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Chapter 4

Global Distribution of the Dominant Vector Species of Malaria

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Additional information is available at the end of the chapter

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1. Introduction

Human malarial protozoa are transmitted by mosquitoes of the genus *Anopheles*. There are 465 formally recognised species and more than 50 unnamed members of species complexes [1]. Approximately 70 of these species have the capacity to transmit human malaria parasites [2] and 41 are considered here to be dominant vector species/species complexes (DVS), capable of transmitting malaria at a level of major concern to public health [3, 4] (Tables 1-3).

The aim of this chapter is to document the distribution of these DVS using global and regional maps. In addition, behavioural summaries are provided for the most important species, i.e. those on each continent that are considered the most dangerous and responsible for most malaria transmission, and hence have the greatest impact on human health. Only the primary vectors in those regions with current and problematic malaria transmission are discussed further here (i.e. the vectors of Europe and the Middle-East are not included – but more details can be found in Sinka *et al*. [5]) The regions covered include the Americas, Africa and the Asian-Pacific.

The maps presented (e.g. Figure 1) provide species location information and highlight the existence of a greater number of vector species than is often considered, many in sympatry, across the malarial zones. Amongst these DVS, there are often important behavioural characteristics that must be considered if successful vector control is to be applied. For example, some species do not always enter houses to bite, are most active in the early evening, and prefer to rest outdoors after feeding, such as many of the species common in South America (e.g. *An. albopictus*, *An. marajoara, An. nuneztovari*), *An. dirus* in South-East Asia and *An. farauti* in the Australian-Pacific region. Others are highly opportunistic in their feeding habits (including *An. darlingi*, the most 'dominant' south American species amongst the South American DVS); biting readily indoors or out. As such, a large investment in insecticide treated bednets (ITNs) or insecticide residual spraying (IRS) will not reduce malaria transmission where such species

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occur. Thus, to appreciate where different malaria control methods are best applied, one must know what *Anopheles* species exists in an area *and* understand their behaviour. A map clearly and simply addresses the first of these needs, and if accompanied by a behavioural summary, than informed decisions about how to combat malaria transmission can be made.

Maps clearly illustrate the spatial extent of a species' distribution. Often, even within a single *Anopheles* species range, behaviour can vary depending on location. The best known example is the *An. gambiae* complex. The *An. gambiae* complex was initially considered as a single species. Clear differences in behaviour reported across its distribution caused it to be examined more closely and now this complex is considered to include eight species [1, 6] including the DVS: *An. arabiensis, An. gambiae, An melas* and *An. merus. Anopheles arabiensis,* is considered mostly zoophilic, when compared to the highly anthropophilic *An. gambiae,* but still plays a very important role in malaria transmission – indeed, its presence and propensity to rest outdoors is attributed (amongst other factors) to the 'failure' of the mass indoor residual spraying program intended to control malaria in Nigeria during the Garki project [7]. Variability in behaviour within the *An. gambiae* species (rather than the complex) is also commonly reported [5]. Such spatially dependant variability amongst the DVS will be discussed further within this chapter.

The maps presented in this chapter are not a comprehensive analysis of all anophelines. They show only those species designated as DVS; a categorisation initially based on information taken from a number of authoritative reviews [8-12] ([10] translated and updated:[13]) and with additional guidance from a technical advisory group of vector experts [3, 5, 14, 15]. This chapter will also briefly touch upon the methodology behind creating the distribution maps for these DVS including what information is needed to ensure increasingly accurate maps can be produced in future.

2. Global

The global DVS map (Figure 1) gives a clear overview of the variability in vector complexity across the world. Africa appears to show a relatively simple picture of a small number of highly dominant species covering large areas of the continent and although the 'secondary DVS' are not shown (see Figure 4), even with their influence, the comparative complexity between African and Asia is very different. The Asian-Pacific region has 19 DVS [14] (16 of which are shown on the multi-species maps presented here (Figures 1 & 5) – see below) whereas Africa has only seven DVS [5], with the three 'primary' DVS shown on the global map (Figure 1 - see below). Of the 19 species in the Asian-Pacific, nine are now considered species complexes, whereas of the seven African DVS, only *An. nili* is a confirmed species complex (the *An. gambiae* complex is not included here, as specific individual members of the complex are categorised within these seven African DVS) [1, 6, 16]. It is unclear what is the cause of the high diversity of vectors found in the Asian-Pacific region, but it may be simply a factor of the large number of islands, and hence a consequence of limitations in dispersal and specialisation within a restricted environment. Whatever the reason, the Asian-Pacific region maintains a high number of vectors and species complexes and even within individual species, behaviours can vary hugely depending on location (e.g. *An. annularis* – see below).

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North America (excluding Mexico) shows a simple vector profile (Figure 2). There are only two species considered here as DVS: *An. freeborni* found in northwestern USA and the *An. quadrimaculatus* complex, found in the southern regions of the country. In Latin America, however, the situation is a little more complex. Despite a number of sympatric species on the continent, *An. darlingi* is considered the most important vector in the neotropical region [13] and hence is shown dominating all localities where it occurs. In Central America this species does not have such a great influence and both *An. albimanus* and *An. pseudopunctipennis* are considered of greater importance.

The individual regions (Americas, Africa, and Asia-Pacific) are discussed in more detail in the following sections.

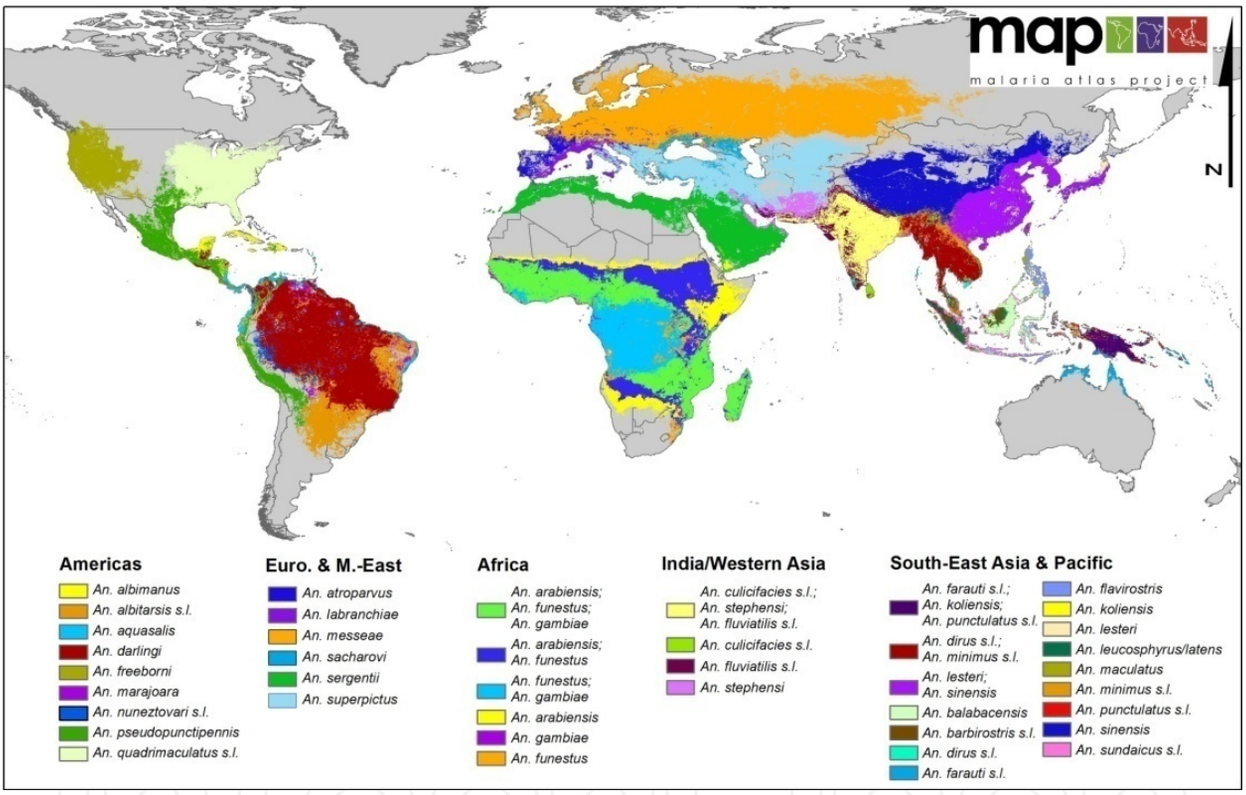


Figure 1. The global distribution of 34 DVS. (Map reproduced from Sinka *et al.* [4]); s.l.: *sensu lato*, meaning 'in the broad sense' referring to species complex

