Larger mangrove forests carry lower and healthier ones higher malaria risk: the importance of integrating mangrove conservation with vector management at local scale

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Abstract

Malaria remains a major public health challenge causing an annual estimated 600,000 deaths and 250 million infections. While most malaria vector control efforts focus on freshwater mosquito species, saltwater-tolerant mosquitoes inhabiting coastal ecosystems like mangrove forests remain understudied. Historically, mangrove forests have been perceived as breeding grounds for malaria vectors, which is often a motivation for their destruction. However, mangroves provide crucial ecosystem services, and their impact on malaria transmission remains unresolved. This study presents the first African multi-country analysis linking mangrove forests to malaria prevalence. We employed piecewise structural equation models (SEMs) to examine the relationships among mangrove land cover and mangrove vegetation health across coastal settlements in 27 African countries. We combined satellite-derived land cover, vegetation, and weather data alongside malaria incidence records from 1996 to 2020. We found two key associations. First, increased mangrove land cover is associated with lower malaria prevalence at coarse spatial resolution, challenging the traditional view of mangroves as disease-promoting environments. This reduction may reflect ecological factors such as limited densities of saltwater mosquitoes, reduced larval development due to shading, or the presence of natural predators. Second, at fine and coarse spatial resolutions, healthier mangrove forests (i.e. more vegetation) are correlated with increased malaria prevalence. This trend may be driven by higher mosquito abundance and biodiversity in vegetatively rich mangrove areas, aligning with other studies showing vegetation as a positive predictor of mosquito population density. Our results suggest that mangrove forests generally carry a low risk of malaria transmission. From this low baseline, transmission is higher in healthier mangrove forests. How large this difference is will likely depend on the locality and configuration of the forests. These findings highlight the importance of integrating mangrove conservation with context-specific vector management strategies.

Keywords

Africa, NDVI, dilution effect, disease ecology, parasite, *Plasmodium falciparum*, structural equation modelling

Introduction

Understanding how environmental conditions influence disease transmission is essential for effective public health and conservation strategies (Adisasmito et al., 2022; Lambin et al., 2010). Malaria kills approximately 600,000 people every year and infects 250 million (WHO, 2024). Substantial effort has been put into controlling malaria and its vectors (Duffy et al., 2024; Mbanefo & Kumar, 2020; Messenger et al., 2023), particularly mosquitoes that lay their eggs in freshwater bodies. However, several malaria vector species also inhabit brackish and saltwater environments in coastal areas (Ramasamy & Surendran, 2012).

Mangrove forests are one of the most widespread ecosystems along tropical and subtropical coastlines (Dahdouh-Guebas et al., 2022). Mangrove forests, like many wetlands, have historically been considered to promote disease transmission (Dahdouh-Guebas et al., 2021; Friess, 2016). This perception originated in the now-disproved “miasma theory”, which attributed malaria to the “bad air” of wetland environments (Friess, 2016). Saltwater-tolerant mosquitoes can transmit malaria in mangrove forests (Diop et al., 2002; Pock Tsy et al., 2003; Sy et al., 2023), although their real impact on malaria prevalence remains unresolved. Their suggested role in disease transmission has led to the purposeful destruction of mangrove forests (Valiela et al., 2001). Mangrove research in past decades has spent significant efforts highlighting the ecological and social benefits of these habitats for local communities (Dahdouh-Guebas et al., 2020, 2021; Friess, 2016), including ecosystem services such as fisheries production (zu Ermgassen et al., 2021, 2025), timber (Dahdouh-Guebas et al., in press), firewood (Satyanarayana et al., 2021), coastal protection (Barbier et al., 2011; Strain et al., 2022), carbon storage (Duarte et al., 2013), cultural significance (Dahdouh-Guebas et al., 2021; Moore et al., 2022), and tourism (Spalding & Parrett, 2019). While mangrove ecosystems have been managed or restored to maximise these benefits (Dabalà et al., 2023), it remains unclear how their loss, conservation, or restoration affects the malaria burden of coastal communities.

Human malaria is a major public health issue in sub-Saharan Africa, the region with the world's highest malaria burden (WHO, 2024). The role of African saltwater-tolerant mosquitoes (*Anopheles merus* Dönitz, 1902 and *An. melas* (Theobald, 1903)) in malaria transmission is poorly understood (Bartilol et al., 2021), although some studies indicate that these species are relevant vectors, e.g. in East Africa (Bartilol et al., 2021; Cuamba & Mendis, 2009). Over time, vector communities (Musiime et al., 2019; Mwangangi et al., 2013) and their feeding behaviour (Russell et al., 2013) can change, for instance, as a result of mosquito control programmes. Therefore, mosquitoes in mangrove forests could become an important source of malaria transmission in the future. Saltwater-tolerant mosquitoes also transmit other tropical diseases that are less well documented, such as lymphatic filariasis, another parasitic disease (Kipyab et al., 2013; Pi-Bansa et al., 2019). The problem of coastal malaria and other diseases transmitted by saltwater-tolerant mosquitoes might further be exacerbated by global warming and rising sea levels, which may lead to more flooding, increasing the impact of saltwater-tolerant vectors in coastal areas (Ramasamy & Surendran, 2012). These trends underscore the need to better understand how coastal environments such as mangrove forests shape disease risks, particularly in vulnerable tropical regions.

Counter to the potential threat posed by saltwater-tolerant mosquitoes, mangrove forests might also limit malaria infections. Several factors have been hypothesised to play a role. Natural predation, e.g. by fishes, insects, crustaceans, and flatworms, on adult and larval mosquitoes can directly reduce mosquito abundance (Arthiyan et al., 2024; Griffin & Knight, 2012; Kaura et al., 2023; Kumar & Hwang, 2006; Louca et al., 2009; Tranchida et al., 2009). Shading could slow down larval emergence by reducing water temperatures (Burkett-Cadena & Vittor, 2018). More broadly, biodiversity may yield dividends for public health. In some ecosystems, greater biodiversity is linked to reduced disease transmission. For instance, Lyme disease infection risk in North America can be diluted by the addition of less-competent hosts to forest communities (Wood & Lafferty, 2013). While this 'dilution effect' provides a strong motivation to conserve ecosystems (Wood & Lafferty, 2013), the generality of these negative biodiversity–disease relationships has been questioned, as many examples exist of systems in which biodiversity destruction has reduced disease transmission—including malaria, which can be eradicated through wetland draining (Hudson et al., 2006; Rohr et al., 2019; Wood, 2025; Wood et al., 2014; Wood & Johnson, 2015). Whether mangrove biodiversity contributes to such a dilution effect remains an open question.

How mangrove forests affect malaria infections likely depends on the spatial resolution at which this relationship is studied. Previous studies showed that the relationship between mosquito-borne diseases and landscape characteristics changed depending on the spatial resolution. For example, Brock et al. (2019) found that changes in forest canopy cover influenced zoonotic malaria burden (*Plasmodium knowlesi* Sinton and Mulligan, 1932) at resolutions of 0.5 km. In contrast, habitat fragmentation was an important predictor at a resolution of 4–5 km (Brock et al., 2019). This example illustrates a broader trend regarding the relationships between ecological factors and disease distributions. Disease burdens correlate most strongly with biotic factors at fine spatial resolution ('local scales'), whereas abiotic factors correlate at coarse spatial resolution ('regional scales') (Cohen et al., 2016; Rohr et al., 2019) [but see also evidence to the contrary in Magnusson et al. (2020)]. The rationale is that species interactions occur at fine spatial resolution, whereas the influence of abiotic conditions, such as weather or topography, generally becomes detectable at regional and not local level. For instance, mosquitoes rarely travel beyond 5 km from their breeding sites (Jansson et al., 2021; Thomas et al., 2013). Therefore, if malaria transmission in mangrove forests is influenced by biotic interactions like predation, these effects are likely the strongest when measured at fine spatial resolution. In contrast, the effects of abiotic factors including weather, seasonality, salinity, and population density on the mangrove-malaria relationship may only become detectable at coarse spatial resolution.

