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Mosquito vector diversity and malaria transmission

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Malaria is the most important parasitic disease in the world, killing over half a million people a year. Globally, we have made gains toward eliminating this disease but our progress has stalled in the last decade. Much of our control efforts and predictive models are focused to a few well understood systems such as *Plasmodium falciparum* transmission by species within the *Anopheles gambiae* complex. However, in many areas of the world, variation in the diversity of mosquito vectors significantly shape malaria transmission dynamics, seasonal persistence, and geographic range. This perspectives piece will focus on vectors of human malaria parasites and the impact of vector diversity on disease transmission by exploring how: 1) *Anopheles* species richness and abundance influence daily malaria transmission, and how differences in host feeding behavior and vector competence within a species-rich vector community influence local transmission, 2) diverse species contribute to persistence of malaria across seasons and spread through different ecotypes, and 3) species-specific parasite-vector interactions determine the genotypes of the malaria parasite that are successfully transmitted and shape parasite population structure. Finally, we will discuss future areas of research that should be prioritized toward understanding a more complete picture of malaria transmission dynamics in the context of diverse vector species.

KEYWORDS

malaria, vector diversity, *Plasmodium*, *Anopheles*, transmission

Introduction

Malaria is one of the most deadly infectious disease in the world, with a third of the human population at risk of infection. Human malaria parasites are transmitted by *Anopheles* mosquitoes. There are around 500 different species of anophelines, about 100 of which have been implicated in malaria transmission (Kiszewski et al., 2004; Sinka et al., 2012). Research on malaria vectors is focused almost exclusively on groups of species that we consider to be primary vectors, those that we believe are responsible for transmitting the majority of infections. These primary vector species often have high vector competence, indoor resting and feeding behaviors, and a propensity to feed on humans over other hosts. In the last decade, there has been an increasing recognition of the role of understudied vector species in sustaining malaria transmission, including species that bite and rest

outdoors and have more generalist feeding habits (Antonio-Nkondjio et al., 2006; Fornadel et al., 2011; Edwards et al., 2019a).

Malaria risk can change throughout the day, over seasons, and across different types of landscapes. Changes in risk of infection are largely driven by the abundance and biting behaviors of malaria vector species. Human exposure to malaria infectious mosquito bites is determined by a number of factors including densities of local vector mosquitoes, how often those mosquitoes feed on humans, and how well malaria parasites can develop in local vectors. In many endemic regions, malaria prevalence is strongly associated with seasonal conditions, like increased rainfall, that provide abundant breeding habitats for mosquito larvae and result in an increased abundance of adult *Anopheles* mosquitoes. Different communities of *Anopheles* species have specialized to exploit different types of habitats. Land use change has resulted in increasingly fragmented landscapes, bringing humans into closer contact with diverse outdoor-biting vector species in high abundance in forest and forest fringe habitats as well as those that have recently adapted to breeding in agricultural sites. In regions of rapid deforestation, particularly in South America and Southeast Asia, people involved in wood harvesting operations experience an increased risk of exposure to infectious bites (Cui et al., 2012; da Silva-Nunes et al., 2012). Exposed forest workers can also bring malaria parasites back into their communities where there are local vectors capable of transmission, initiating local outbreaks of infection (Sluydts et al., 2014; Edwards et al., 2019a). As humans move through different environments, the diversity of anophelines across these landscapes provide opportunities for malaria transmission and spread.

The life cycle of malaria parasites is complex, with multiple distinct life stages in the human and mosquito hosts. While malaria parasites build to huge population sizes in a human host, particularly during blood stages, very few mosquito-infective sexual stage gametocytes are ultimately picked up by a suitable mosquito. Malaria parasites must then persist through multiple life stages in the vector, including invasion, replicative development, and escape from multiple mosquito tissues. The most dramatic bottlenecks in parasite population size occur within the mosquito (Alavi et al., 2003), so slight differences in the success or failure of parasite development during these mosquito stages ultimately determine the parasite populations that are successfully transmitted. Different *Anopheles* species have been shown to be variably susceptible to infection by different populations of *Plasmodium falciparum* and *P. vivax*, the two species of human malaria that cause the greatest disease burden worldwide (Zollner et al., 2006; Molina-Cruz et al., 2012; Goupeyou-Youmsi et al., 2020). To combat malaria, we need to understand the interaction of human malaria parasites and the many different *Anopheles* species that transmit them.