3. The Americas

On a global scale, the nations of the Americas benefit from having the lowest *P. falciparum* morbidity, with stable risk areas typically having low levels of endemicity ($Pf\text{PR}_{2\text{-}10} \leq 5\%$) [17]. Such reduced levels of malaria transmission coupled with continuing reports of decreasing mortality and morbidity for all major *Plasmodium* species across the region (e.g. between 2000 and 2007) [18] have been credited to an increasing use of integrated vector control [19].

Integrated vector control/management relies on a number of factors, but foremost (as given in the World Health Organisation (WHO), strategic framework for integrated vector management [20]) is the 'selection of proven vector control methods based on knowledge of local vector biology and ecology, disease transmission and morbidity'; essentially, knowing which vector species is present and understanding how it behaves.

There are nine DVS in the Americas (Figure 2, Table 1) [15], with two species having their distributions contained entirely within North America (*An. freeborni* and *An. quadrimaculatus*), and the remaining six species encompassing areas from southern North America, through Central America and into South America, incorporating the northern reaches of Argentina. As stated above, in South America, *An. darlingi* is considered to be the most important of the DVS where it is found [13]. However there is increasing evidence of the importance of other species, including members of the *An. albitarsis* complex (e.g. *An. marajoara*), that may have a higher influence in malaria transmission than previously thought [21]. As such, and due to the dominance across the continent indicated by the *An. darlingi* distribution in Figure 2, single species maps are also shown for *An. albitarsis, An. marajoara, An. nuneztovari* and *An. pseudopunctipennis* (Figure 3).

Many of the American species show great variability in their adult behaviour, with most showing little preference for biting either humans or animals [15] (Table 1), tending to feed on whichever host they first encounter. This variability is also reflected in their propensity to bite both indoors and out. Overall, the majority of DVS in the Americas will rest outside after biting (Table 1, [15]).

Despite similar adult behaviour amongst many of the South American DVS, there are a number of behavioural characteristics found in the larval stages that do differentiate the species (Table 1). For example *An. aquasalis*, whose name means salt (salis) water (aqua), is a vector found in coastal environments. Its larvae prefer clear, non-polluted water bodies such as mangrove swamps, lagoons and ditches [22, 23]. They can develop in fresh water sites, but it is considered a poor competitor in such habitats, especially against *An. albimanus* [15], which may be causal in tending to restrict the range of *An. aquasalis* to brackish locations.

Anopheles darlingi larvae are characteristically associated with patches of floating debris found along river margins in rural and lowland forested areas [24]. *Anopheles marajoara* is also found in lowland areas but is more common in secondary forests and is able to adapt to environments that have undergone some human intervention [21, 25] which may be a causal factor in its increasing dominance over *An. darlingi* in some localities. Forest clearance and pollution will decrease sites suitable for *An. darlingi* but increase the availability of sunlit marshy areas and ponds more suitable for *An. marajoara* [21, 26].

The *An. pseudopunctipennis* complex is known to be able to survive and transmit malaria at altitudes higher than many other DVS, up to 3000 m [27, 28]. Its larvae also have a defining characteristic; an apparent obligate association with filamentous *Spirogyra*-type green algae [23, 27, 29-31] (Table 1). Indeed, the removal of such algae has been shown to be a viable method of control for this species [31].

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Species	Larval site characteristics	Host		Biting		Resting		Other
		Anthropo-philic	Zoophilic	Endophagic	Exophagic	Endophilic	Exophilic	
An. albimanus	Sunlit, brackish or fresh, clear, still or flowing water, containing higher plants or algae	●	●		●		●	Bites at dusk/night
An. albitarsis complex	Sunlit, fresh, clear or turbid, still water with some higher plants or algae	●	●	●	●	○	●	Bites at dusk/night
An. aquasalis	Sunlit, brackish or fresh, clear or turbid, still or flowing water with some higher plants or algae	●	●	●	●	-	●	An ability to utilise brackish coastal larval habitats raises this species from a relatively poor vector to a DVS. Has been found biting in the day but mostly bites at dusk/night
An. darlingi	Shaded (occasionally sunlit), fresh (occasionally brackish), clear or turbid, still or flowing water with higher plants or algae	●	○	●	●	-	●	Bites at dusk, night and dawn
An. freeborni	Sunlit, fresh, clear, still water with higher plants or algae	●	●	●	●	-	●	Bites at dusk, night and dawn
An. marajoara	Sunlit (occasionally shaded), fresh, clear or turbid, still or flowing water with higher plants or algae	●	●	●	●	-	●	Bites at dusk/night
An. nuneztovari complex	Sunlit or shaded, fresh, clear or turbid, still or flowing water with higher plants or algae		●		●	-	●	Bites at dusk, night and dawn
An. pseudopunctipennis	Sunlit, brackish or fresh, clear or turbid, still or flowing water with higher plants or algae	●	●	●	●	●	●	Larval habitats are strongly associated with filamentous algae, and species can exist at high altitudes (up to 3000 m). Bites at night
An. quadrimaculatus complex	Sunlit, fresh, clear or turbid, still water with higher plants or algae. Occasionally no vegetation		●	-	●	-	●	Bites at dusk, night and dawn and occasionally in the day

Table 1. Summary of bionomics of the DVS of the Americas (created by cross referencing TAG and literature searches). Filled dot (●) indicates typical behaviour, open dot (○) indicates non-typical behaviour but examples exist, and dashes (-) indicate no data.