The present study examines how (i) mangrove land cover and (ii) mangrove health affect malaria prevalence directly or indirectly, and (iii) at which spatial resolution these relationships are the strongest. To achieve these goals, we conducted a multi-country analysis of satellite-derived land cover, vegetation, and weather data alongside malaria incidence records from 1996 to 2020. Using piecewise structural equation models (SEMs), we disentangled the direct and indirect effects that influence the mangrove-malaria relationships. This study is the first continent-wide analysis of the relationship between mangrove forests and malaria burden.

Methods

Overview

Classical statistical methods in ecology such as linear and mixed models test for direct effects between variables. The mangrove–malaria relationship might, however, be shaped by many indirect relationships, which these models cannot fully capture. Therefore, we opted to use structural equation models (SEMs), an approach specifically designed to test for direct and indirect effects. We would like to point out that SEMs are a confirmatory analysis, meaning that we built the model structure based on postulations about causal relationships between the variables of interest. This model structure is then tested against the data. Importantly, we do not aim to model all possible variables influencing malaria prevalence, but rather to test whether the postulated mangrove–malaria relationship is confirmed or rejected by our data. To account for potentially missing or superfluous causal connections, the model building was followed by an optimisation procedure. The final optimised models were used for interpreting the support for the individual causal relationships of the SEM structure.

To contextualise the performance of our SEM approach, we also benchmarked the results by running a series of supervised machine learning algorithms (Supplementary File S1) on the same input data (Bailly et al., 2022; Chen & Guestrin, 2016; Chollet, 2015; Pedregosa et al., 2011; Python Software Foundation, 2023; Richardson et al., 2024). The comparison aims to highlight how well the SEM approach is at fitting models compared with the predictive performance of the machine learning approach that does not explicitly test for indirect effects.

Malaria prevalence data were obtained through the MalariaAtlas project, which is the most extensive malaria database currently available (Guerra et al., 2007). The project is a curated collection of georeferenced malaria surveys from various peer-reviewed sources and the Demographic and Health Surveys (DHS) Programme (ICF, 2007). The observations listed in the MalariaAtlas project include information on the number of tested individuals, number of infected individuals, survey methodology (microscopy or rapid diagnostic testing – RDT), and start and end date (month and year) of the survey period. We focused on infections of *Plasmodium falciparum* (Welch, 1897) because it is the deadliest human malaria agent and most prevalent on the African continent (WHO, 2024). For the other variables, we adopted a hypothesis-driven approach. This meant only including those variables that could plausibly modulate the relationship between malaria and mangrove forests based on hypotheses posited in previous publications. Four sets of variables were collected: *mangrove-related*, *human impact*, *weather*, and *geographical variables*. We then extracted and assembled data from vector and square-shaped raster layers for each georeferenced malaria survey site (see *Data collection, extraction, and assembly*), limiting this selection to years with corresponding mangrove-related data.

Variable selection

The mangrove-related variables included mangrove land cover and vegetation health, measured by NDVI (normalised difference vegetation index). Mangrove land cover captures the potential effect of mangrove forests increasing malaria prevalence, as has been suggested in historical documents (Friess, 2016). Mangrove NDVI was selected as a proxy for mangrove health (Ruan et al., 2022; T. V. Tran et al., 2022). We employed NDVI to reflect the concept of the dilution effect: Healthier mangroves should support greater biodiversity as suggested for fishes (L. X. Tran & Fischer, 2017), birds (Mohd-Azlan et al., 2015), and macrobenthic organisms (Leung & Cheung, 2017). This higher biodiversity might buffer the transmission of malaria to humans through, e.g. natural predation of mosquito larvae and adults. Furthermore, we selected NDVI over similar indices as a trade-off between availability of long-term and spatially resolved data layers (Didan, 2021).

For the *human impact variables*, we selected two factors to capture anthropogenic pressure. The use of population density alone as an indicator of human impact on mangrove forests (Chien et al., 2024) and malaria prevalence (Mbouna et al., 2019) has previously been questioned. Therefore, we also included agricultural land cover, which has been reported as one of the main drivers of mangrove loss (Goldberg et al., 2020) and is also associated with increased childhood malaria in Africa (Shah et al., 2022).

For the *weather variables*, temperature and precipitation are known to affect mosquito biology and, hence, malaria infection rates. But these effects might occur with a time lag (Craig et al., 1999; Donkor et al., 2021; Ikeda et al., 2017), i.e. rainfall can initially lower temperature and reduce mosquito activity, but later increase in egg laying activity after the rain has passed. To account for this effect, we included mean temperature and precipitation values both during the malaria survey period (P, T) and the means over six-months leading up to the survey (P_{-6}, T_{-6}). The six-month window was chosen to capture the potential lagged effects of the weather on malaria prevalence. Some previous studies have suggested time lags of one to two months as best predictors (Donkor et al., 2021). However, as many data layers, including the mangrove variables, were only available at annual resolution, we opted to use the six-month average as a proxy for seasonality to harmonise the coarser temporal resolution of the key parameters (such as mangrove land over) with the more granular weather variables. Beyond baseline weather conditions, weather anomalies have increasingly been linked to mosquito abundance (Nosrat et al., 2021; Sorenson et al., 2025) and the health of mangrove forests (Duke et al., 2017; Servino et al., 2018). Therefore, we also calculated the deviation of temperature and precipitation from the long-term average, both during ($P_{Anomaly}$, $T_{Anomaly}$) and prior to ($P_{Anomaly-6}$, $T_{Anomaly-6}$) the malaria survey period.

As an additional *geographic variable*, we included the distance to the coastline. This variable was added to account for the area covered by open sea, which does not host mosquito populations. This was done to incorporate the possible effect of salinity on mosquito abundance and, hence, malaria prevalence.

Data collection, extraction, and assembly

The resulting dataset was compiled from existing sources on malaria prevalence, mangrove, human impact, and weather variables (Table 1). Furthermore, we extracted additional variables that are traditionally used to predict malaria infection rates, but these data were only used for imputing missing values (Supplementary Table S2) (Bertozzi-Villa et al., 2021; Rathmes et al., 2020; Smits & Permanyer, 2019; Tangena et al., 2020; Weiss et al., 2018, 2020; Wiebe et al., 2017). Malaria prevalence data with associated geocoordinates were downloaded using the package *MalariaAtlas* v1.6.3 (Pfeffer et al., 2018) in R v4.4.0 (R Core Team, 2024). We filtered data to include only those in sites located within 50 km of the coastline and within the years, for which mangrove land cover data were available (1996, 2007–2010, 2014–2020) (Bunting et al., 2022). Egypt was not included as no malaria prevalence data were available for these specific years in proximity to mangrove forests. We also excluded small island nations (Cape Verde, São Tomé and Príncipe, and the Comoros) because of their unique geographical features (e.g. disproportionately large size of ocean surface and lack of inland data points).

Mangrove variables including mangrove land cover and mangrove NDVI, were derived for each georeferenced malaria survey location. We calculated mangrove land cover both for the year of the malaria survey and the preceding year. In both cases, mangrove land cover was computed for different spatial resolutions *r*, from 1 to 50 km at 1-km intervals (Fig. 1A). This means that for each year and location we obtained 50 different values of mangrove land cover. Mangrove NDVI was calculated as the mean NDVI within the mangrove-covered area for each *r* during the year of the malaria survey (Fig.1B). In absence of mangrove forests (mangrove land cover = 0%), mangrove NDVI could not be computed and the corresponding data points were, therefore, excluded from subsequent analyses.

