, as before, added to the seasonal averages in malaria case numbers $\overline{A}$. To check statistical consistency, transfer function model residuals were tested against Gaussianity, homoscedasticity, and independence, using the Kolmogorov-Smirnov, Bartlett and Portmanteau test, respectively.

Figure 4 shows the posterior probability distributions for the parameters of both models applied to the Mpumalanga data. It can be seen that calibration converged to well defined optimal values. On the other hand, parameter uncertainty is significant.

3 Results and discussion

The seasonal component of malaria dynamics explained on average 41 % of the variability in cases (Table 1). None of the linear regressions between deseasonalised climate forcing and deseasonalised malaria cases explained significant variability in malaria case anomalies, resulting in at most a Nash efficiency (Nash et al., 1970) of 14 % for the rainfall-malaria correlation with a zero month time lag in the province of KwaZulu-Natal (Table 1). Introducing time lags did not improve the results. These results indicate that a direct and linear association between climatic variables and malaria dynamics is not statistically supported, beyond seasonal effects.

We therefore considered whether soil water content dynamics may be associated with malaria case anomalies. The eco-hydrologic model was able to explain a significant fraction of the variation in malaria cases in all three provinces (Fig. 3 and Table 1). Furthermore, the parameter estimates of the eco-hydrologic model, including the slope of the regression between soil water content anomalies and malaria case anomalies, are biologically and physically interpretable (Table 2). Estimates of the parameter m, the rate at which soil water is lost, yielded values between 0.1 and 0.44 months^{-1}, although the related 95 % confidence limits, also shown in Table 2, show the presence of significant parameter uncertainty. This result was expected in view of the values of the explained variance. The optimal parameter values translate in soil water transit times of 2–10 months, which highlight the persistence of perturbations induced in malaria cases by higher than usual precipitation. 95 % confidence limits of the transit times allows one not to reject the hypothesis that they are identical in all the three locations. Values of the soil water loss rate m between 0.3 and 0.5 months^{-1} are comparable with estimates from other systems (Katul et al., 2007a), while the smaller estimate of this parameter for Limpopo suggests the possible presence of a biological delay in the disease dynamics not explicitly considered here (Pascual et al., 2008; Hay et al., 2000). As a whole, from a physical perspective, these results suggest that unusually wet periods result in anomalously high surface and soil water storage, and thereby higher mosquito densities, ultimately yielding anomalously high malaria case numbers.

In our eco-hydrologic model, all of the delays between favorable environmental conditions and malaria incidence are assumed to be induced by soil water dynamics. This is consistent with observed biological delays (in both the mosquito population and in disease dynamics) that are shorter than a month (e.g. Chitnis et al., 2008), while the memory induced by surface water storage is generally longer (e.g. Katul et al., 2007a). The proposed simplified model neglects compound delays and nonlinear interactions that might result in long delays between climatic forcing and malaria cases (Pascual et al., 2008; Hay et al., 2000). Our results are therefore likely to underestimate surface water loss rates m to some degree, since we attributed all physical and biological delays to soil water content dynamics alone.

For the transfer function statistical model, first note that we expect different parameter values because deseasonalisation of standard deviation was carried out. However, the resulting transit times are consistent with those obtained with the eco-hydrologic model. The results show that the hypotheses of Gaussianity and homoscedasticity of the residuals cannot be rejected at the 95 % confidence level in all three of the time series, therefore providing support for the assumption of model linearity. On the other hand, all the residuals exhibited the presence of a slight but still statistically significant correlation (at the 95 % confidence level). This outcome is due to the inability of the model and the selected climatic determinants to fully account for the persistence of the malaria case anomalies. Such persistence could presumably be accounted for by other factors; however, this would introduce more parameters and thus uncertainties in their estimation. Alternatively, the residual correlation could be eliminated introducing a further autoregressive component in the regression model to account for previous malaria cases, which would summarize the effects of the additional inputs above (see, for instance, the approach adopted by Zhou et al., 2004). However, this solution was not used here because it induces equifinality, therefore hindering the efficient identification of the causal relationship between rainfall/soil water content and malaria. Looking at the statistical model performance (Table 1) one can see that they are comparable with those of the eco-hydrologic model, with some differences depending on location.

