
Ecology of Larval Habitats

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<http://dx.doi.org/10.5772/55229>

1. Introduction

Mosquito-borne diseases, including malaria are undergoing a global resurgence [1-7]. The factors responsible for the re-emergence are very complex, and management requires integrated cooperation at many levels, however, a need to better understand the ecology of disease vectors remains critical for any control program to succeed. In the case of malaria, the spatial and temporal changes in anopheline mosquito abundance, quantification of transmission potential of vector populations, characterizations of climatic conditions, and description of distributions of host (human) populations are necessary prerequisites for predicting high-risk malaria areas and implementing an effective disease control program [5, 8]. Tools such as remote sensing and geographic information systems (GIS), which are increasingly being used in studies of disease transmission and vector ecology have greatly enhanced our abilities to analyze landscape level relationships of vectors and diseases. Yet these tools can be successfully used only in combination with a thorough understanding of ecologic and epidemiologic processes of disease transmission.

Among the most important determinants of adult mosquito abundance and distribution is the presence and quality of larval habitats.¹ An understanding of the dynamics and productivity of larval habitats in the changing environment is required if efforts to model and predict adult abundance and ultimately limit the disease spread are to succeed [8-12]. While biology of adult mosquitoes has been reviewed from multiple perspectives [13-15], there has been no recent comprehensive review of mosquito larval habitats.²

¹ terms larval habitat, breeding site, breeding habitat have been used interchangeably for descriptions of places where mosquito females oviposit eggs, larvae hatch, grow and pupate [16]. We will be using the term larval habitat throughout the paper.

²*Anopheles* species included in Sinka's et al [17] list of dominant vector species plus *An. vestitipennis* have been included in this review.

A vast amount of literature on malaria vectors is available. More than 60 years ago, Marston Bates wrote in the Introduction to his *The Natural History of Mosquitoes*: “Mosquitoes in general, and the malaria carriers in particular, have been the subject of a tremendous amount of study, whose results have been reported in the voluminous literature. Much of this literature is an uncritical accumulation of facts that were easy to record, or of facts that were related to some momentarily fashionable subject of study, or of facts that were needed for the attainment of some immediately practical objective. This accumulation awaits to be converted into an orderly and useful structure of knowledge” [18]. It is hard not to feel the same today, with the Web of Science responding with > 600 references to an inquiry for *Anopheles* larval habitats. We won’t be able to provide “an orderly and useful structure of knowledge” in this short chapter, but we will attempt to cover a few important topics:

- History of description of larval habitats
- Determinants of larval habitats
- Habitat selection
- Landscape context
- Human impact and adjustment to new habitats
- Implications for vector control
- Future priorities

Research and reporting efforts and resulting available information are disproportionately distributed and heavily skewed towards the most important malaria vector, *An. gambiae* with over 5440 references in the Web of Science, followed by *An. stephensi*, *An. arabiensis* and *An. funestus* with 1557, 744 and 537 references respectively. The majority of remaining species from Sinka’s [17] list are referenced < 200 times with the exception of *An. albimanus*, *An. quadrimaculatus*, *An. darlingi* and *An. dirus* referenced 592, 456, 264 and 255 times, respectively. However, in most cases these species are primary vector species. In considering potential vector replacement following the environmental change (see examples further in the text) it will be important to keep in mind that secondary, little studied and less efficient, vector species might be found replacing primary malaria vector species.

2. History of description of larval habitats

Much of what we know about the detailed behavior of individual insect vectors resulted from observations made during the pre-DDT era of the 1920’s and 1930’s [8, 19], when programs for malaria control through environmental management and regular larvicidal treatment of larval habitats were developed across Europe, Middle East, Asia, and the Americas [20, 21]. Examples of successful treatment schemes [21] show that they were all accomplished based on a good knowledge of larval ecology. The concept that the prevalence of malaria can more effectively be reduced by destroying vector mosquitoes in their adult stage than in their aquatic, larval

stages became central to antimalarial efforts practiced throughout the world's tropical regions beginning first with pyrethrum and later with DDT spraying. Success of those efforts led start-up of the Global Malaria Eradication Strategy, GMES [20, 22]. One of the unfortunate consequences of GMES was a substantial reduction in funding for research related to larval ecology, it was even credited with "exterminating more medical entomologists than mosquitoes" [20]. However, as early as 1983, Service [23] pointed out that "the general disillusionment with chemical control methods has led to the resurrection of biological control from the pre-DDT era" and although funding has not been easy to come by, the 1990's saw an exponential increase in studies on larval ecology and larval habitats. Laird's *The Natural History of Larval Mosquito Habitats* [24] provided an important source of information.