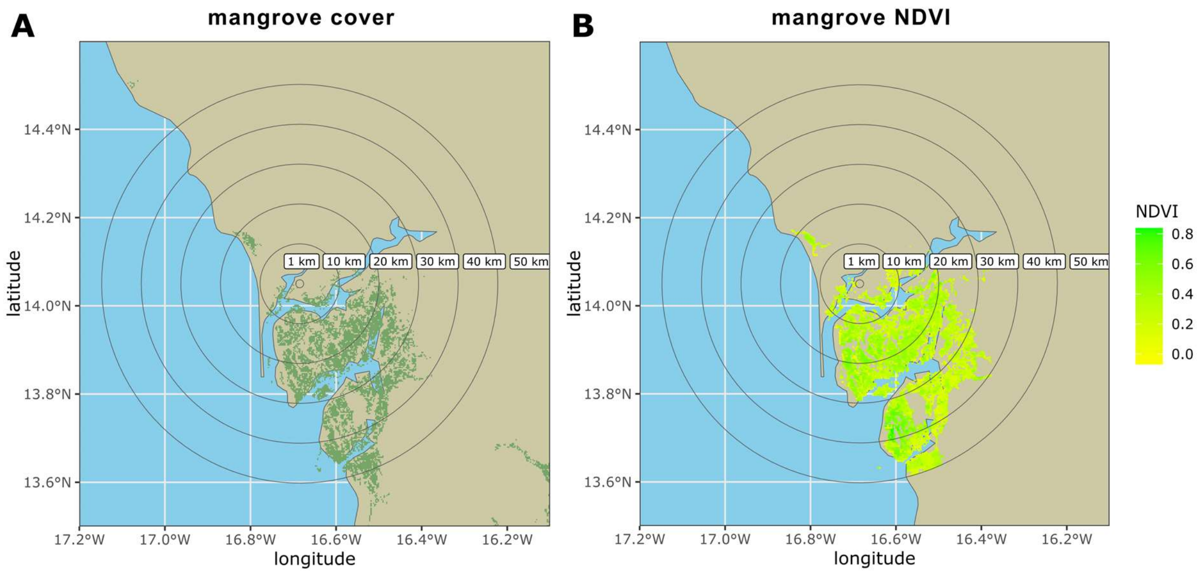

Figure 1. Example for calculation of mangrove variables (Senegal, Saloum Delta). A, mangrove land cover was calculated as share of land covered by mangrove forests for each spatial resolution *r* from 1 to 50 km in 1-km intervals (only selected values of *r* are shown). B, mangrove NDVI was calculated as mean value of NDVI inside the mangrove area and each *r*. Data sources: mangrove land cover (Bunting et al., 2022), NDVI (Didan, 2021), coastline (http:// naturalearthdata.com).

All other variables were assembled using a fixed *r* of 10 km to manage computational constraints. For raster layers with annual values (one or more years), we took the mean (weather variables, population density) or total value (agricultural land cover) within the 10-km radius. For variables with multiple observations per year, we averaged the values over the duration of the malaria survey. The *r* of 10 km was selected as trade-off between accuracy and sensitivity of these estimations. Malaria transmission could have occurred anywhere near the geographic location of the survey. A smaller *r* might therefore result in a higher number of inaccurate estimates due to human travel (Marshall et al., 2018), while a larger *r* risks masking differences between nearby locations. We recognise that the fixed *r* of 10 km might be an oversimplified approximation of human travel distance. However, global human mobility estimates are currently only available for a single year (Kraemer et al., 2020) and, therefore, challenging to harmonise with our multi-annual final dataset.

Spatial operations were performed through *R* packages *sf* v1.0.19 (Pebesma, 2018; Pebesma & Bivand, 2023), *terra* v1.8.15 (Hijmans, 2025), and *exactextractr* v0.10.0 (Baston, 2023), with the coordinate reference system adapted to each country (Supplementary Table S3).

Missing data

To deal with missing values in our dataset, we applied k nearest neighbour (kNN) imputation. This approach replaces missing values with the mean of the closest matching observations (‘nearest neighbours’) across the input dataset, with *k* determining the number of nearest neighbours to be selected. We implemented this approach in the *R* package *caret* (Kuhn, 2008), with *k* set to 10. Prior to the imputation, the values were also centred and scaled to prevent large eigenvalues from hampering model convergence. Imputation was performed using the full set of variables (Table 1 and Supplementary Table S2), which includes many variables that are frequently used in modelling malaria prevalence. Including a broad set of variables improves the selection of nearest neighbours and results in more accurate kNN estimates. The robustness of the results to the kNN imputation by producing a separate dataset, where all observations with missing values were excluded. We, then, applied the same optimisation procedure for the SEMs detailed below to this ‘reduced’ dataset.

The weather variables accounted for more than half of all variables included in our analysis (8 of 15). To avoid overfitting models with collinear variables, we assessed pairwise relationships in the dataset resulting from kNN imputation using Pearson’s pairwise correlation coefficient ρ through the *R* package *GGally* v2.2.1 (Schloerke et al., 2024). We considered $\rho > 0.7$ as indicative of collinearity (Dormann et al., 2013), but as no such case (see Supplementary Fig. S4) was found, we proceeded with the resulting dataset as it was.

Table 1. Information variables and respective data sources for machine learning analysis and structural equation modelling. r, spatial scale at which land cover and other variables were calculated.

Variable group	**Variable**	**Temporal resolution**	**Spatial resolution**	**Explanation**	**Reference**
Disease variables	Malaria prevalence (*P. falciparum*)	1980s–present	–	MalariaAtlas project through the associated R package	Pfeffer et al. (2018)
	Coastline distance	–	–	Distance of each disease data point to coastline	Coastline vectors (large scale: 10 m, v4.1.0), Natural Earth (https://naturalearthdata.com)
Mangrove variables (per km of radius r: 1–50 km)	Mangrove land cover	1996, 2007–2010, 2014–2020	max. 25 m	Percentage of mangrove surface inside *r* between 1995–2020	Bunting et al. (2022)
	Mangrove land cover (year – 1)	see above	max. 25m	Percentage of mangrove surface inside r preceding the malaria survey period	see above
	Mangrove NDVI	2000–present	250 m	Mean NDVI inside of mangrove polygons	AppEEARS Team, (2024); Didan (2021)
Human impact variables (r = 10 km)	Agricultural land cover	1992-present	300 m	Percentage of agricultural land cover inside *r* = 10 km	Copernicus Climate Change Service (2019)
	Population density	1990–2020	0.08° x 0.08°	Mean population density inside *r* = 10 km	Liu et al. (2024)
Weather variables (r = 10 km)	Temperature (survey period)	1979–present	0.25° x 0.25°	Weather data are provided in 16-day intervals (mean T and sum of P)	Copernicus Climate Change Service (2019)

	Temperature (survey period)	see above	see above	see above	see above
	Precipitation (survey period)	see above	see above	see above	see above
	Temperature (previous 6 months)	see above	see above	see above	see above
	Precipitation (previous 6 months)	see above	see above	see above	see above
	Temperature anomaly (survey period)	see above	see above	see above	see above
	Precipitation anomaly (survey period)	see above	see above	see above	see above
	Temperature anomaly (previous 6 months)	see above	see above	see above	see above
	Precipitation anomaly (previous 6 months)	see above	see above	see above	see above

Structural equation models

To investigate potential causal relationships among variables, we used structural equation models (SEMs) to test whether the final dataset fitted to the hypothesised causal relationships. SEMs have been successfully used in ecological studies to understand direct and indirect effects leading to changes in ecological communities (Ali et al., 2022; Byrnes et al., 2011; Roland et al., 2019). Several studies have also employed SEMs to understand the role of environmental change on host-pathogen interactions, including for human malaria (Duo-quan et al., 2013), bacterial infections (Ferguson et al., 2023), and fungal diseases (Vacher et al., 2008). Two separate methodologies are widely used to estimate SEMs: global and local estimation. Global estimation uses a single variance-covariance matrix to capture relationships amongst all variables included in the SEM. It assumes normality and a sufficient sample size to produce unbiased parameter estimates (Grace et al., 2015). Local estimation (piecewise SEMs) allows relationships to be estimated separately for each response variable, which also allows for the use of non-Gaussian distributions, mixed effect models, and autocorrelation terms (Lefcheck, 2016; Shipley, 2000).

Because of the binary nature of prevalence data and the need to use random effects and autocorrelation terms, we employed piecewise SEMs in the present study. All SEM operations were performed through the *R* package *piecewiseSEM* v2.3.0.1 (Lefcheck, 2016) and *glmmPQL* in *MASS* v7.3.64 (Venables & Ripley, 2002). Model fits were assessed using Shipley's test of directed separation (d-test) (Shipley, 2000) by comparing Fisher's *C* statistic. The d-test assesses whether adding further relationships to the SEM structure improves the model fit, with $p \leq 0.05$ indicating that adding specified effects significantly improves the model fit. A value of p above 0.05 means that the d-test fails to reject the model. To drop relationship from the models, we assessed the significance of single causal relationships the significance tests provided by *piecewiseSEM*, which are based on type II analyses of variance (ANOVA) (Lefcheck, 2016).