4 Conclusions

Through an application to time series of malaria cases from three South African provinces, we showed through two sets of analyses – the eco-hydrologic model and the transfer function model – that soil water content is an important driver of malaria dynamics. These analyses required a series of consecutive assumptions to be made in order to interface these models with the climate data and malaria data that were available. Nevertheless, we found a statistical association between modelled soil water content and malaria cases in all three provinces, with parameter estimates that were biologically and physically interpretable. Future work, with more extensive time series, should therefore focus on coupling soil water content dynamics to full epidemiological models (Eqs. 1–4), which require a larger number of parameters, but that maintain the non linear feedbacks that are known to be important for malaria dynamics in endemic regions (Koelle and Pascual, 2004; Pascual et al., 2008; Laneri et al., 2010).

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Table 1. Nash efficiencies for the seasonal component of malaria dynamics, the eco-hydrologic model, and the transfer function model for the three South African provinces of Mpumalanga, Limpopo and KwaZulu-Natal.

	Equation	Mpumalanga	Limpopo	KwaZulu-Natal
Seasonal cycle		0.496	0.388	0.337
Rainfall-malaria correlation				
(0 month time lag)		0.117	0.027	0.140
(1 month time lag)		0.027	0.033	0.125
Minimum temperature-malaria correlation				
(0 month time lag)		0.016	0.005	0.026
(1 month time lag)		0.046	0.001	0.069
Ecohydrologic model	(17)–(19)	0.351	0.160	0.313
Seasonal+ecohydrologic		0.674	0.491	0.545
Transfer function model	(20)–(21)	0.351	0.190	0.156
Seasonal+transfer function		0.752	0.454	0.569

Table 2. Best set of model parameters (and 95 % confidence level) of the eco-hydrologic and transfer function models for the three provinces illustrated in Fig. 1.

Model	Parameter	Units	Mpumalanga	Limpopo	KwaZulu-Natal
Eco-hydrologic model	*m*	month^{-1}	0.442 (0.164 ÷ 0.780)	0.107 (0.063 ÷ 0.359)	0.267 (0.180 ÷ 0.551)
	b	cases mm^{-1} month^{-1}	2.697 (1.394 ÷ 3.686)	0.673 (0.338 ÷ 1.135)	8.855 (5.457 ÷ 13.393)
Transfer function model	*n*	-	0.916 (0.726 ÷ 0.945)	0.871 (0.698 ÷ 0.931)	0.745 (0.103 ÷ 0.864)
	d	-	0.145 (0.108 ÷ 0.311)	0.242 (0.131 ÷ 0.362)	0.214 (0.074 ÷ 0.449)