Although earlier papers are not often cited in the contemporary literature, there are several reasons why older papers are important and should not be ignored:

They provide records of species distributions: The older papers often describing simple surveys or even just few locations where a particular species was found provide historical evidence of species distribution prior to human interference [25, 26]. *Example:* Positive records of the presence of *An. darlingi* in southern Belize (then British Honduras) published by Komp [25] and Kumm and Ram [26] and a report of absence of this species 30 years later by Bertram [27], made one of the authors of this chapter (DR) suspects that disappearance of *An. darlingi* was most probably a response to DDT house-spraying [28]. The species was eventually recorded again from Belize (a consequence of the interruption of DDT-spraying?). The whole story points to the need to continuously study changing roles of malaria vectors in different geographical areas.

They contain important ecological and ecophysiological observations: Already in the 1940's mosquito entomologists realized what many recent papers present as a new discovery, i.e., that human interference can lead to a vector change. As described by Muirhead-Thomson [29] from the coastal zones of Sierra Leone, draining and dyking of mangroves, which used to be very productive habitats for *An. melas*, and changing land use to rice cultivation, resulted in very productive habitat for *An. gambiae* and eventual replacement of *An. melas* by *An. gambiae*. Goma [30, 31] discarded a long time belief that high incidence of malaria in Uganda is related to the extensive papyrus swamps hypothesizing [30, 31] and eventually experimentally proving [32] that interior of a papyrus swamp is unsuitable for anophelines and only the swamps altered by human activities are significant providers of larval habitats. Numerous interesting observations and results of simple experiments on oviposition and larval development as influenced by environmental factors were published [18, 33] and are well summarized in Bates's *Natural History of Mosquitoes* [34].

There can be a good information on well executed larval control: A series of detailed studies on larval habitats originated from the US Tennessee Valley Authority, TVA (TVA is a federally owned corporation in the US created in 1933 to provide navigation and flood control, electricity generation, fertilizer manufacturing and economic development in the Tennessee Valley, a region strongly affected by the Great Depression; <http://www.tva.com/abouttva/history.htm>).

This watershed area of the fifth largest river system in the United States was transformed into a series of reservoirs encompassing more than 11,000 miles of shoreline. Because the impoundment of the river provided enhanced breeding opportunities for *An. quadrimaculatus* in (then) malaria-endemic region, antimalarial measures were required as integral parts of all TVA projects. The general philosophy was to control mosquito breeding through natural measures and limit larvicidal and other temporary controls to an absolute minimum [35]. Papers by Hinman et al [36], Penfound [37], Hess and Hall [38], Hall [39] focused on the importance of aquatic vegetation in anopheline larval habitats (see section on Vegetation).

Older correlative studies can provide a good starting point for hypotheses testing through experimental studies: Starting in early 1990's there is a progression of studies that include habitat characteristics and attempts to relate the presence of larvae to these characteristics [17, 40-51]. An important change compared to the majority of older papers was that in these correlative studies, environmental characteristics of both, larvae positive and negative habitats were recorded. As more information became available on the relationships between larval presence and habitat characteristics, attempts to classify anopheline larval habitats appeared. As an example Rejmankova et al. [44] classified larval habitats of *An. albimanus* on the coastal plain of Chiapas into 16 habitat-types based on the dominant aquatic vegetation. The goal was a hierarchical system of habitat classification that could be universally used for larval habitat description in the study area and it became a basis for many future studies on larval ecology by the Tapachula-based Center for Malaria Studies [52-54]. The analytical methods and hierarchical system described in Rejmankova et al [44] article are applicable to a wide range of studies on phytoecological relationships of vectors to aquatic habitats.

The need for regional classification of larval habitats into higher units became more urgent with the increasing use of remote sensing technology in malaria vector studies [55-57]. The step-wise approach (paradigm) advocated by Roberts and Rodriguez [58] became widely applied [59, 60]. These steps included the following: 1) developing an understanding of vector ecology and defining the environmental determinants for its presence and abundance (this step is based on field studies); 2) constructing a database that characterizes the landscape elements associated with the important aspects of vector biology and human habitation (RS and GIS are suitable tools for this step); and 3) formulating and verifying predictions of vector abundance.