We developed an initial hypothesised SEM structure based on prior knowledge of the relationships among variables (Fig. 2). We do not claim that this structure fully reflects the true relationships among all variables; it served as an informed starting point for further model optimisation, which tested for missing or superfluous causal relationships (see next paragraph). For each value of *r*, we implemented this initial SEM structure using three generalised linear mixed models (Table 2) in the piecewise SEM framework. As we expected autocorrelations to be an important factor in our models, we dealt with these challenges following examples suggested by Lefcheck (2016). Time – with the year and month the malaria survey was initiated as a proxy variable – was included as random effect to account for temporal autocorrelation. An exponential autocorrelation term across the latitude and longitude data was modelled to account for spatial autocorrelation. We also accounted for the difference in survey technique (microscopy *vs* RDT, see 'Overview') by including the survey method as another random effect. Weather extremes might decrease values of mangrove and malaria variables, which might indicate a non-linear relationship. Therefore, we also tested whether using a quadratic term for weather variables led to improved model fits.

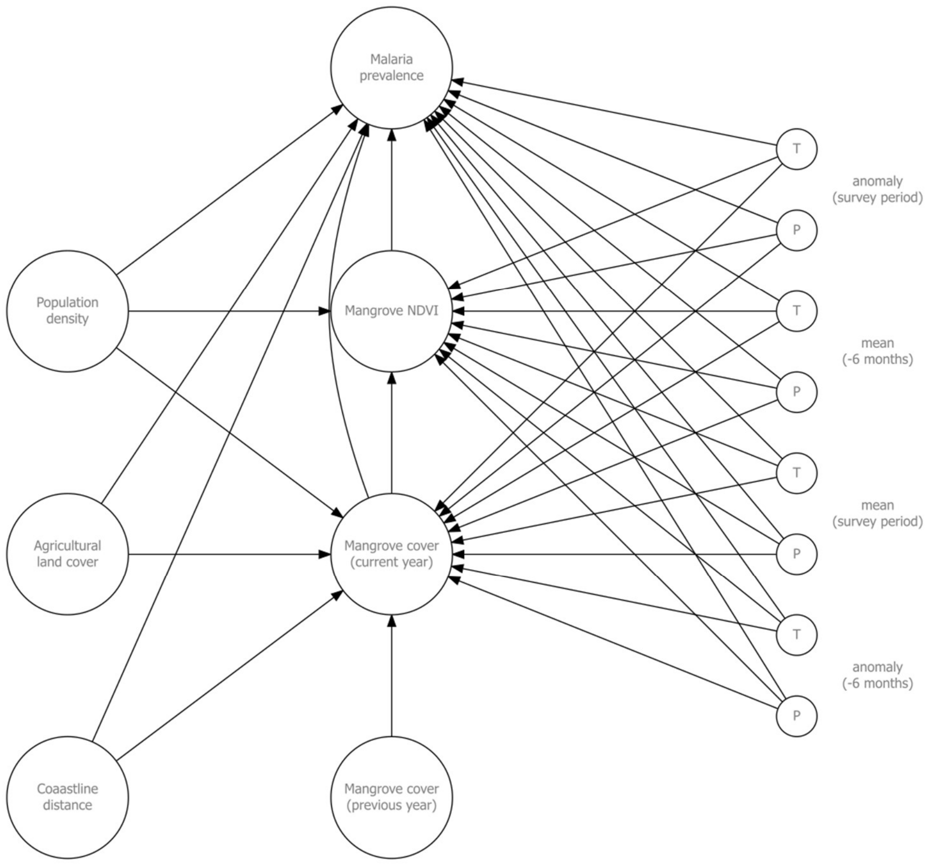

Figure 2. Path diagram of initially hypothesised structure of structural equation models with each hypothesises causal relationship of variables marked with an arrow. T: temperature variables, P: precipitation variables.

Table 2. List of dependent and independent variables of initially hypothesised structure of structural equation models illustrated in Fig. 2, including specification of respective generalised linear mixed models, and relationships dropped and added in model optimisation steps.

Dependent variable	**Independent variables**	**Model specification**	**Independent variables after optimisation, and steps used for optimisations**		
			Full dataset, missing values imputed (two steps)	**Full dataset, with quadratic terms for weather variables (two steps)**	**'Small' dataset: observations with missing values dropped (four steps)**
Malaria prevalence	• Mangrove NDVI • Mangrove cover (current year) • Population density • Agricultural land cover • Coastline distance • Weather variables	Binomial distribution with logit link	• Mangrove NDVI • Mangrove cover (current year) • Population density • Agricultural land cover • Coastline distance • Weather variables ($T_{Anomaly}$, $P_{Anomaly}$, T, T_{-6}, P_{-6})	• Mangrove NDVI • Mangrove cover (current year) • Population density • Agricultural land cover • Coastline distance • Weather variables: $T_{Anomaly}$, T, P, P_{-6}, $T_{Anomaly-6}$, $P_{Anomaly-6}$ • Weather variables (quadratic terms): $T_{Anomaly}$, T, $T_{Anomaly-6}$, T_{-6}, P_{-6}	• Mangrove NDVI • Mangrove cover (current year) • Population density • Agricultural land cover • Weather variables ($T_{Anomaly}$, $P_{Anomaly}$, $T_{Anomaly-6}$, T_{-6}, P_{-6})
Mangrove NDVI	• Mangrove cover (current year) • Population density • Weather variables	Gaussian distribution	• Mangrove cover (current year) • Mangrove cover (year-1) • Population density • Agricultural land cover • Coastline distance • Weather variables ($T_{Anomaly}$, $P_{Anomaly}$, T_{-6})	• Population density • Agricultural land cover • Coastline distance • Weather variables: $T_{Anomaly}$, $P_{Anomaly}$, T, T_{-6}, P_{-6}, $T_{Anomaly-6}$, $P_{Anomaly-6}$ • Weather variables (quadratic terms): $T_{Anomaly}$, T, P, T_{-6}, P_{-6}, $T_{Anomaly-6}$	• Mangrove cover (current year) • Mangrove cover (year-1) • Population density • Coastline distance • Weather variables ($T_{Anomaly}$, $P_{Anomaly}$, T, $T_{Anomaly-6}$, $P_{Anomaly-6}$, T_{-6}, P_{-6})
Mangrove cover (current year)	• Mangrove cover (year-1) • Population density • Agricultural land cover • Coastline distance • Weather variables	Gaussian distribution, as approximation[1]	• Mangrove cover (year-1) • Population density • Agricultural land cover • Coastline distance • Weather variables ($P_{Anomaly}$, T, $T_{Anomaly-6}$, $P_{Anomaly-6}$, T_{-6}, P_{-6})	• Mangrove cover (year-1) • Population density • Agricultural land cover • Coastline distance • Mangrove NDVI • Weather variables: $T_{Anomaly}$, $P_{Anomaly}$, T, P, T_{-6}, P_{-6}, $T_{Anomaly-6}$, $P_{Anomaly-6}$	• Mangrove cover (year-1) • Population density • Agricultural land cover • Coastline distance • Weather variables ($T_{Anomaly}$, T, P, T_{-6}, P_{-6})

	• Weather variables: $T_{Anomaly}$, P, T_{-6}, P_{-6}, $T_{Anomaly-6}$

[1] Beta or gamma distribution to fit values limited by 0% and 100% are currently not implemented in *piecewiseSEM*.

To optimise the SEMs, relationships that were not significant ($p < 0.05$) across all 50 models were all removed in a single step. Simultaneously, we applied Shipley's test of directed separation (d-test) to detect any potentially missing causal relationships. We added causal relationships if the d-test suggested their inclusion for more than 5 of the 50 models. This threshold was based on informed selection as below this value the model optimisation procedure was unstable, leading to the repeated addition and removal of the same paths. The optimisation was continued until no further effects needed to be removed or added according to these criteria. Path diagrams were visualised using the package *DiagrammeR* v1.0.11 (Iannone & Roy, 2024). Other graphs were plotted using the package *ggplot2* v3.5.1 (Wickham, 2016).