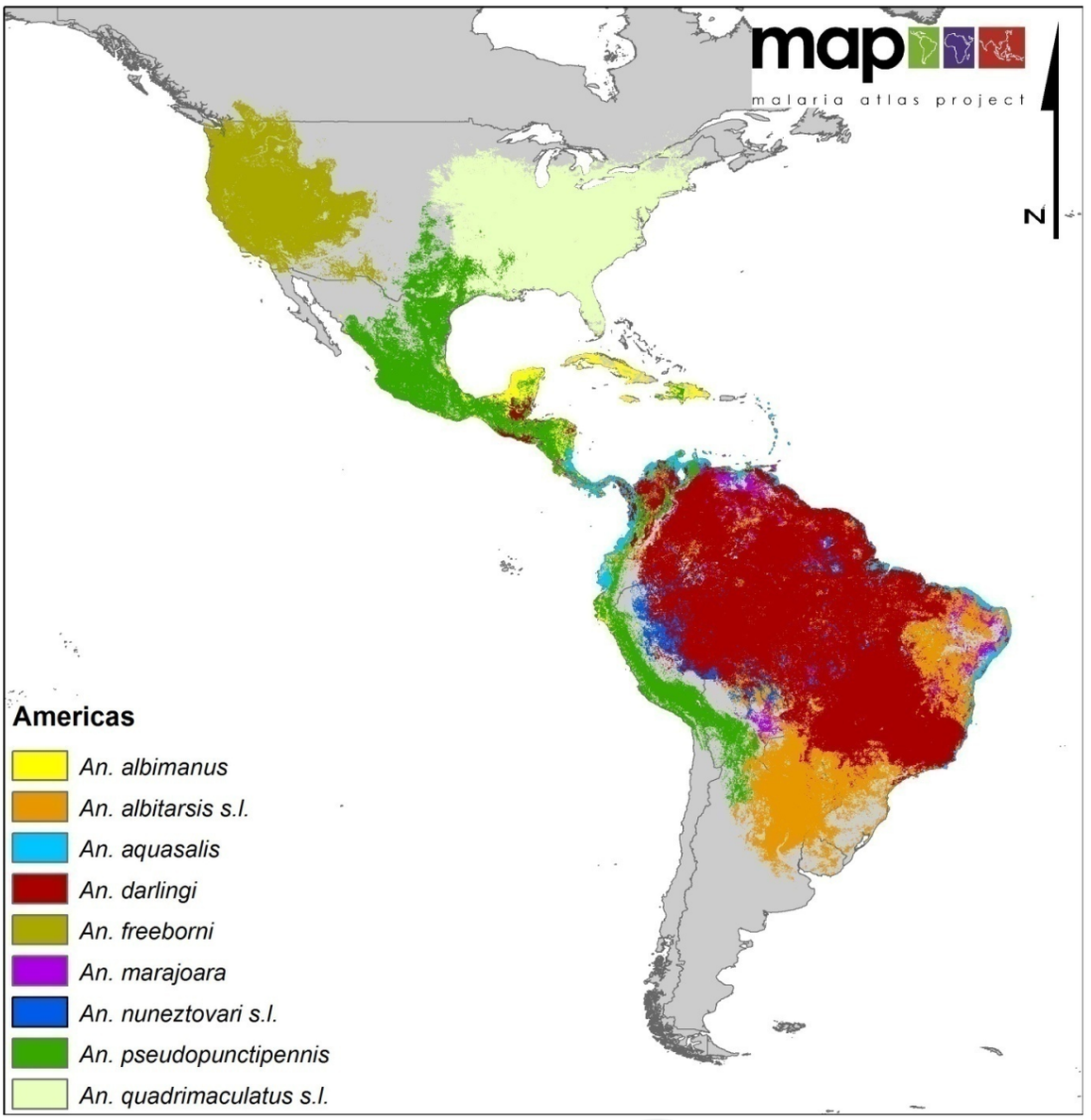


Figure 2. Multi-species map of the nine DVS of the Americas (map reproduced from Sinka *et al*. [4])

4. Africa

Across the huge and variable landscape of the African continent, there is a corresponding variability in the intensity of malaria transmission [32, 33]. Sub-saharan Africa is, however, home to localities suffering from the highest global malaria transmission levels, and hence, morbidity and mortality of malaria [17, 32, 34-36]; a consequence of the wide spread presence of the most effective and efficient vector currently known, *An. gambiae* [37, 38]. *Anopheles gambiae* is a member of the *An. gambiae* complex, which also contains other DVS including *An. arabiensis*, *An. merus* and *An. melas* [6, 39-42]. Also found in Africa is the widespread *An.*

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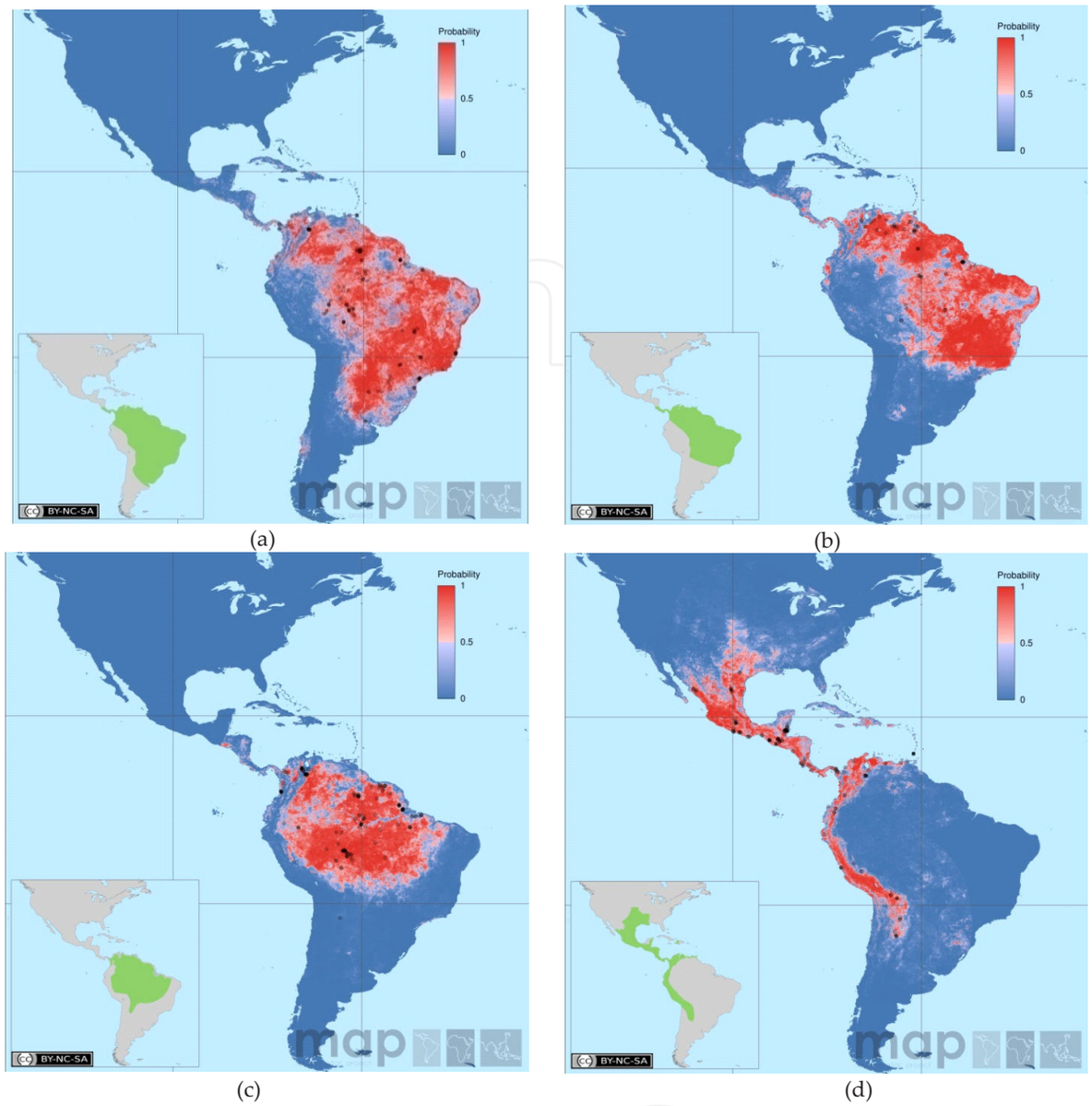


Figure 3. Predicted distribution maps for a) *An. albitarsis* s.l. (n = 138); b) *An. marajoara* (n = 56); c) *An. nuneztovari* (n = 171); d) *An. pseudopunctipennis* (n = 156). The insert map in each shows the expert opinion distribution for that species (Maps reproduced from Sinka et al, [15]).

funestus subgroup of which *An. funestus* is another highly effective vector, and possibly the first species to adapt to make use of humans as a food/blood source [43]. The more restricted, but still highly anthropophilic *An. moucheti* and the more widespread *An. nili* complex add to a suite of vectors within Africa that have proved highly efficient in malaria transmission and equally difficult to control [5].