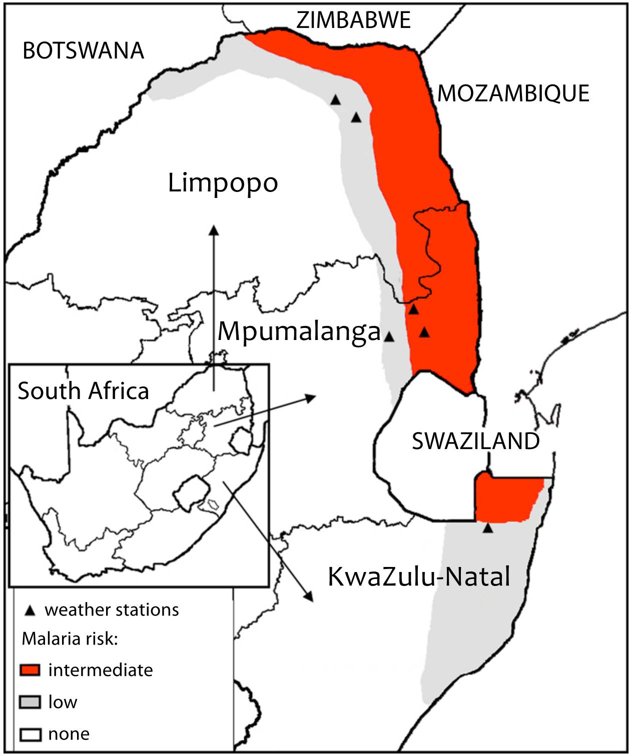

Fig. 1. Map of the investigated provinces in South Africa, colored by level of malaria risk. The locations of the weather stations for each province are marked with black triangles (see: http://www.malaria.org.za/Malaria_Risk/Risk_Maps/risk_maps.html).

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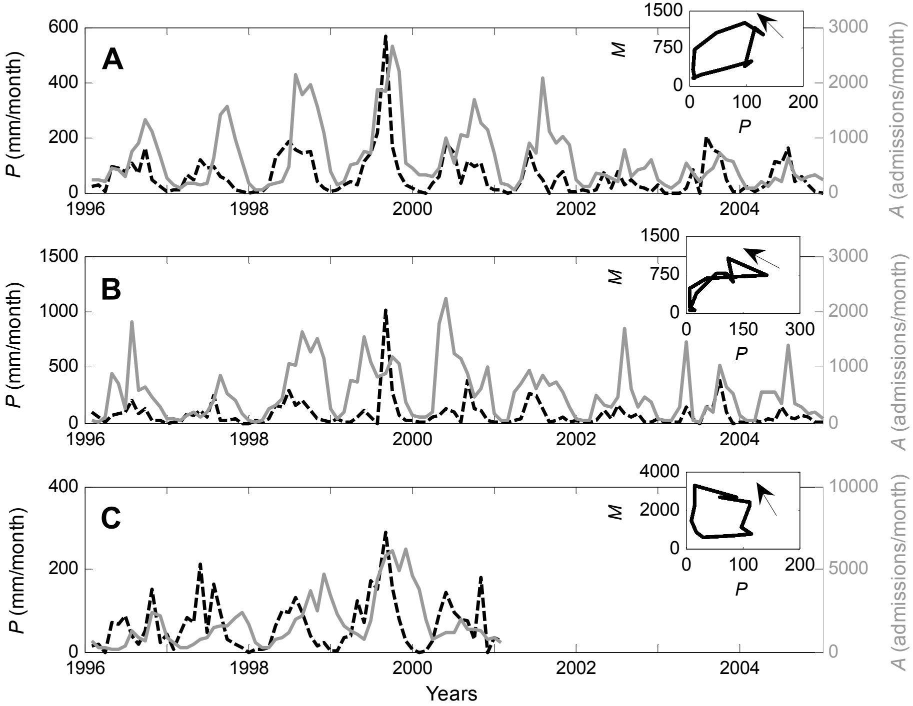

Fig. 2. Monthly malaria cases and rainfall levels for **(A)** Mpumalanga, **(B)** Limpopo, and **(C)** KwaZulu-Natal provinces. Insets, seasonal averages of malaria cases and rainfall levels(time proceeds according to the arrows).