Results

Data assembly

In total, we assembled 79,005 individual observations from 1,898 unique malaria survey locations (Fig. 3A) across 27 African countries in the years 1996, 2007–2010, and 2015–2020. Depending on the spatial scale (Fig. 3B), this number varied ranging from 289 values at 1 km to 2,069 values at 50 km. Mangrove land cover in the previous year ('*mangrove land cover (year–1)*') and *mangrove NDVI* had 19% and 8% of missing values, respectively. These values were non-random as for no *mangrove land cover (year-1)* no values could be calculated for 1996, 2007, and 2015 due to lack of mangrove land cover data. No NDVI data were available for the year 1996. All other variables had no missing values. We detected only low levels of collinearity in the weather variables, with no variable pairs exceeding a correlation coefficient of 0.7 (Supplementary Fig. S4).

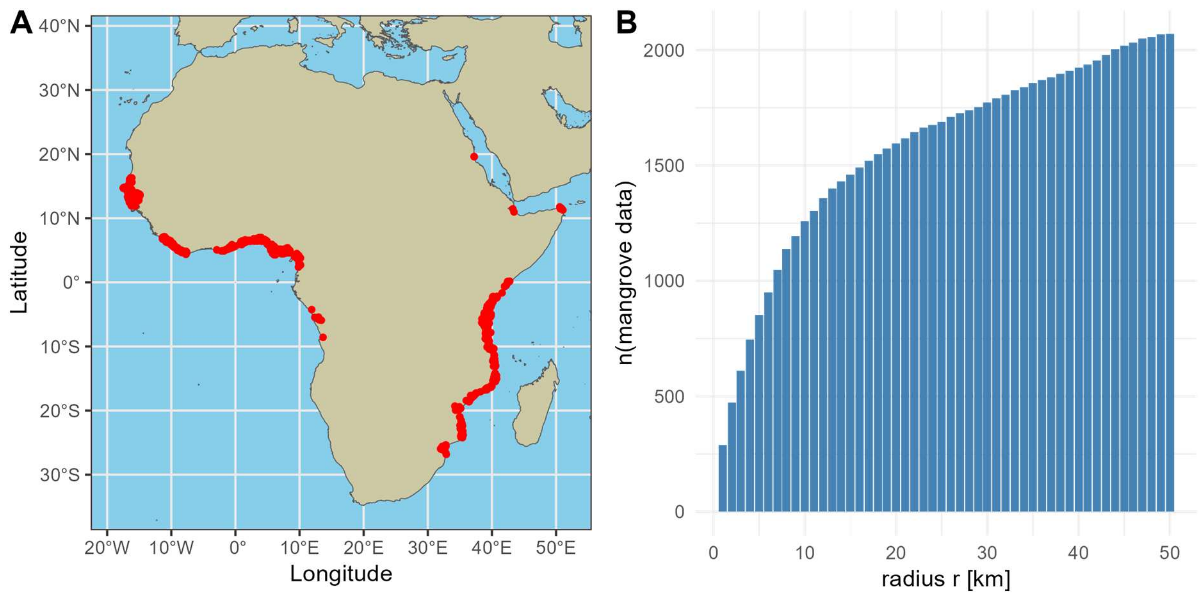

Figure 3. Overview of malaria survey data used in the final dataset. A: Geographic locations indicated in red. B: Number of observations per radius *r* at which mangrove variables (cf. Table 1) were calculated.

Structural equation modelling

Two to optimisation steps were performed for the models without the quadratic terms for the weather variables. Five steps were needed for the model with the quadratic terms. However, the non-linear terms for the weather variables did not improve model fits and were, therefore, not considered further (Fig. 4). Furthermore, the 'reduced' dataset, for which observation with values were dropped, produced similar SEM structures, albeit with a few differences concerning some of the weather variables (Table 2). A closer look at the final models (selected for the same value of *r* as resulting from the final dataset, Fig. 5) revealed that fewer relationships were well-supported (Supplementary Fig. 5). Some weaker relationships also changed from positive to negative and vice versa. However, these differences did not substantially our main conclusions, unless referred to in the discussion. The resulting path diagrams are supplied in Supplementary Fig. S5,

A total of ten causal relationships were dropped from the initially hypothesised SEM structure and three paths following optimisation (Table 2). Notably, benchmarking with supervised machine learning detected no links between malaria prevalence and the other variables (Supplementary File S1), highlighting the importance of accounting for indirect effects.

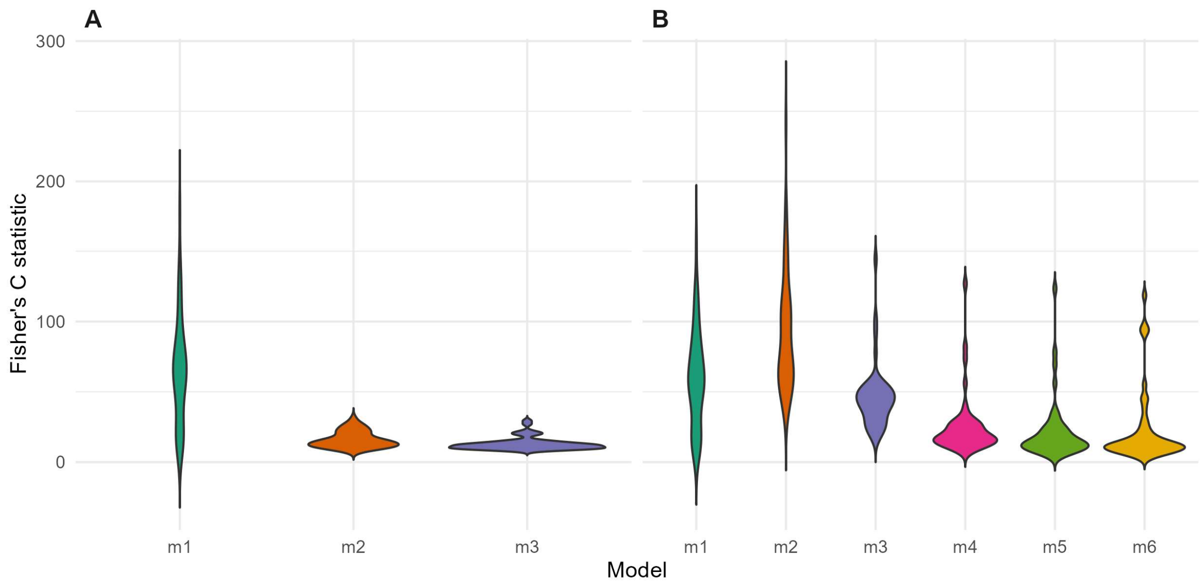

Figure 4. Distribution of Fisher's *C* for piecewise structural equation models (SEMs) with mangrove variables (land cover and NDVI) calculated at spatial resolutions of 1–50 km and model optimisation steps (m1–m6). Models without (A) and with (B) quadratic term for weather variables.

The final optimised models contained 28 causal relationships and the majority of the models (48 of 50) were supported, meaning that the d-test was rejected ($p > 0.05$). The standardised effect sizes of the estimated relationships varied across the spatial resolution *r* that was used to calculate mangrove variables. To best represent the impact of *r*, we show the path diagrams of the best supported model overall (40 km), as well as a well-supported model (28 km) in the middle range (between 10 and 30 km) and another model (3 km) the lower range (< 10 km) in Figure 5. In addition, a Shiny application is provided on GitHub (https://github.com/HU-AquaticBiodiversity/MangroveMalaria-SpatialAnalysis/src/Mangrove-Malaria_ShinyApp) to explore changes of the causal relationships for each *r* (1–50 km). Furthermore, we visualised changes in the standardised effects sizes of key relationships across r (Fig. 6A). We also plotted the malaria prevalence data against mangrove NDVI at 3-km resolution (Fig. 6B) and against mangrove land cover at 40-km resolution (Fig. 6C).