Recently, studies describing larval habitats of anophelines were included in the global database on 41 dominant vector species, DVS, of human malaria. The contemporary distribution of each of the DVS, alongside a comprehensive description of the ecology and behavior of each species, has been published in a series of papers by Sinka and coauthors [17, 61-63]. The authors stated that simple, universal species-specific statements regarding the biology of these vectors are nearly impossible due to the behavioral plasticity of most species, in some cases sympatric distributions of sibling species, changing taxonomic categorization and the influence of environmental disturbance, all contributing to a high level of complexity.

While the descriptive and correlative studies of larval habitats have mushroomed in the 1990's and 2000's, good experimental studies explaining the hypothetical relationships between larvae and the habitat characteristics are still relatively lacking. They are increasingly called for [11, 22], e.g., by proposing development and application of enclosed, pathogen-free, semi-field mesocosms in which vector populations can be experimentally manipulated. There are a few exceptions such as Goma's [31] study from the papyrus swamps in Uganda. Based on his observations on the absence of *An. gambiae* larvae from the swamp interior, Goma hypothesized that the larvae are not found there because the conditions are unfavorable for their development. He conducted a series of experiments in which known amounts of larvae of different instars were placed in floating cages in different locations throughout a swamp and confirmed that larvae in the swamp interior suffered significantly higher mortality and those surviving took longer to develop into adults than larvae in cages placed at the swamp periphery. The high mortality has been later explained as a result of inhibition of larval breathing due to the surface layer of oil produced by papyrus [64]. For other examples of hypotheses driven experimental studies see, e.g., [10, 65-76] and other examples provided in further text.

2.1. Dichotomy between medical entomologists and ecologists in larval studies

There has been quite a deep divide between medical entomologists and ecologist in their approach to studying mosquito larval habitats [22, 77]. Medical entomologists generally study larval habitats with the focus on design of efficient control interventions and often don't realize that it is the ecological approach to studying larval habitats in the context of other ecosystem components that can eventually lead to a thorough understanding of the larvae – habitat relationships. A relatively small number of researchers realize that filling the gap between ecologically based and epidemiologically based information is a necessity [77]. As Chase and Knight [78] put it: because larval mosquitoes are components of a much larger metacommunity of interacting species, the interplay between biotic interactions (competitors and predators) and abiotic constraints (temperature, habitat drying) is essential for understanding the controls on mosquito abundance. By placing mosquitoes into a broader community context, a much better predictive framework can be developed for understanding and predicting year-to-year variation in mosquito abundances [79, 80]. Ecology should—like other basic disciplines such as molecular biology and bioinformatics—be considered an enabling science essential for defining the target product profiles of completely new control technologies and delivery systems [22].

3. Environmental determinants of larval habitats

Larval habitats or breeding sites - places where eggs are laid, larvae hatch, change instars, pupate, and adults emerge - are primary drivers of adult distribution, abundance and fitness [5, 9, 10, 81]. They are always composed of water bodies, natural or man-made, permanent or

temporary, large or small, freshwater or saline. The mosquito reproduction is successful only if larval habitats remain stable for a duration equivalent to the development of immature stages [82]. The great diversity of habitats, often combined with inaccessibility, makes studies of the ecology of larval anopheline mosquitoes methodologically quite difficult [9].

Larval densities are controlled by interactions between abiotic (hydrology, temperature, light/shade, pH, salinity, nutrient availability) and biotic (predation, competition) factors [78, 83-85]. For comprehensive analyses of patterns in the productivity of larval habitats the studies should incorporate a landscape context, because presence and abundance of mosquito larvae in aquatic habitats and consequently the number of adults capable of malaria transmission are regulated by a variety of ecosystem processes operating and interacting at several organizational levels and spatial/temporal scales [86]. The conceptual scheme in Figure 1 summarizes the main factors and processes important for good understanding of interactions between larvae and their habitat characteristics in the larger ecosystem context. Humans can affect habitat availability and quality through ecosystem and landscape changes such as deforestation/ reforestation, desertification, irrigation and other hydrological changes, and agricultural practices (see further). In the following text we will focus on the main determinants of larval development.