Figure 1 shows those vector species that can be considered the 'primary' DVS of Africa: *An. gambiae, An. arabiensis* and *An. funestus*. Figure 4 indicates the more 'secondary' DVS, including *An. moucheti, An. nili, An. melas* and *An. merus*. Examining only the 'primary' species (Figure 1), the vector situation in Africa appears relatively simple. However for each of these species

to have an extensive spread across such a large geographical area suggests a high level of adaptability and plasticity in behaviours and tolerances within all of these DVS. This plasticity is becoming more apparent as the taxonomy of the species complexes are untangled. The *An. gambiae* complex is a case in point. Originally considered as one species, the discovery of saline tolerant larval '*An. gambiae*' coastal specimens which, in cross mating experiments, produced sterile male progeny, confirmed that the salt-water tolerant and fresh-water '*An. gambiae*' were reproductively incompatible, and identified *An. melas* on the west coast and *An. merus* on the east [44-47]. The Gambiae complex is now known to consist of at least eight species [1, 6] yet this taxonomic categorisation is still a relatively recent occurrence, with the provisional inclusion of *An. quadriannulatus* B only reported in 1998 [6, 48]. Moreover, behavioural and ecological plasticity within the *An. gambiae* species itself have highlighted further potential speciation; there are now five recognised chromosomal forms (Savanna, Mopti, Forest, Bamako and Bissau) and two molecular forms (M and S) [49-51]. The M and S forms have distinctive and separate behaviours, specifically in terms of preferred larval habitats, with the S form utilising larval sites considered typical for *An. gambiae* (i.e. temporary pools or puddles that only occur after rain) whereas larvae from the M form are found in more permanent sites such as rice fields or flooded areas [52-57]. Overall, *An. gambiae* is considered highly anthropophilic (Table 2), a characteristic that is held as greatly influential in the designation of this species as the most effective malaria vector. It also tends to be reported as biting indoors and during the night when people are asleep and therefore more vulnerable [5]. Although these traits do tend to hold true in a general sense, the variability of *An. gambiae* does extend to adult behaviour and there are a number of localities where this species does not follow these commonly reported behaviours [5].

The extensive distribution of *An. arabiensis* (Figure 1) also indicates a vector with a wide range of behaviours [40, 58, 59] and although it is classified as zoophilic and exophagic (Table 2) this is often only reported in comparison with the generally highly anthropophilic and endophagic *An. gambiae* or *An. funestus* [5, 60]. *Anopheles arabiensis* is more tolerant of drier environments than the other DVS, as can be seen in Figure 1 where its range extends north (the Sahel) and south (desert and steppe of Namibia and Botswana) beyond those of either *An. gambiae* or *An. funestus.* It is noticeably absent from the humid, forested areas of western Africa (Figure 1).

Despite the zoophilic label, the feeding behaviour of *An. arabiensis* varies greatly depending upon location, host availability and the local genotype [40, 58, 59, 61] and there is some suggestion that *An. arabiensis* populations are more anthropophilic, endophilic and endophagic in western Africa whereas those in the east are more zoophilic and exophilic [62].

Beside the apparent inability to exist in the forested west of Africa, *An. arabiensis* appears to tolerate a much greater range of larval sites than *An. gambiae*. Similar to its sibling, it makes use of sunlit, temporary, shallow fresh-water habitats and the larger more permanent sites as characterised by *An. gambiae* M form, but it is also able to survive in flowing water, turbid or polluted sites and even, on occasion, brackish habitats [5, 63-66]. It readily makes use of rice fields, although its propensity for sunlit water means it is primarily found when the rice plants are small and larval numbers reduce substantially as the plants mature [67-70]. The adapta-

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Species	Larval site characteristics	Host		Biting		Resting		Other
		Anthropo-philic	Zoophilic	Endophagic	Exophagic	Endophilic	Exophilic	
An. arabiensis	Sunlit (occasionally shaded), fresh (occasionally brackish), clear or turbid, still or flowing water with higher plants or algae (occasionally without vegetation)	●	●	○	●	○	●	Bites at dusk/night and occasionally at dawn. Species shows high behavioural plasticity and readily adapts in response to control
An. funestus	Sunlit or shaded, fresh (occasionally brackish), clear, still or flowing water with higher plants or algae (occasionally without vegetation)	●	○	●	●	●	○	Bites at dusk, but mainly during the night and to a lesser extent at dawn
An. gambiae	Sunlit (occasionally shaded), fresh (occasionally brackish), clear or turbid, still or flowing water with or without higher plants or algae	●	○	●	●	●	●	Larval site characteristics are influenced by molecular and/or chromosomal form
An. melas	Sunlit or shaded, fresh or brackish, clear or turbid, still water with higher plants or algae	●	●	●	●	○	●	Unlike other DVS, *An melas* densities tend to link to tides rather than rainfall
An. merus	Sunlit or shaded, fresh or brackish, clear or turbid, still water with higher plants or algae	●	●	○	●	○	●	Despite also being a coastal vector, *An. merus* is not influenced by tides like *An. melas*, nor can it tolerate the same levels of salinity.
An. moucheti	Sunlit (occasionally shaded), fresh, clear (occasionally turbid), still or flowing water with higher plants or algae	●	○	●	○	●	○	Range entirely restricted to equatorial forests. This vector is highly anthropophilic and endophilic.
An. nili complex	Sunlit or shaded, fresh, clear, still or flowing water with higher plants or algae	●	○	●	●	●	●	Behaviour depends on sibling, with *An. nili* being highly anthropophilic and the most important vector of the complex

Table 2. Summary of bionomics of the DVS of Africa (created by cross referencing TAG and literature searches) Filled dot (●) indicates typical behaviour, open dot (○) indicates non-typical behaviour but examples exist, and dashes (-) indicate no data.

bility, plasticity and general tendencies for *An. arabiensis* to feed outdoors on animals (Table 2) means that this species does not readily succumb to traditional methods of control such as IRS or ITNs [59, 71, 72].

Anopheles funestus, is a highly adaptable species with a large distribution across sub-saharan Africa (Figure 1). It is also a highly effective vector, and in some cases, due to a relatively high longevity plus a preference for human blood and late night biting (Table 2), is even more efficient at transmitting malaria than *An. gambiae* [38, 40, 73]. *Anopheles funestus* is the only member within the Funestus Subgroup regarded as an important vector [73], and can only be morphologically distinguished from other members at certain stages in their development, again highlighting the importance of correct species identification [38, 40, 73, 74]. Indeed, for this subgroup, such identification is rarely reported, and hence the distributions illustrated here (Figure 1) cannot distinguish the true range of this specific vector. For example in Ethiopia, only one known study has performed PCR identifications of the Funestus Group [75], indicating that only *An. parensis* (a non-vector member of the Funestus Subgroup) is present.

Anopheles funestus is a highly anthropophilic mosquito [5, 38, 76, 77] and its endophilic behaviour adds to a suite of behaviours that enhance its ability to effectively transmit malaria [5]. It is comparably consistent in its behaviour and has been subject to successful control via both IRS and ITNs, but some populations have shown a rapid development of insecticide resistance to pyrethroids which was considered the primary cause of epidemic malaria reported in South Africa in the late 1990s [73, 78].

The larvae of *An. funestus* are found in large permanent or semi-permanent bodies of freshwater such as swamps, large ponds or lake edges [5]. They are also associated with rice cultivation in some localities, favouring older fields with mature rice plants [79-81].