Anopheles species richness and abundance can increase daily malaria transmission

Vector species diversity complicates our estimates of transmission as key descriptive features that enable us to predict

malaria transmission risk are not well described in understudied malaria vectors (Smith and Ellis McKenzie, 2004; Lobo et al., 2015). These include measures of vector competence, the innate susceptibility of a single species or population to malaria infection, as well as measures of host preference, population density, daily survival rate, and how long it takes for a mosquito to become infectious after taking an infected bloodmeal (extrinsic incubation period). Vectors that are not as competent can be extremely abundant and biting at high enough rates to sustain transmission (Sallum et al., 2019). Studies have shown that in some environments with multiple *Anopheles* species, any one of those species could sustain malaria transmission (Billingsley and Sinden, 1997; Kweyamba et al., 2025). The risk of malaria exposure from multiple vector species in a single place is additive, increasing the total risk of daily exposure of one person to potentially infectious bites.

Our lack of information about understudied species perpetuates itself, with scientists necessarily expending limited resources on known and well-studied vector species, ultimately dismissing vectors that we have very little data about. Locations across the tropics have diverse communities of anophelines, many of which are capable of transmitting malaria (Kiszewski et al., 2004; Antonio-Nkondjio et al., 2006; Cui et al., 2012; Sriwichai et al., 2016; Kyalo et al., 2017; Davidson et al., 2020; Lee et al., 2022; Kweyamba et al., 2025). Randomized screening of *Anopheles* mosquitoes collected in medium and high transmission areas has resulted in the detection of more than a dozen species in a single location having malaria parasites in their salivary glands, being potentially infectious (Lobo et al., 2015; St Laurent et al., 2016a; St Laurent et al., 2016b; Mustapha et al., 2021). Studies of diverse vector communities in the Kenya highlands and Zambia showed that species considered secondary or non-vector species had a sporozoite prevalence comparable or exceeding those in species considered primary vectors from the same collections (Lobo et al., 2015; St Laurent et al., 2016a). Due to our lack of data about natural infection rates in most *Anopheles* species, we cannot predict the role of diverse outdoor biting species in sustaining infection, representing a gap in our understanding of malaria transmission.

Differences in host feeding behavior and vector competence influence local transmission and enable diverse species to avoid vector control

Malaria control is often only targeted at a few malaria vector species that are regularly interacting with humans. Vector control measures that are centered around human households like long lasting insecticide-treated nets (LLINs) and indoor residual spray (IRS) only impact *Anopheles* species that bite humans in and around houses. Diverse species that bite humans outdoors can act as reservoirs for transmission while also avoiding common interventions centered around human habitation, such as LLINs and IRS (Cooke et al., 2015; Sherrard-Smith et al., 2019).

A diverse vector community is also more resilient to control. During trials of high coverage distribution of LLINs in Tanzania, malaria transmission shifted from one anthropophilic vector species *An. gambiae* transmitting near houses to several species of exophilic vectors, *An. funestus* and *An. arabiensis*, that then sustained malaria transmission outdoors (Russell et al., 2011). Shifts in vector populations in response to LLIN and ITN coverage from primary vectors biting indoors to other species biting outdoors have been observed in other high transmission areas across Africa (Reddy et al., 2011; Sherrard-Smith et al., 2019). The presence of outdoor biting species can further extend transmission risk outside of areas of human habitation (Figure 1C) (Edwards et al., 2019b), and outdoor behaviors make these species more difficult to monitor.

Many outdoor-biting species tend to be more generalist in their feeding behavior, exhibiting zoophilic or opportunistic feeding. Mosquitoes that are generalists only need to have bitten an infected human in their first few bloodmeals and survive long enough to bite a human again once they are infectious to transmit parasites. Occasional biting of humans may help these generalist mosquitoes avoid the killing or fitness reducing effects of insecticidal human-centered interventions, as well as increasing the risk of zoonotic disease transmission (Hawkes et al., 2019). Generalist feeding and zoophilic mosquitoes can have high vector competence. A study of East African vectors showed that species with substantially different human host preferences can have similar human-infective sporozoite loads from infections (Kweyamba et al., 2025). We currently have very little data about the vector competence of most *Anopheles* species.