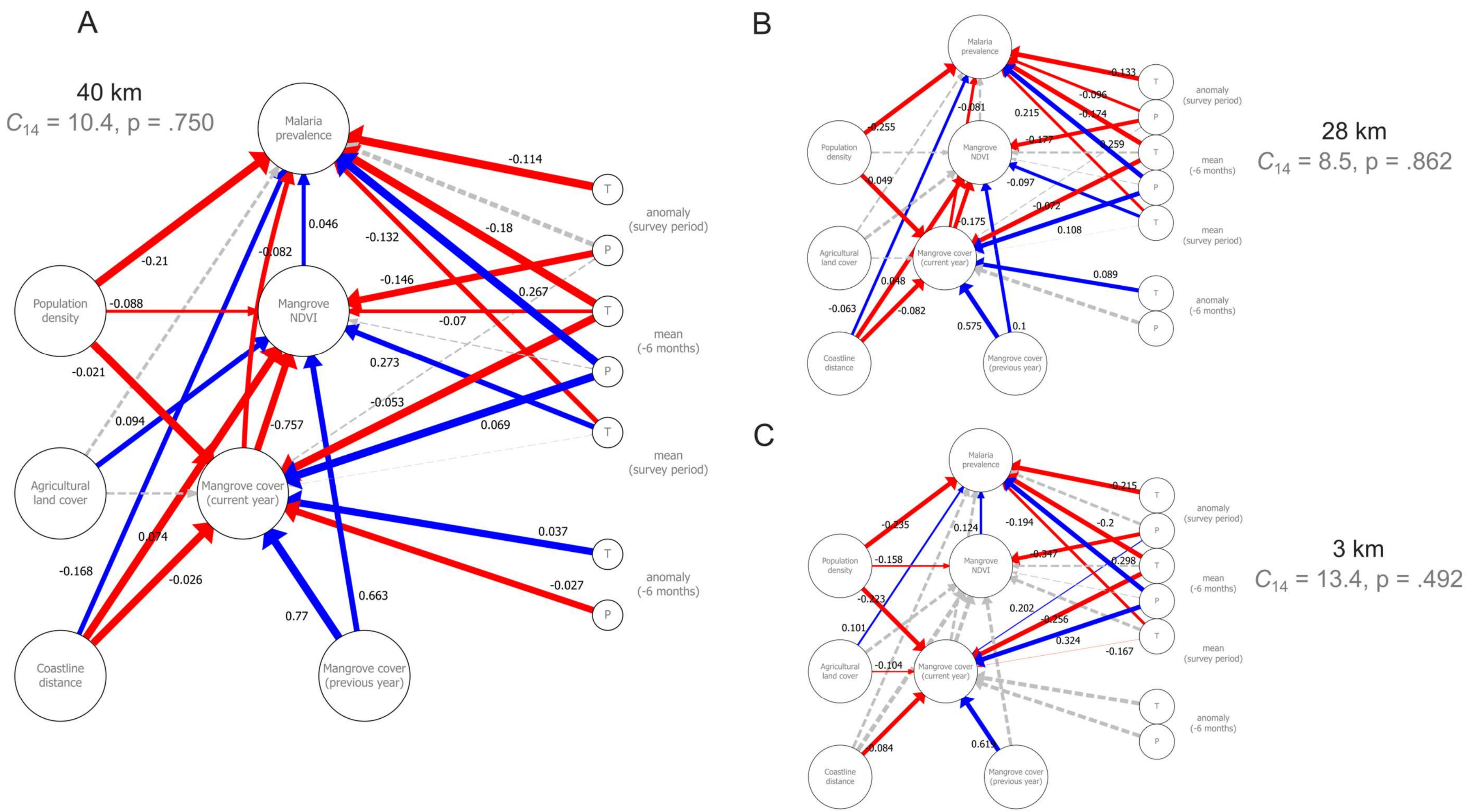
A
40 km
C_{14} = 10.4, p = .750
Malaria prevalence
Mangrove NDVI
Population density
Agricultural land cover
Coastline distance
Mangrove cover (current year)
Mangrove cover (previous year)
T
P
anomaly (survey period)
mean (-6 months)
mean (survey period)
anomaly (-6 months)
-0.114
-0.21
0.046
-0.082
-0.132
-0.18
-0.146
0.267
-0.088
-0.07
-0.021
0.273
-0.053
0.094
-0.757
0.069
0.074
0.037
-0.168
-0.026
-0.027
0.663
0.77
B
28 km
C_{14} = 8.5, p = .862
C
3 km
C_{14} = 13.4, p = .492

Figure 5. Selected structural equation models with different spatial resolution *r* explaining the causal relationship (arrows) between mangrove ecosystems and malaria prevalence. A: r = 40 km, the best supported model, B: r = 28 km, a well-supported model at intermediate spatial resolution, and C: r = 3 km, a well-supported model at fine spatial resolution. Statistical support of models: result of Shipley's test of directed separation (d-test) including Fisher's C statistic and *p* values; with $p > 0.05$ the d-test is rejected and, therefore, model is considered a good fit. Arrow colour: blue – significant positive effect, red – significant negative effect, grey & dashed – non-significant effect. Arrows thickness: number of models (*r* between 1 and 50 km) that supported each causal relationship. Values on arrows: effect sizes of the causal relationship, indicating the directionality of the causal relationships. The effect sizes serve to compare the relative influence of the relationships on the dependent variable, but should not be interpreted as absolute values due to standardisation and centring of the input dataset. Other abbreviations: see Fig. 2.

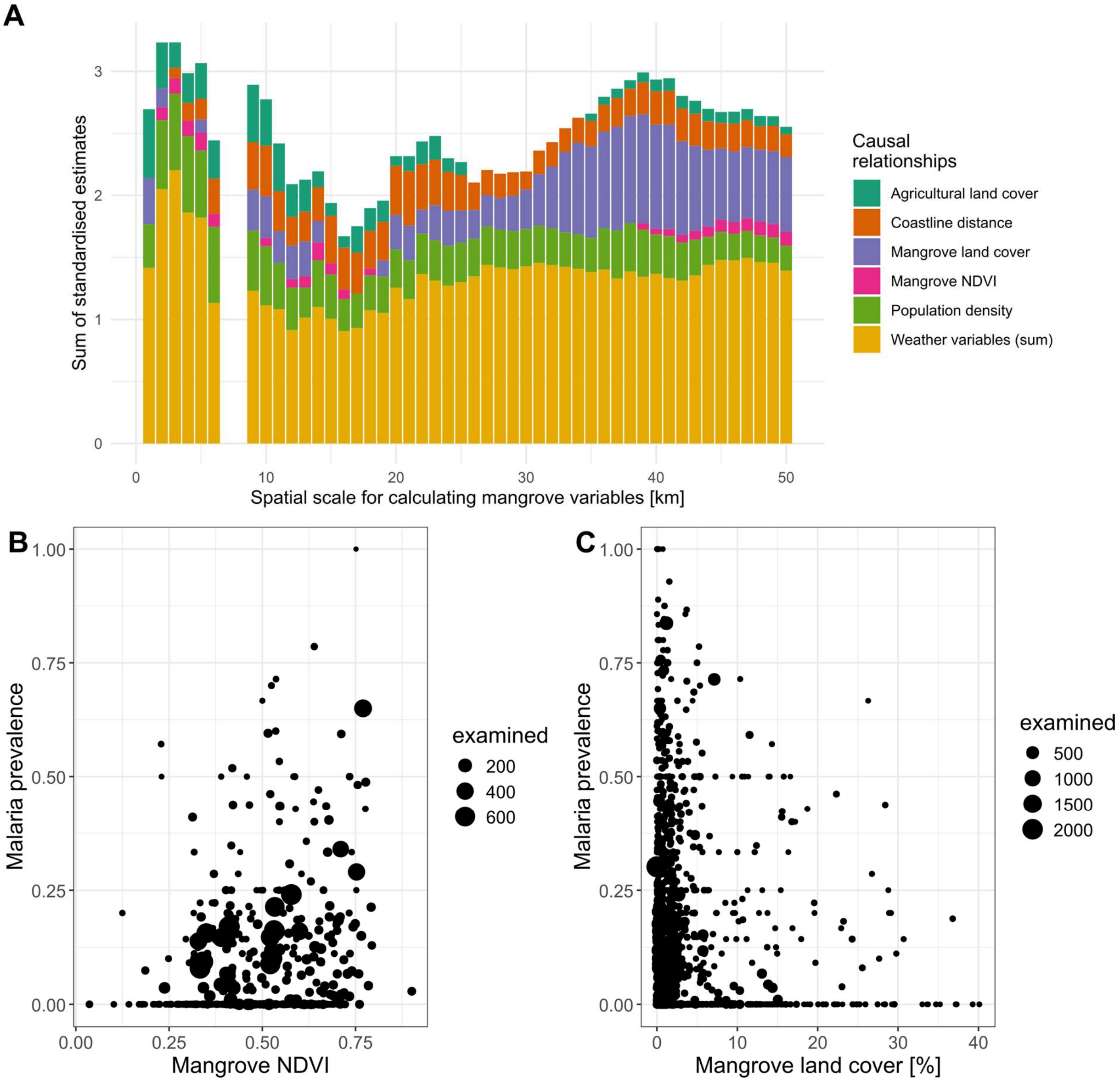

Figure 6. Relationships of different variables in the optimised structural equation models. (A) Sum of absolute standardised effect sizes of causal relationships as function of spatial resolutions (1–50 km) at which mangrove variables (mangrove land cover, mangrove NDVI) were calculated, grouped by independent variables in optimised SEMs. Only significant causal relationships were included. The trends detected through the SEM analysis are visible within the raw data: (B) Malaria prevalence as function of mangrove NDVI showing an increasing trend at fine spatial resolution (*r* = 3 km) and (C) a decreasing trend at coarse spatial resolution (*r* = 40 km).