5. Asia

The region of Central, South and East Asia is home to 46% of the global populations at risk (PAR) of stable falciparum malaria [82] and suffers a particularly high impact of vivax malaria, with an estimated 82% of the world's PAR of *P. vivax* transmission [83]. Indeed within the 'top 10' of countries with the highest global *P. vivax* PAR estimates, seven are from Asia (China, Indonesia, Pakistan, Vietnam, the Philippines, Myanmar and Thailand) [84]. The complexity of the vector situation in the Asian-Pacific region increases the problems associated with understanding the vector/transmission environment. This region has a greater number of DVS than any other and amongst these, there are a greater number of species complexes and taxonomic complexities than anywhere else [1, 6, 16].

With at least nine out of 19 DVS found in the Asian-Pacific now considered as a species complex [1, 6], the impetus to correctly identify both the vectors and their behaviours at a specific location is even greater in this region than elsewhere. Indeed, even within those species not currently considered as part of a complex, behavioural variability is common, depending upon location, and in some cases to such an extent that a species considered a vector in one location

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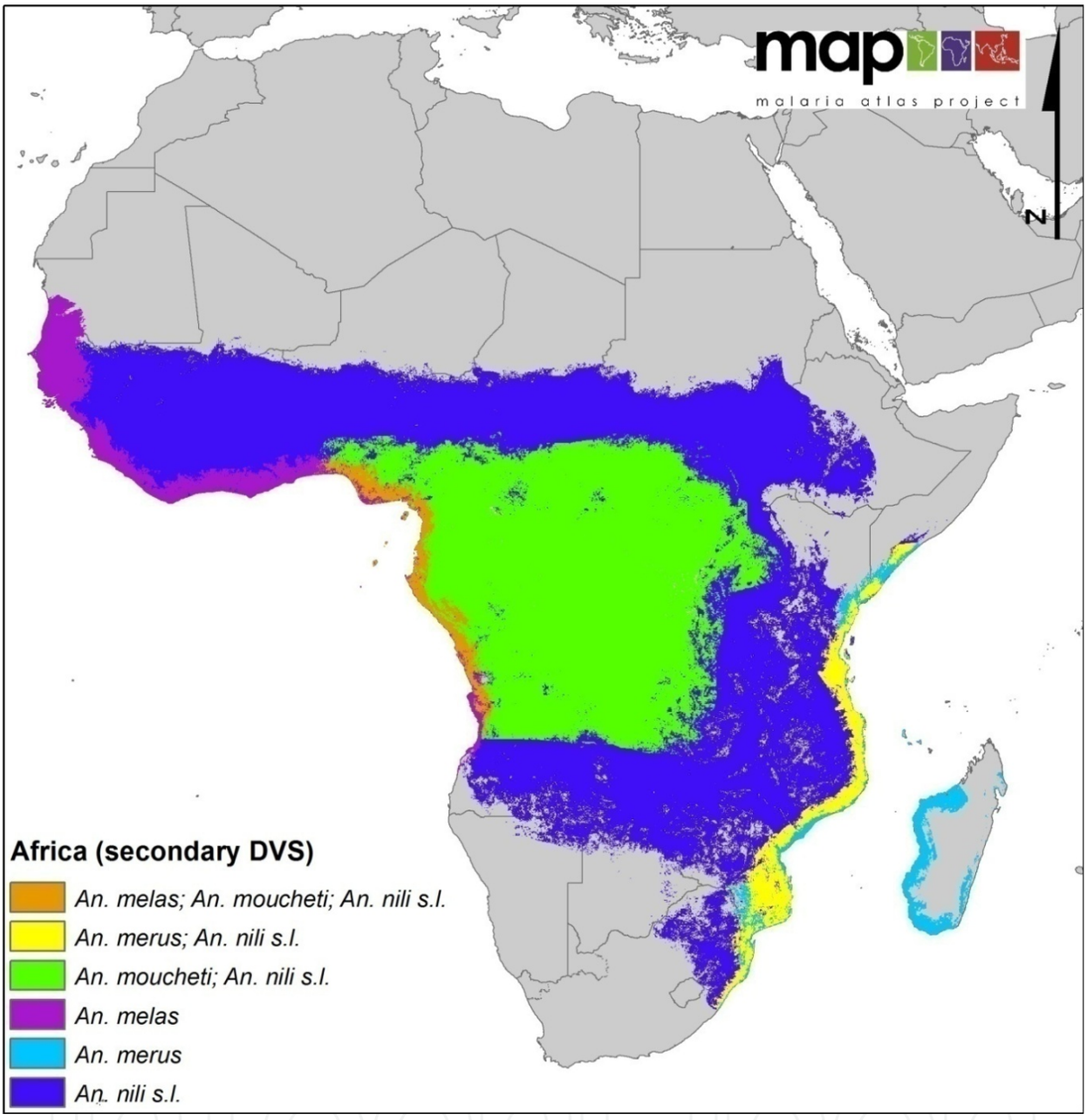


Figure 4. Multi-species map of Africa indicating the distributions of the four 'secondary' but still important, DVS. (map reproduced from Sinka et al. [4]).

may be only of secondary importance, or even a non vector in another [14]. For example, *An. annularis* has a range extending across India, down through South-East Asia, across many of the Indonesian islands down to and including Timor Island [14]. However, it only has a focal role in malaria transmission in selected areas of India. Elsewhere it is considered of little importance [85-91] (hence, *An. annularis,* along with *An. aconitus* and *An. subpictus*; all listed in Table 3 as DVS, are not included in the multi-species maps shown here in Figure 1 and Figure 5, as overall, they do not have as great an impact in malaria transmission as other species in the region).

Species	Larval site characteristics	Host		Biting		Resting		Other
		Anthropo-philic	Zoophilic	Endophagic	Exophagic	Endophilic	Exophilic	
An. aconitus	Sunlit, fresh, clear (occasionally turbid), still or flowing water with higher plants and algae (occasionally without vegetation)	○	●	●	●	○	●	Particularly favours both coast plain and upland rice fields as larval sites
An. annularis	Sunlit, fresh, clear (occasionally turbid), still or flowing water with higher plants and algae (occasionally without vegetation)	○	●	●	●	●	○	Vector role depends on location. Possible complex of two (species A and B) siblings, but these do not appear to be linked to variable vector capacity
An. balabacensis	Shaded (occasionally sunlit), fresh, still water with or without higher plants or algae	●	-	●	●	●	○	Primarily found in forested environments
An. barbirostris complex	Sunlit or shaded, clear or turbid, still or flowing water with higher plants or algae (occasionally without vegetation)	○	●	○	●	○	●	The siblings within the complex are yet to be fully resolved and their distributions are unclear.
An. culicifacies complex	Sunlit, fresh (occasionally brackish) clear (occasionally turbid), still or flowing water with or without higher plants or algae	●	●	●	●	●	○	Bionomics dependent on sibling: Sp E = Anthropophilic; Sp A, B, C , D = Zoophilic)
An. dirus complex	Shaded, fresh, clear or turbid, still water without vegetation	●	○	●	●	-	●	Bionomics dependent on sibling but the two main vectors are *An. dirus* and *An. baimaii*. *Anopheles scanloni* is also anthropophilic but plays more focal role in transmission in Thailand
An. farauti complex	Sunlit or shaded, fresh or brackish, clear or turbid, stagnant (occasionally flowing) water with higher plants or algae (occasionally without vegetation)	●	○	●	●	○	●	*Anopheles farauti*, *An. hinesorum* and *An. farauti* No. 4 are the only siblings considered to be important malaria vectors
An. flavirostris	Shaded, fresh, clear, flowing (occasionally still) water with higher plants or algae (occasionally without vegetation)	○	●	●	●	○	●	Historically confused/misidentified as *An. minimus*. All records of *An. minimus* from the Philippines, Sabah (Malaysia) and Indonesia are now considered to be *An. flavirostris*
An. fluviatilis complex	Sunlit, fresh, flowing (occasionally still), water with higher plants or algae (occasionally without vegetation)	●	●	●	●	●	●	Bionomics dependent on sibling. Species S is the most anthropophilic and endophilic and is the main vector of the complex. Species T and U are primarily zoophilic, exophagic and exophilic and non or poor vectors in India.