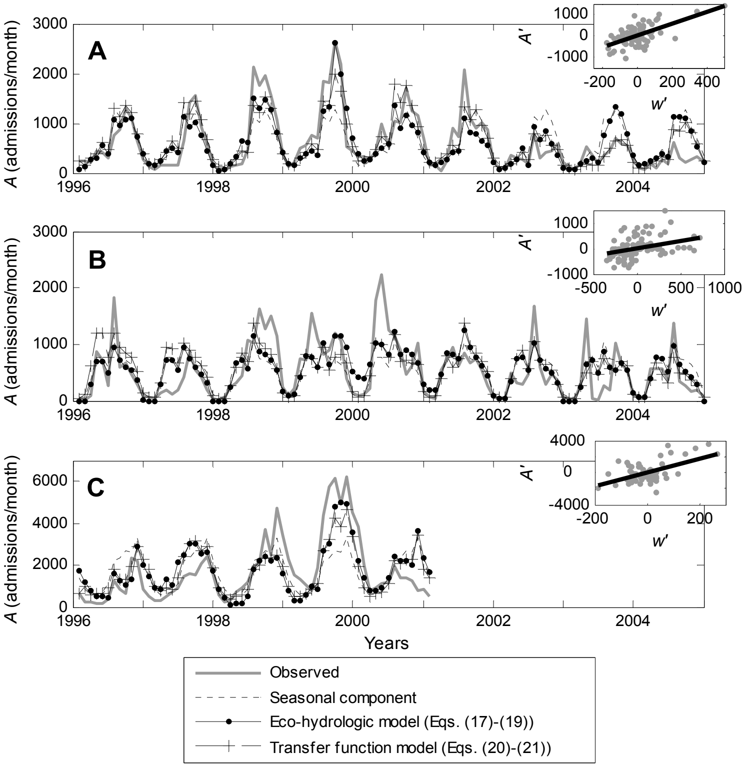

Fig. 3. Observed and modeled monthly malaria incidence for **(A)** Mpumalanga, **(B)** Limpopo and, **(C)** KwaZulu-Natal provinces. Observed incidence is shown alongside seasonal averages, case estimates form the eco-hydrologic model, and case estimates from the transfer function model. Insets are scatter plots of soil water content anomalies against malaria case anomalies for each province (dots, observations; solid lines, modeled relationships using (Eq. 17 and 19). Best fit parameters are reported in Table 2).

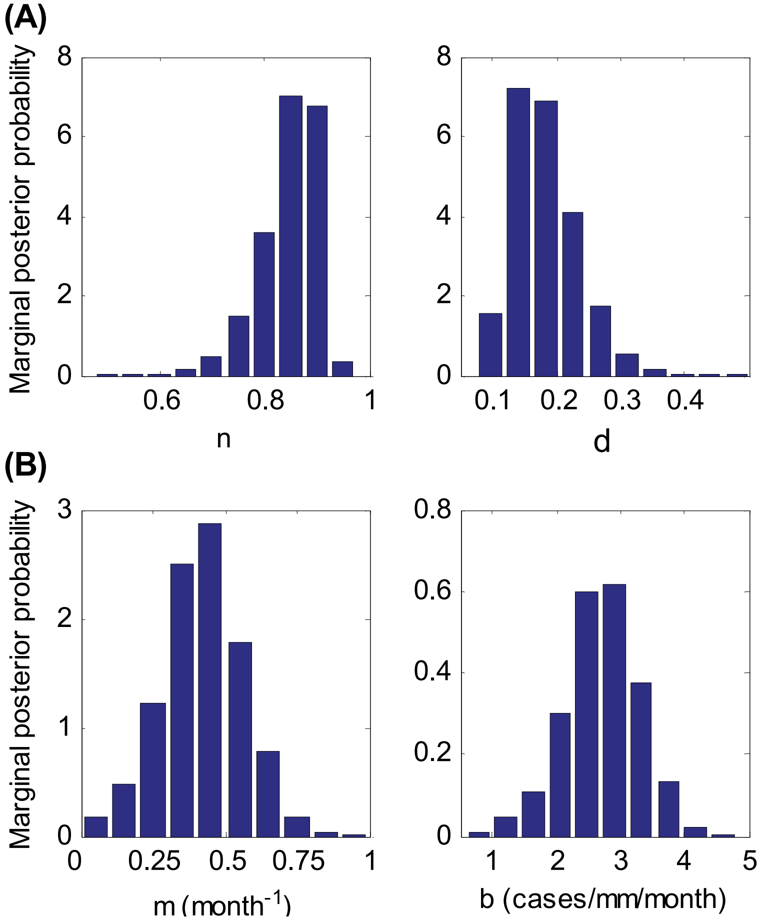

Fig. 4. Posterior parameter distributions for **(A)** eco-hydrologic and **(B)** transfer function models at Mpumalanga. 95 % confidence bands for the parameters are given in Table 2.