Within our models, the weather variables accounted for the largest share of total absolute effect sizes across all spatial resolution (Fig. 6A). However, their direct influence on malaria prevalence and mangrove NDVI was much smaller at fine spatial resolution (Fig. 5C). Mangrove land cover also contributed substantially, albeit only at coarse and intermediate spatial resolution (Fig. 6A, B). Specifically, it showed no significant effect on malaria prevalence at fine spatial resolutions (3 km: 0.005, $p = 0.849$) (Fig. 5C), whereas at coarse resolution, it decreased prevalence (40 km: -0.082, $p < 0.05$) (Fig. 5A). All other variables contributed relatively little to the total effect sizes (Fig. 6).

Mangrove NDVI had a significant positive effect on malaria prevalence at fine (3 km: 0.124, $p < 0.001$) and coarse (40 km: 0.046, $p < 0.05$) spatial resolution (Fig. 5A, C; 6B, C), but showed no effect at intermediate spatial resolution (28 km: -0.008 , $p = 0.711$) (Fig. 5B). At coarse spatial resolution, mangrove land cover indirectly decreased malaria prevalence by reducing mangrove NDVI (40 km: -0.757, $p < 0.001$) (Fig. 5A). However, '*mangrove land cover (year-1)*' increased mangrove NDVI (40 km: 0.663, $p < 0.001$) and, therefore, indirectly increased malaria prevalence.

Coastline distance had a significant positive direct effect on malaria prevalence at coarse spatial resolution (Fig. 5A, Fig. 6A), but indirectly decreased malaria prevalence *via* mangrove NDVI and increased it *via* mangrove land cover. Among the human impact variables, population density had a significant negative effects on the mangrove variables, decreasing malaria prevalence as a result at fine spatial resolution (Fig. 5C), but increasing it at intermediate spatial resolution (Fig. 5B). At coarse spatial resolution, both these indirect effects were present. The effect size of population density on malaria prevalence remained relatively constant across all spatial resolutions (Fig. 6A). Agricultural land cover reduced mangrove land cover at fine and intermediate spatial resolutions (Fig. 5A, B; Fig. 6A), but its indirect effects on malaria prevalence (*via* mangrove land cover) was not well-supported.

Discussion

We present the first multi-country African study on the role of mangrove forests in mosquito-borne diseases. Our goal was to answer whether the historical perception of mangrove forests as a source of disease is empirically supported. This notion has long been criticised as negative views of mangrove forests led to their large-scale destruction in the 20th century (Dahdouh-Guebas et al., 2020; Friess, 2016) and subsequent loss of valuable ecosystem services. Specifically, we tested how mangrove land cover (the percentage of land covered by mangrove forests) and mangrove NDVI (a vegetation index to characterise the greenness/health of the mangrove forests) influence malaria prevalence using satellite and health data. We also tested the role of spatial resolution by altering the radius at which the two mangrove variables were calculated. With this study, we assembled the most expansive dataset on malaria near mangrove forests to date.

Lesson 1: At coarse spatial resolutions, higher mangrove land cover means less malaria transmission

Our results show that mangrove land cover has a negative indirect (Fig. 5A) or direct (Fig 5A, B; Supplementary Fig. S5A) effect on malaria prevalence at coarse spatial resolution . This finding is consequential as it not only counters long-held beliefs of mangrove forests as sources of infectious disease (Friess, 2016), but also has practical implications for ecosystem managers. Malaria transmission is still listed as a potential ecosystem disservice of mangrove landscapes in the recent literature (Awuku-Sowah et al., 2022). But our results indicate that, at least in Africa, the presence of mangroves alone decreases malaria transmission.

Previous studies reported that increased mangrove cover led to higher abundance of mosquitoes locally, but these findings were based on much smaller spatial resolutions to calculate mangrove land cover (500 m, Claflin & Webb, 2017) or raster data (30-m resolution, Pope et al., 1994). As such, these observations may not be directly comparable to the negative mangrove land cover–malaria relationship at coarse spatial scale found in our study. However, they might align with the positive relationship we observed between mangrove NDVI and malaria prevalence (see below). While our models do not account for all non-mangrove landscape types, they certainly suggest that the presence of mangrove forests is better for malaria control than their absence. Therefore, we hypothesise that malaria may be less frequently transmitted in mangrove forests than other landscape types. For example, agricultural landscape cover increased malaria prevalence in our models (directly: Fig. 5A; indirectly: Supplementary Fig. 5A), a positive relationship that has been reported before (Shah et al., 2022). Further studies are needed to compare the impact of different coastal landscape types on malaria prevalence in detail, but here we show that mangrove forests are among those landscapes that may reduce malaria transmission.

The low levels of malaria in mangrove forests raise the question of what makes mangrove forests less suitable habitats for malaria vectors than other landscapes. One reason might be the limited number of mosquito species that lay eggs in brackish or saltwater (Ramasamy & Surendran, 2012). Some species have adapted to these conditions and are competent malaria vectors (Ramasamy & Surendran, 2012), but these species are generally few compared to those in freshwater, which might limit malaria transmission. Saltwater-tolerant mosquito species might also have a lower ability to carry malaria parasites (vectorial capacity) than their freshwater relatives. For instance, two coastal African malaria mosquitoes, *An. merus* and *An. melas*, appear to have a lower proportion of infective female mosquitoes than freshwater species (Bryan, 1983; Cuamba & Mendis, 2009), although similar rates have been observed in some cases (Temu et al., 1998).

Importantly, saltwater alone does not explain reduced malaria levels near mangrove forests in our models. In fact, coastline distance as a factor did not eliminate the mangrove land cover–malaria relationship, but rather showed an indirect effect whereby malaria prevalence decreased with increasing distance from the coast due to reduced mangrove land cover. Low malaria transmission in mangrove forests might, therefore, be more than just a phenomenon of closeness to the coast.

An alternative explanation is that coastal wetlands, like mangrove forests, provide refuge for a range of natural predators including fishes, crustaceans, and insects that might control mosquito populations (Arthiyan et al., 2024; Griffin & Knight, 2012; Louca et al., 2009; Roberts, 1995). Unfortunately, the role of vector predation in mosquito control remains poorly studied in mangrove ecosystems, particularly in Africa, because measuring these effects is difficult due to the heterogeneity of mangrove ecosystems and complexity of predator–prey relationships [see detailed discussion by Griffin & Knight (2012)]. In addition, shading of mangrove trees may slow down larval development by reducing water temperatures (Wamae et al., 2010). This effect has been suggested as an ecosystem service of forested landscapes, especially in the Amazon basin (Burkett-Cadena & Vittor, 2018), although a more recent analysis of malaria prevalence and deforestation across Africa found no correlation (Bauhoff & Busch, 2020). In the present study, we found no support for such an effect of mangrove vegetation as all direct causal relationships between temperature variables and malaria prevalence were negative.

Lesson 2: 'Healthier' mangrove forests increase malaria transmission

We found that healthier mangrove forests (i.e., 'greener', ones with higher NDVI) tended to increase malaria prevalence at fine and coarse spatial resolutions. At first glance, this observation appears to contradict our earlier finding (Lesson 1). If more mangrove land cover decreases malaria prevalence, why would healthier mangrove ecosystems increase it?