Table 3a. Summary of bionomics of the DVS of the Asian-Pacific (created by cross referencing TAG and literature searches) Filled dot (●) indicates typical behaviour, open dot (○) indicates non-typical behaviour but examples exist, and dashes (-) indicate no data.

Species	Larval site characteristics	Host		Biting		Resting		Other
		Anthropo-philic	Zoophilic	Endophagic	Exophagic	Endophilic	Exophilic	
An. koliensis	Sunlit (occasionally shaded), fresh, clear, still water with higher plants or algae (occasionally without vegetation)	●	○	●	●	○	●	Currently considered a single species but new evidence suggests it may be a complex of two or more species
An lesteri	Shaded, fresh water with higher plants or algae	●	●	?	?	●	-	*Anopheles lesteri* is synonymous with *An. anthropophagus.*
An. leucospyrus/latens	Shaded, fresh, clear or turbid, still water	●	-	●	●	-	●	Most reported information for *An. leucosphyrus* probably actually refers to *An. latens*
An. maculatus (group)	Sunlit (occasionally shaded), fresh, clear (occasionally turbid), still or flowing water with higher plants or algae (occasionally without vegetation)	○	●	●	●	○	●	Vector role of individual species is unclear due to previous misidentifications based solely on overlapping morphological characteristics and due to apparent variability within species depending on location
An. minimus complex	Shaded (occasionally sunlit), fresh, clear, still or flowing water with higher plants or algae (occasionally without vegetation)	●	●	●	●	●	●	Within the complex, only *An. minimus* and *An. harrisoni* are current vectors of malaria
An. punctulatus complex	Sunlit (occasionally shaded), fresh, clear or turbid, still water without vegetation (occasionally with higher plants or algae)	●	○	●	●	○	●	Within the complex, only *An. punctulatus* is a known vector of malaria
An. sinensis complex	Fresh, clear, still (occasionally flowing) water with higher plants or algae (occasionally without vegetation)	○	●	-	●	-	●	Possibly refractory to *P. falciparum* but an important vector of *P. vivax*
An. stephensi	Sunlit or shaded, fresh (occasionally brackish), clear or turbid still (occasionally flowing) water with higher plants or algae (occasionally without vegetation)	○	●	●	○	●	-	One of the few anophelines able to flourish in urban areas
An. subpictus complex	Sunlit, brackish or fresh, clear or turbid, still (occasionally flowing) water with higher plants or algae (occasionally without vegetation)	○	●	●	●	●	○	The complex is currently considered to consist of four siblings: Species A, B, C and D although there is some confusion in the identification of Sp. B in some localities (may be a member of *An. sundaicus* complex)
An. sundaicus complex	Sunlit (occasionally shaded, brackish (occasionally fresh), clear or turbid, still (occasionally flowing) water with higher plants or algae (occasionally without vegetation)	●	○	●	●	●	●	The complex is currently considered to consist of four allopatric siblings:

Table 3b. Summary of bionomics of the DVS of the Asian-Pacific (created by cross referencing TAG and literature searches) Filled dot (●) indicates typical behaviour, open dot (○) indicates non-typical behaviour but examples exist, and dashes (-) indicate no data.

Unfortunately the high number of vectors in this region, and their complexity, have not equated to a higher level of knowledge, despite considerable effort from local scientists as well as from US military entomologists during WWII and the Vietnam War. Indeed, amongst all 41 DVS mapped [5, 14, 15], the two species with the lowest number of occurrence points, were both from the Asian-Pacific region (*An. leucosphyrus*/*An. latens* (12 points) and *An. balabacensis* (14 points)). There are also limitations when attempting to categorise vector behaviour as again, some species are very poorly studied, or those data that do exist are compromised by unreliable identifications due to the lack of robust techniques that are now available. Hence the summaries given here should be considered as potentially transient and may be updated as more data is collected and systematic PCR-based assays for species identification are applied [92-94]. Accepting these caveats, it must also be noted that the behavioural information presented is the culmination of a comprehensive review of the published literature combined with the 'on the ground' knowledge of highly competent and experienced experts and as such, do represent the best currently available species distribution maps and bionomics knowledge. Here focus is on the species and species complexes designated as the most influential across the region, including *An. culicifacies, An. fluviatilis* and *An. stephensi* across the Indian subcontinent; *An. dirus* and *An. minimus* within south-east Asia and the DVS members of the Punctulatus Group in the Pacific region. More detailed bionomics information and single species distribution maps for all 19 Asian-Pacific DVS are given in Sinka *et al.* [14].

5.1. Indian subcontinent (Bangladesh, Bhutan, India, Nepal, Pakistan, Sri Lanka)

The Indian subcontinent is densely populated giving rise to very high figures for the population at risk from malaria, however, the levels of risk are typically lower than those found in sub-saharan Africa. The majority of people at risk are living in areas of low endemicity (<5% prevalence) or areas of unstable malaria transmission where the disease is not endemic. This is true for both falciparum and vivax malaria. A smaller number of people living in India itself are at risk of much higher levels of falciparum malaria (>40% prevalence), possibly equalling the levels of risk found in sub-saharan Africa although there is a need for more data to support these figures [82].

The range of the *An. culicifacies* complex extends far beyond the Indian subcontinent; it also encompasses large areas of Southeast Asia including Vietnam, Cambodia, Lao PDR and southern China and reaches as far as Yemen in the Middle East with a small distribution in Eritrea as well as Nepal, India, Pakistan and Sri Lanka [14] (Figure 1). Despite this extensive distribution, the complex has only been studied in any detail in India and Sri Lanka [95-100]. Of the five species (A, B, C, D, E) of the complex, four are considered vectors in India (A, C, D and E) [101]. Of these four, species E is a particularly efficient vector due to its highly anthropophilic and endophilic behaviour and is considered the most important vector of both *P. falciparum* and *P. vivax* in southern India and Sri Lanka [102, 103]. The remaining three species (A, C and D) are primarily zoophilic and tend to be considered as playing more minor roles in malaria transmission [97]. Indeed, the highly zoophilic behaviour of Species B means it is often considered a non-vector [99, 104].

Members of the complex are found at a wide range of altitudes, from plains to hilly and mountainous areas [100]. The habitats they utilise are also varied and include forested and deforested ecotypes and irrigated areas. Consequentially, the larval sites they inhabit are also wide-ranging and include man-made habitats such as irrigation canals, borrow pits, domestic wells, tanks and gutters as well as natural sites such as stream margins and rock pools [96, 100, 101, 104-107]. A tolerance to brackish water has also been reported [96, 108], although fresh-water sites appear to be preferred. With many aspects of behaviour dependent on sibling, further investigations, coupled with confirmed identifications of each species, are needed before targeted vector control can be applied.

Again, despite a large distribution (Figure 1) [14], the behaviour and ecology of the *An. fluviatilis* complex has only been studied in any detail in two countries: India and Iran. The complex consists of three species, currently and informally designated species S, T and U [109] and an as yet unconfirmed form V [110]. The complex is distributed widely across the forested hills and mountains of southwestern Asia (Iran, Pakistan, Afghanistan, India, Nepal, Bangladesh and Myanmar) [104, 111-114]. Members of the complex also exhibit behavioural differences, with the anthropophilic and endophilic *An. fluviatilis* S categorised as a highly efficient vector in India [112], whereas both the zoophilic Species T and U, which also tend to feed and rest outdoors, are considered poor or non-vectors [115, 116]. However, species T is considered an important vector in Pakistan, Nepal and Iran [117, 118]. The larvae of this complex are associated with slow-flowing water in streams or river margins [119-124] (Table 3a).