Species-rich vector communities exhibit a range of biting behaviors. Differences in the timing of peak biting by different *Anopheles* species can extend transmission risk through different parts of the night, and even into daytime hours (Figure 1A). Species that bite during dawn and dusk hours when people are active present an increased risk for infection and a gap in protection from LLINs or IRS (Cooke et al., 2015; Mwema et al., 2022). In Southeast Asia, multiple forest species have been found to exhibit biting behavior during the day, unusual for *Anopheles* mosquitoes (Vantaux et al., 2021; Boyer et al., 2025). Daytime biting of forest mosquitoes endangers workers harvesting wood and others who work in forest-fringe areas. This diversity in the timing of biting by different species increases the risk of infectious bites per day.

Diverse species contribute to persistence of malaria across seasons and spread through different ecotypes

Malaria transmission risk can change throughout the year. The number of malaria cases is often strongly associated with seasons where *Anopheles* population densities are high. While populations of individual species can sustain malaria transmission, combinations of species enable an expanded transmission season, and stabilize malaria transmission across seasons, including an increased risk multiple infections for an individual per year (Bompard et al., 2020) (Figure 1B). Since anopheline species respond to environmental

changes differently, a high diversity of *Anopheles* mosquitoes can contribute to an extended malaria transmission season for multiple human malaria parasite species. In South Asia, milder dry seasons and large stretches of forested regions sustain many different *Anopheles* species year-round, with continual malaria transmission (Tainchum et al., 2014; Sriwichai et al., 2016; Bourke et al., 2018; Al-Amin et al., 2023; Boyer et al., 2025). In regions with a more extreme dry seasons, diversity of vector species can extend malaria transmission through dry periods compared to areas with fewer anopheline species where transmission might be interrupted (Cross et al., 2022). In Zambia, *An. arabiensis* and *An. funestus* were found to sustain malaria transmission through extreme drought when the primary vector population of *An. gambiae* had been decimated (Kent et al., 2007).

Combinations of species across landscapes expand the geographic range of malaria transmission (Kiszewski et al., 2004) (Figure 1D). Variations in abundance of difference species has been associated with changes in land use (Hii et al., 1997; da Silva-Nunes et al., 2012). Classic examples include vector species that occupy specific and sometimes overlapping niches along an altitudinal or land use gradient (Overgaard et al., 2003). For example, in a single village in Northeastern Cambodia, someone would have a risk of exposure to infectious bites from highly competent *An. dirus* in the forest, *An. barbirostris* and *An. maculatus* in forest-fringe areas, and species like *An. minimus* and *An. aconitus* that take advantage of permanently available larval habitats in rice cultivation near human habitation (Sinka et al., 2011). Outdoor and generalist feeding anophelines that exploit rice paddies and other agricultural plots come into regular contact with humans and other hosts and can emerge in high numbers and persist across extreme dry periods.

One pressing issue of land use change is deforestation, which can create patchy forest plots and developed landscapes that also bring humans in closer regular contact with competent forest vectors that are sometimes highly abundant (Hawkes et al., 2019; Oliveira et al., 2021). In Bangladesh, vector community composition was distinct between forested and non-forested ecotypes (Hawkes et al., 2019), including differences in *P. falciparum* and *P. knowlesi* infection rates. Another study in Thailand showed that mosquito abundance and diversity was highest at forest fringe sites (Tainchum et al., 2014), with high potential for contact between humans and vector mosquitoes. Land use change in the Amazon has been a major driver of malaria transmission risk, with increases in vector species diversity and abundance associated with recently deforested areas where new larval habitats are created (da Silva-Nunes et al., 2012). In these shifting landscapes, diverse vector species can maintain malaria transmission (Cross et al., 2022).

Species-specific vector-parasite interactions determine the genotypes of the malaria parasites that are successfully transmitted and shape parasite population structure

The most extreme population bottlenecks for the parasite occur within the mosquito (Alavi et al., 2003; Soontarawirat et al., 2017).