The answer lies in what the two variables measure. Mangrove land cover measures the availability of mangrove habitats. It is, therefore, a physical parameter that distinguishes mangrove forests from other landscape types. Mangrove NDVI is a vegetation index and, therefore, a biological parameter that measures the health of mangrove forests (T. V. Tran et al., 2022). Previous studies also reported positive correlations between NDVI and malaria across sub-Saharan Africa (summarised in Ebhuoma & Gebreslasie, 2016), often attributing this relationship to precipitation (Amadi et al., 2018; Fastring & Griffith, 2009). Our results suggest that weather variables alone were not enough to account for the mangrove NDVI–malaria relationship. The strongest associations were observed at fine spatial resolution (Fig. 5C; Supplementary Fig. 5C), indicating that this trend may reflect processes other than precipitation.

We hypothesise that the NDVI–malaria relationship is rooted in biotic interactions. Higher NDVI is associated with greater plant biomass (Ruan et al., 2022), structural complexity (LaRue et al., 2018), and species richness of macrobenthos, fishes, and plants (Arfan et al., 2024; Ram et al., 2025; Wang et al., 2016). Therefore, the relationship between mangrove NDVI and malaria at fine spatial resolution may indicate a role for biodiversity on malaria transmission, but not in the direction that is typically presumed; this relationship contradicts the dilution effect hypothesis, instead suggesting a potentially positive relationship between biodiversity in mangrove forests and disease risk. Our finding is consistent with studies in North America showing that canopy height in mangrove forests coincided with higher mosquito abundance (Pope et al., 1994), possibly linked to decreasing water flow and increasing water retention rates through dense mangrove vegetation after floods and rainfalls (Knight, 2011; Partani et al., 2024). Furthermore, the positive correlation between NDVI and mosquito numbers and diversity has been well documented in the literature (Ferraguti et al., 2024), although this relationship varies among mosquito species (Roiz et al., 2015). African mosquitoes in mangrove forests may, therefore, follow the broad pattern where a biodiverse ecosystem is also one that is richer in pathogens and their vectors (Hudson et al., 2006; Wood, 2025; Wood & Johnson, 2015).

Why, then, is the NDVI–malaria relationship significant only at fine and coarse but not intermediate spatial resolution? At fine resolution, this association can perhaps be explained by the spatial scale of biotic interactions (Dáttilo et al., 2023). Mosquitoes are known to rarely travel more than 5 km (Jansson et al., 2021; Thomas et al., 2013), making local habitat conditions particularly relevant. At coarse resolution, the effect of NDVI appears to be linked to several indirect effects. For instance, the positive relationship of mangrove NDVI with lagged *mangrove land cover (year-1)* suggests that older, more established, and, therefore, healthier mangrove forests (with higher NDVI) are linked to a higher malaria burden (Fig. 5A, B). Therefore, the direct effect of mangrove-associated mosquitoes on malaria prevalence is probably strongest at fine spatial resolution whereas the indirect effects of mangrove land cover, weather variables, and coastline distance become detectable at coarse spatial resolution (Fig. 6C). At intermediate spatial resolution, the NDVI signal may be diluted by the noise introduced by adding more distant datapoints, in which case local biotic effects become less distinct, while broader indirect effects are not yet strong enough to be detectable.

Does this result mean that mangrove forests pose a health hazard? Not necessarily. Rather our findings should be interpreted in the context of *Lesson 1*. Mangrove forests carry a lower risk of malaria compared to alternative coastal or inland landscape types. From this relatively low baseline, malaria transmission may be higher in healthier mangrove forests than in degraded ones. How large this difference is will depend on locality and mangrove forest type.

Our pan-African approach aimed at identifying broader trends across a wide geographical range, rather than site-specific risks of malaria. However, the study highlights the need for more surveys of malaria and its vectors in mangrove ecosystems. Further attention should be given to regions outside of Africa, where saltwater-tolerant mosquitoes are already important malaria vectors. For instance, the East Asian mosquito *An. aquasalis* Curry, 1932 transmits malaria in coastal regions of Central and South America (Póvoa et al., 2003). *Anopheles sundaicus* (Rodenwaldt, 1948) has been confirmed as a competent malaria vector in Asia (Sugiarto et al., 2016). These cases are especially relevant as parasites and vectorial capacities can shift over time because of human intervention. For instance, vector control measures have led to shifts in vector composition in East Africa (Musiime et al., 2019; Mwangangi et al., 2013) and the southwest Pacific (Russell et al., 2013). Therefore, regions outside of Africa may hold valuable information about which specific factors might influence malaria burden in mangrove forests. Such information could help understand the specific mechanisms in African mangrove forest, maintaining the low levels of malaria transmission today.

Concluding remarks: managing malaria in mangrove forests

What do our results imply for managing mangrove ecosystems in the context of malaria? Malaria control as a potential ecosystem service is certain to further improve the public image of mangrove forests. This insight also strengthens the case for mangrove reforestation of coastal areas. In recent years, mangrove restoration programmes have been expanded (Friess et al., 2022) and can be successful if neighbouring communities are allowed to participate and benefit (Del Cid-Alvarado et al., 2024; Lhosupasirirat et al., 2023). Our findings could further boost mangrove conservation by offering a counterargument to long-held beliefs that associate mangroves with infectious diseases. However, we would also caution against an overly optimistic interpretation of our findings. As our models show in areas immediately adjacent to mangrove forests, malaria transmission may increase with the amount of mangrove vegetation, although it would still remain lower than without any mangrove forests in the area.

We suggest that studies examining the links between mangrove forests and malaria at local level could provide a better understanding of effective management strategies for mangrove-associated malaria in the future. These strategies might include reducing human exposure to mangrove-associated mosquitoes (Ismail et al., 2018; Kipyab et al., 2013; Tuno et al., 2010), managing coastal ecosystems to reduce mosquito breeding (Breitfuss et al., 2003; Brockmeyer et al., 2022; Dale & Knight, 2012; Jones et al., 2004), or promoting natural predation on mosquitoes (Griffin & Knight, 2012). Given the importance of mangroves to coastal communities in Africa and worldwide, any malaria-related management strategies should carefully consider their impact on other ecosystem services. Lastly, as malaria control programmes become more successful in human settlements, mangrove forests and other less disturbed ecosystems may increasingly act as reservoirs of malaria transmission (Mwangangi et al., 2013). Understanding the mechanisms of malaria transmission in coastal Africa and developing appropriate management strategies for these regions remains vital, even when transmission levels are currently low compared to other landscapes.

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Author contributions

AJCL: conceptualisation, funding acquisition, methodology, data curation, formal analysis, validation, visualisation, writing – original draft, writing – review and editing. FDG: supervision, funding acquisition, writing – review and editing. DDM: validation, writing – review and editing. OK: data curation, validation, writing – review and editing. MPMV: funding acquisition, supervision, writing – review and editing. CLW: conceptualisation, funding acquisition, validation, supervision, writing – original draft, writing – review and editing.

Data availability statement

The R and Python scripts that support the findings of this study are available in GitHub at https://github.com/HU-AquaticBiodiversity/MangroveMalaria-SpatialAnalysis/. The data that support the findings of this study are available from the DHS programme (https://www.dhsprogram.com/) and via the MalariaAtlas database (https://github.com/malaria-atlas-project/malariaAtlas). Restrictions apply to the availability of these data, which were used under license for this study. Data are available from the MalariaAtlas database with the permission of DHS programme.

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List of Supplementary Files

Supplementary File S1. Machine learning analysis

Supplementary File S2. Overview of additional variables used to impute missing data

Supplementary File S3. Coordinate reference systems (CRS) applied for geometric measurements by country

Supplementary Figure S4. Correlation matrix of weather variables, with each column and row representing a variable pair. Plots below the diagonal are scatterplots of the column variables as a function of the row variables; above the diagonal the Pearson's pairwise correlation coefficient of the variable pairs is shown; the plots on the diagonal show the density of the column variables. The variables we selected showed no signs of strong multicollinearity.

Supplementary Figure S5: Selected structural equation models obtained through 'reduced' dataset, for which observations with missing values were excluded, with r indicating the radius at which mangrove variables were calculated. A: r = 40 km, B: r = 28 km, and C: r = 3 km. Values of r were selected to match those in Fig. 5. For further explanation concerning path diagrams and abbreviation, see Fig. 5.