The ability of the larval stages of *An. stephensi* (Table 3b) to develop in urban areas, making use of artificial containers such as domestic wells, overhead water tanks, room coolers, cisterns and roof gutters and in water bodies in construction sites and other industrial localities, brings malaria transmission into densely populated areas including the major cities of India such as Delhi [125, 126]. In general, malaria is considered to be a disease confined to rural environments, as a simple consequence of the tendency of anophelines to search for clean and unpolluted larval habitats and thus the existence of *An. stephensi* in such areas is a defining characteristic of the species.

Anopheles stephensi is found across the Indian subcontinent [14], extending from the Arabian Peninsula, through Iran and Iraq, across to Bangladesh, southern China, Myanmar and Thailand (Figure 1) [127-129]. It is typically described as an endophilic and endophagic species despite a tendency to bite outdoors during warmer months when people are more active outdoors [130, 131]. Host availability seems to be a driver to a variable anthropophily for this species, and therefore in urban areas, there appears to be a greater tendency for biting humans [132, 133], and therefore an increased risk of malaria transmission.

5.2. Southeast Asia (Cambodia, Laos, Myanmar, Thailand, Vietnam)

Human populations in Southeast Asia, with the exception of Myanmar, are typically exposed to low levels of falciparum and vivax malaria endemicity, unstable malaria transmission or are living in malaria-free areas. The majority of the population in Myanmar live in areas with low malaria endemicity but significant numbers live in areas of moderate (5-40% prevalence) and high (>40% falciparum prevalence or >7% vivax prevalence) risk. There is increasing

evidence that knowlesi malaria is transmitted from monkeys to humans in this region, particularly in the South, but the level of risk is currently unmeasured [82, 83, 134, 135].

The Dirus and Minimus complexes both contain species considered particularly efficient in transmitting malaria. Indeed, the *An. dirus* complex, due to its longevity and the highly anthropophilic behaviour of its members (Table 3a), is considered to be the dominant vector group in any area where its species exist [136]. However, due to its close relationship with members of the Leucosphyrus Complex, there has been considerable confusion in its identity in the published literature [137]. Species of the *An. dirus* complex are forest dwellers, existing in mountains and foothills, cultivated forests and forest fringes. There are eight members, *An. dirus* (formerly *An. dirus* species A), *An. cracens* (formerly sp. B), *An. scanloni* (formerly sp. C), *An. baimaii* (formerly sp. D), *An. elegans* (formerly sp. E), *An. nemophilous* (formerly sp. F), *An. takasagoensis* and the recently added species informally named *An.* Aff. *Takasagoensis* [138-142]. Of these species, *An. dirus* and *An. baimaii* are vectors of particular note [143-146]. As mentioned above, they are both highly anthropophilic, but their efficiency in transmitting both vivax and falciparum malaria is enhanced through biting humans both in and outdoors and of avoiding most conventional control methods by resting mainly outdoors (Table 3a) [111, 143, 145, 147-150].

Larvae are typically found in small, temporary, shallow and shaded pools of fresh water within the forest environment, such as puddles, pits, animal footprints, wheel ruts, hollow logs and slow flowing streams (Table 3a) [151-154].

Species of the *An. minimus* complex are also found in the hilly forested regions, but unlike the Dirus Complex, are restricted to mainland Southeast Asia (Figure 1) [14]. The complex contains three sibling species, *An. minimus* (formerly species A), *An. harrisoni* (formerly sp. C) and *An. yaeyamaensis* (formerly sp. E) [155-157]. This latter species has a very restricted distribution, only being found in the Ryukyu Archipelago in southern Japan, where it was considered a major malaria vector before the successful eradication of the disease in 1962 [158, 159]. Both *An. minimus* and *An. harrisoni* are, however, still considered primary vectors across their range, which encompasses much of Southeast Asia [14], although all historical records of *An. minimus* in Indonesia are now considered to actually be *An. flavirostris*. *Anopheles minimus* has a more adaptable nature than *An. harrisoni* allowing it to occupy a large variety of habitats, including dense canopy forests to open rice fields [14] and therefore has a greater distribution. *Anopheles harrisoni* tends to be restricted to deforested agricultural sites [160, 161]. *Anopheles minimus* is also highly variable in its behaviour (Table 3b), being an opportunistic mosquito, although in some reports this may be a consequence of the species complex not being fully identified [160]. Larvae of the *An. minimus* complex are found in small or moderate streams with slow-running, clear water. Females lay their eggs in the partially shaded grassy margins (Table 3b)[162-165]. Larvae have also been found in water containers in Hanoi [166].

Anopheles minimus is considered primarily anthropophilic, but its choice of blood meal can also be influenced by the availability of alternative animal hosts such as domestic cattle [148, 167, 168]. Biting habit is also variable (Table 3b), and dependent on location, with reports of endophagic behaviour in India, Thailand and central Vietnam, but exophagic behaviour in Cambodia and northern Vietnam [148, 165, 169]. The same is found for resting behaviour,

although there appears to be a large influence of the use of IRS on resting location and population densities for this species [170, 171]. Overall, *An. harrisoni* appears more consistent in behaviour, generally reported as exophagic, exophilic and zoophilic and thus potentially the less dominant vector [172, 173].

5.3. Asia-Pacific (Indonesia, Papua New Guinea, Philippines, Solomon Islands, Vanuatu, Timor Leste)

Human populations in the Asia-Pacific, with the exception of Papua New Guinea and Indonesian Papua, typically live in areas with low levels of falciparum and vivax malaria endemicity (<5% prevalence), or unstable malaria transmission or that are malaria-free. The majority of the population in Papua New Guinea live in areas with low malaria endemicity (<5% prevalence) but significant numbers live in areas of moderate (5-40% prevalence) risk. [82, 83].

The DVS in the Asia-Pacific region (as categorised here) are dominated by three of the 12 members of the Punctulatus Group, namely *An. farauti* complex, *An. koliensis* and *An. punctulatus* complex (Figure 5). *Anopheles farauti* complex has the widest distribution of these vectors (and of the Punctulatus Group as a whole), extending from the Maluku island group (Indonesia) in the west to Vanuatu in the east, including northern Australia in between. Of the eight species within the *An. farauti* complex, only three are considered to be main vectors, *An. farauti* s.s., *An. hinesorum* (formerly *An. farauti* No. 2) and *An. farauti* No. 4, although there is some, albeit limited and circumstantial, evidence of *An. farauti* No. 6 as a primary vector in the highlands, river valleys and intramontane plains of New Guinea [174, 175].

Despite being the most studied member of the Punctulatus Group, there are still many unknowns regarding the ecology and behaviour of the species of the *An. farauti* complex, with added uncertainty due to apparent variability in behaviour depending on location (based on reports of undifferentiated members of the complex). However, there are some trends that appear relatively consistent, for example, members seem to be mainly anthropophilic, although they will feed on domestic livestock, birds and other animals where available (Table 3a) [14]. Both endo- and exophagic feeding on humans has been reported, and some, albeit limited, endophilic behaviour. On the whole, females tend to be early biters (18.00 – 20.00), biting and resting outdoors [14, 176].

The larvae of *An. farauti* complex are able to make use of a large variety of water sources, both sunlit and shaded, but tend to be found in natural, rain-fed temporary pools through to semi-permanent/permanent bodies of ground water, often with floating or emergent vegetation. Within the complex, a defining trait of *An. farauti* s.s. is its ability to tolerate brackish larval sites, and hence this species is found mainly on the coast in pools within mangroves containing high organic debris and subject to tidal fluctuations. They are also found in natural swamps, oxbows, fish ponds, ditches, borrow pits and pools along stream or river margins [14]. Other members of the complex may have greater or lesser salinity tolerance, but this is one uncertainty that still needs to be confirmed, along with many other aspects of behaviour within the complex.