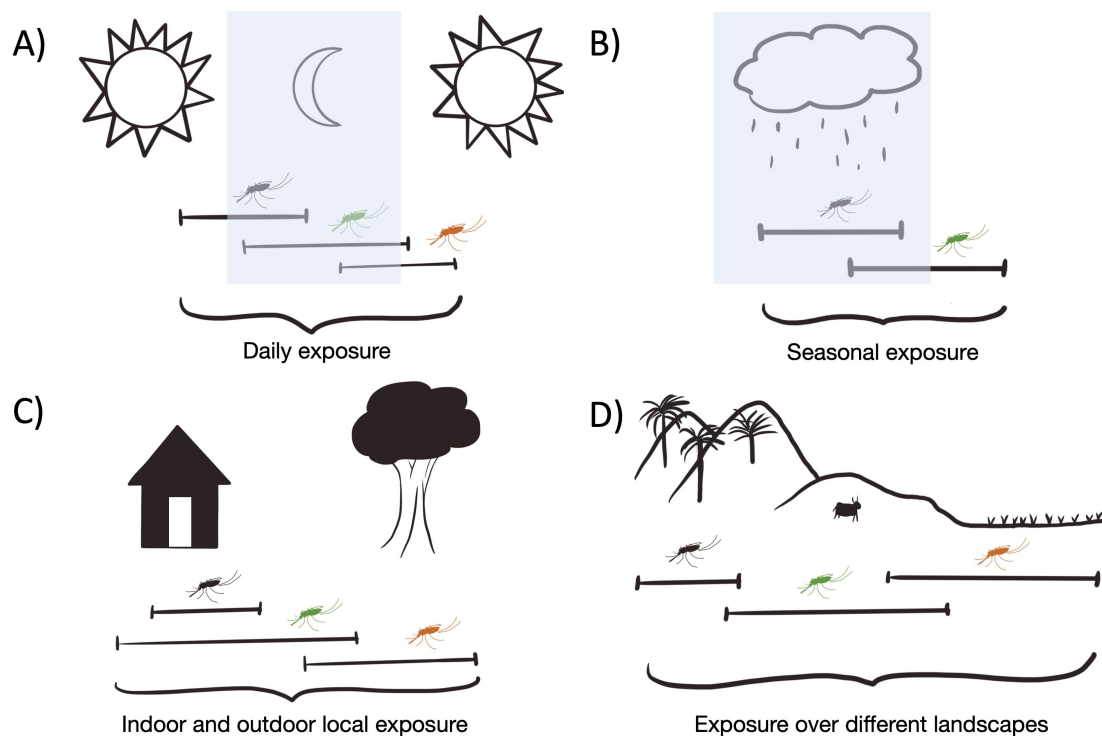


FIGURE 1

Diverse malaria vectors extend exposure to potentially infectious bites over (A) hours of the day, (B) seasons, (C) indoor and outdoor local areas, and (D) different landscape types.

Parasite development in mosquito tissues is largely determined by tissue-specific immune responses, some of which target *Plasmodium* parasites. Slight differences in parasite development at these different mosquito stages can determine whether a parasite gets successfully transmitted by that mosquito or not, and which parasites are transmitted (Figure 2). Sexual reproduction of parasites also occurs within the mosquito, which can increase the genetic diversity of the parasite population. This vector-specific filter of individual parasites shapes the population structure of parasites that are then circulating in humans (Annan et al., 2007; Das et al., 2017; Goupeyou-Youmsi et al., 2020). The selective effect of vectors on parasite populations may be more pronounced under low transmission conditions.

Though species can have varying vector competence, *Anopheles* are often competent for multiple human malaria parasite species. Similarly, all five human *Plasmodium* species are able to infect a wide range of *Anopheles* species (Kiszewski et al., 2004; Sinka et al., 2012; Neafsey et al., 2015). Infections using patient isolates showed successful infections in multiple highly diverged species (St. Laurent et al., 2015; Sriwichai et al., 2016). Field and lab experiments have shown that different species of mosquitoes can select for human malaria parasite species and strains (Somboon et al., 1994; Joy et al., 2008; White et al., 2011; Goupeyou-Youmsi et al., 2020). In other malaria species, parasite lineages are differentially transmitted by different mosquito species, sometimes selected for through different

immune mechanisms (Zollner et al., 2006; Jaramillo-Gutierrez et al., 2009; Das et al., 2017; Gutiérrez-López et al., 2020). With multiple species selecting for different parasites, multiple vectors involved in transmission can contribute to and sustain the genetic diversity of *Plasmodium* populations.

Conclusions

Flexibility in vector behaviors make species rich vector communities able to adapt to our most effective vector control tools and increases potential exposure to infectious bites over the course of a day, over the course of a year, and in different types of habitats. Diverse vector species represent a black box for malaria control, with very little scientific baseline information about dozens of species that contribute to malaria transmission and very few tools available to address malaria transmission by outdoor and generalist feeding species. A diverse vector community is also more resilient to insecticide-based control tools, with a reservoir of genetic diversity, different molecular mechanisms of coping with chemical and oxidative stressors, and adaptive behaviors that avoid insecticidal interventions. These species represent a dangerous unknown in our estimations of persistence of malaria in different types of habitats and the spread of parasites and vectors to new locations.