Anopheles koliensis plays an important role in transmitting malaria wherever it is found, possibly due to its strong anthropophily (Table 3b). Its range is essentially limited to New Guinea Island (Figure 5) with only a patchy distribution in the Solomon Islands, where it is absent in some areas despite a presence of apparently suitable environments [177-179]. Where it is found, it will bite in or outdoors, but is rarely found resting indoors [180]. The larvae of this species are found in more permanent habitats than those of either the *An. farauti* or *An. punctulatus* complexes [180, 181]. Typical larval sites include sunlit irrigation ditches, and ponds containing floating and/or emergent vegetation, often in close association with humans. They are never found in brackish water [14].

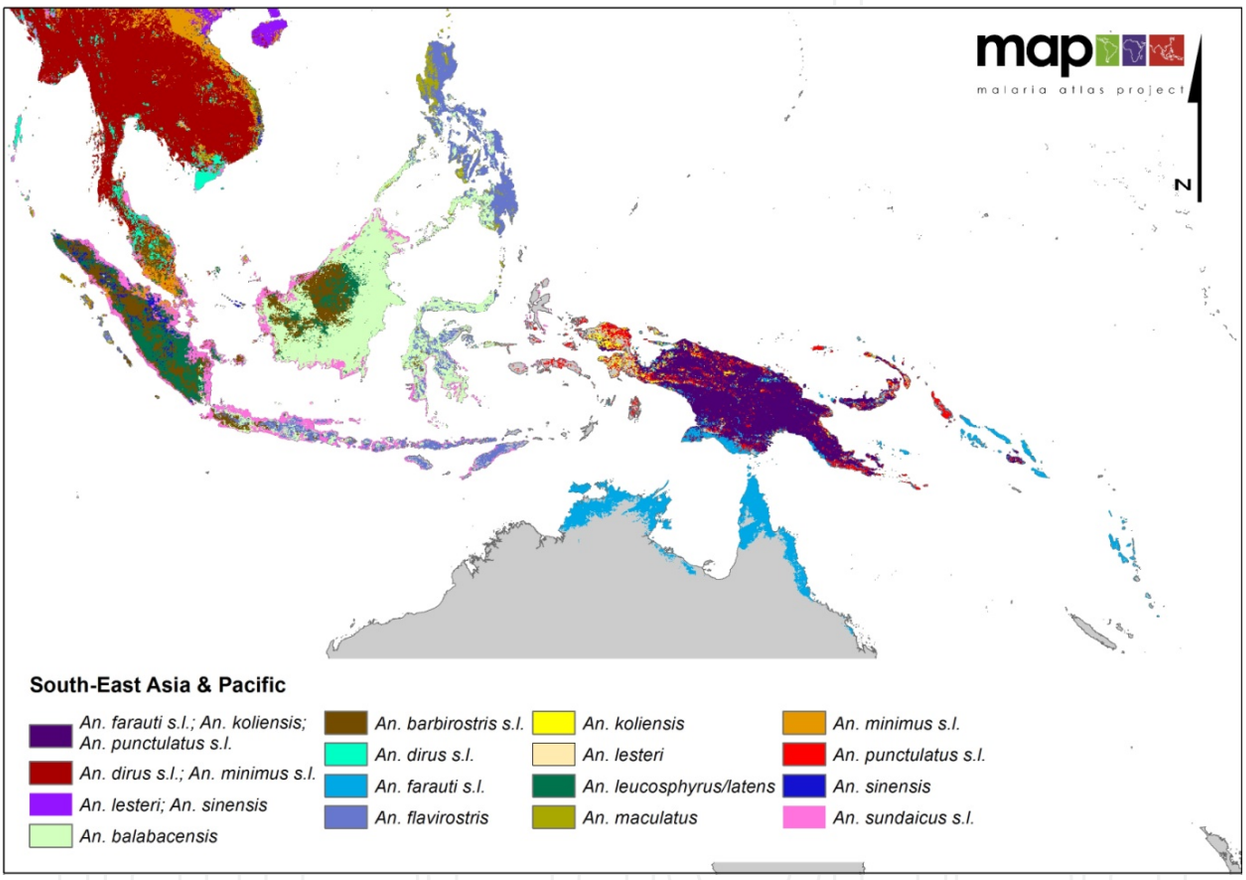


Figure 5. Multi-species map of South-East Asia and the Asia-Pacific region indicating the distribution of 13 DVS of particular importance. (map reproduced from Sinka et al. [4]).

The last DVS in this region is a member of the *An. punctulatus* complex. The complex contains two species, *An. punctulatus* and *An.* sp. near *punctulatus* [182] of which the latter is relatively uncommon and restricted to a few remote highland localities on New Guinea Island where little is known of its ability to transmit malaria. On the other hand, *Anopheles punctulatus* is a highly efficient malaria vector across much of its range, which extends within lowland valleys and plains, and up to altitudes of 2000m across New Guinea Island and the Solomon Islands [174], although its impact and importance as a vector appears reduced in this eastward end of its range [14, 178, 179]. As with other vectors within the Punctulatus Group, *An. punctulatus*

feeds readily on humans both in and outdoors and is mainly found resting outdoors (Table 3b) [181, 183, 184]. This species is particularly adept at exploiting disturbed environments, such as those caused by land clearance or areas subject to drought conditions, where receding rivers result in small temporary pools rapidly colonised by larvae. Such colonisations can result in explosive adult populations and subsequent severe and unpredictable outbreaks of malaria [185, 186]. The typical larval sites utilised by this species reflect the conditions found in such disturbed ecologies, i.e. scattered temporary pools of fresh water, generally sunlit and shallow, containing either clear or turbid water with little or no vegetation [14]. Eggs can cope with some level of desiccation and larvae can survive in damp mud for several days during drought conditions [183]. They are also able to withstand high water temperatures (over 40^{o}C) where they grow rapidly with particularly short development time (5-9 days to adults), occasionally resorting to cannibalism to survive, (Bangs, pers com; [14]).

6. Map methodology

A full description of the methodology used to create the individual and multi-species maps is given in Sinka *et al* [15] and Sinka *et al* [4].

The maps presented here were created using the Boosted Regression Tree (BRT) environmental niche modelling method [187, 188]. This method uses spatially defined presence data and environmental and climatic variables to identify the conditions that typify a species' habitat. The model then identifies all locations where such conditions exist and therefore other localities where the species could potentially occur (i.e. its fundamental niche). It also provides an estimate of the probability of occurrence, i.e. applying a numerical value to indicate the conditions within the acceptable range of a species. The multi-species maps show only presence pixels with a probability value greater than 0.5 for each species.

To create the multi-species maps, the individual species distributions were overlaid ensuring the most dominant species (established through consultation with a technical advisory group of vector experts) was uppermost. Where more than one species was considered dominant in an area the species distributions were merged.

7. Conclusions

The maps given in this chapter are presented with the caveat that they represent only the beginning of a process to establish the distribution of these vectors. As with all species distribution modelling, the accuracy of the output is limited by the amount and quality of the data that is available to the model. The data must be accurately geo-referenced and reflect the true and full identity of the species to be modelled. Our maps were created using the most comprehensive database of species occurrence currently available, yet still, for many of the DVS, the quality of the data is ambiguous and the quantity is poor. However, as more reliable and repeatable methods of species identification are developed, species occurrence data and

the corresponding bionomics will be better understood as the taxonomy of many of these species are resolved. Moreover, a greater commitment for data sharing between research groups, public health officials, modellers and map makers is beginning to increase the quantity and quality of data available and subsequently, increasingly accurate maps and a greater understanding of transmission dynamics, combined with the benefits of targeted vector control, is making the prospect of the global elimination of malaria a much more realistic goal.

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