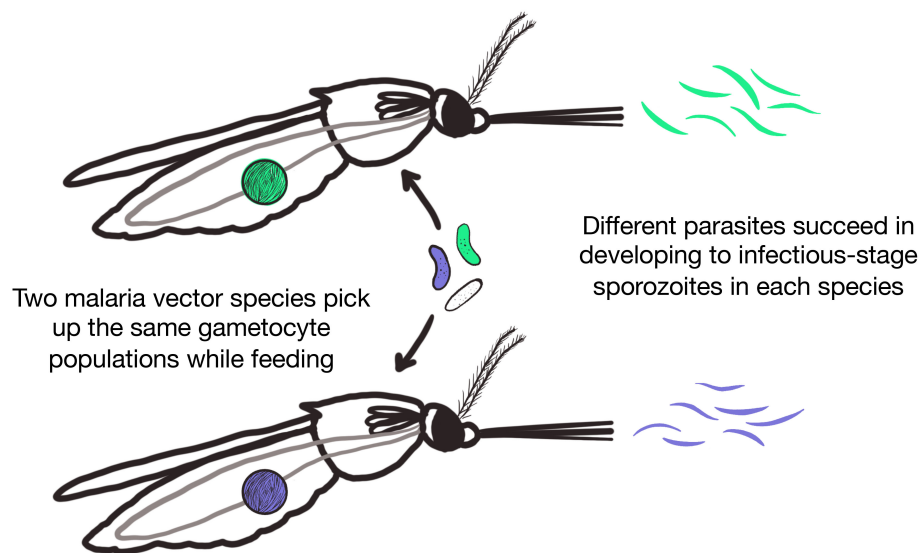


FIGURE 2

Diverse vector species can differentially select for the parasite species and genotypes that get transmitted.

Vector diversity presents a challenge for both established vector control and new control tools that are being developed. Species that are genetically divergent from major malaria vector species will not be effectively controlled by new developments in gene drive and other genetic control tools that typically target conserved gene sequences within a well-studied primary vector species. Diverse species should be represented in our genetic and genomic studies of the natural genetic variation of malaria vectors. Sequence data from diverse *Anopheles* species will allow for more accurate species identification and improved molecular monitoring. More comprehensive field studies are needed to address gaps in our understanding of malaria transmission, including crucial information about natural infection rates of different species and their distributions. The presence of multiple species and shifts in vector populations can make monitoring and evaluating the impact of control tools more complicated (Máquina et al., 2024). Utilizing multiple collection techniques that capture outdoor species and species with different feeding behaviors will capture a broader range of anophelines. A regular assessment of species composition, with random screening of all collected species for infection, should be a part of malaria control program activities where vector control tools are being evaluated.

Our understanding of malaria transmission is also limited by the strains of anophelines and *Plasmodium* that have been studied. Most malaria transmission experiments in the lab involve *Anopheles* colonies of primary vector species that have been kept in the lab for decades, undergoing constant population bottlenecks that limit their genetic diversity and any similarity to wild populations. We need to expand our studies of vector-parasite interactions to include actively circulating malaria parasites and

vectors that represent current real-world populations, including understudied vector species. Vector competence is one important transmission metric that can be evaluated in the lab. Malaria transmission models currently use limited infection data from *An. gambiae* s.l. or *An. stephensi* to predict infection parameters for all other anophelines. Infection studies including diverse *Anopheles* species would help to disentangling the role that different vector species play in malaria transmission, providing better comparative metrics for estimating infection risk across species and across environments with different species compositions.

Diverse vector species make malaria eradication much more difficult to achieve (Fornace et al., 2021). Multiple species that are not well understood sustain malaria transmission through harsh environmental conditions and over seasons, in habitats that are not associated with humans, and through times of the day when people are not protected by bednets or other vector control interventions. These species contribute to what is known as residual malaria transmission, the transmission that remains after highly effective vector control tools have been rolled out to high coverage. It is essential that we work to better understand malaria transmission by diverse outdoor species, as these will harbor and sustain the last reservoirs of infection when we reach the endgame of global malaria eradication.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

Author contributions

BS: Writing – review & editing, Writing – original draft, Visualization.

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Conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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