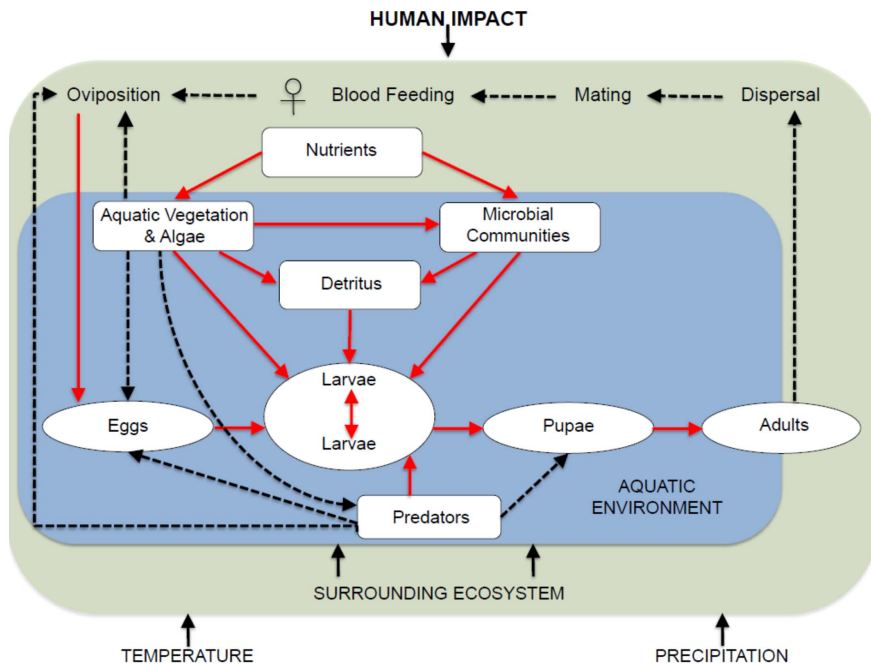


Figure 1. Relationships between larval development and environmental factors on both habitat and ecosystem level. The relationships reviewed in the chapter are indicated in red.

3.1. Temperature

Temperature affects all the important processes such as the rate of larval development and survivorship, pupation rates, larval-to-adult survivorship and larval-to adult development time [81, 87-89]. Water temperature is influenced by various parameters, such as local climate, water depth and movement, habitat size and geometry, land cover type or canopy overgrowth, presence of vegetation and/or algae, soil properties and turbidity [81]. Despite its importance, there are not many detailed outdoor studies on the temperature of larval habitats and the available data are hard to compare due to different methods of temperature measurement (air temperature vs. water temperature; data loggers vs. hand-held thermometers). Available data on *An. gambiae* point to a consensus that one of the main reasons for higher productivity of *An. gambiae* and *An. funestus* in habitats associated with agricultural crops or swamp margins is higher temperature as compared to shaded dense papyrus swamps [72, 90, 91]. Additional proof comes from Wamae et al [88] who compared *An. gambiae* densities in shaded (by napier grass, *Pennisetum purpureum*) and unshaded water channels in reclaimed sites in Western Kenya highlands. In these studies, the shading reduced anopheline larvae by >75%, apparently due to ~3 degrees C reduced water temperature. High water temperature pools (30-33 degrees C) were reported as the most productive habitats for *An. gambiae* in Gambia [92]. In South America, Marten et al [93] found the majority of *An. albimanus* larvae on the coastal plain of Colombia associated with sun-exposed sites with a mid-day temperature range of 27.5 - 30.0° C. Pinault and Hunter [94] report minimum water temperatures that might limit the upper altitudinal distribution of *An. albimanus* (18.7° C) and *An. pseudopunctipennis* (16.0° C). Larvae are not generally able to survive temperatures over 40 degrees C as documented by Muirhead-Thomson [29] for *An. minimus*, (but see *An. bwambae* in hot springs, [95]). Recent detailed study on the longevity and mortality of *An. gambiae* under a wide range of temperatures [87] concluded that under extremely cold (10–12°C) or hot (38–40°C) temperatures all larvae died within a few days. While the low temperature range is rarely experienced in larval habitats of *An. gambiae*, the higher temperatures are frequently encountered in most tropical regions. In nature, however, such high temperatures occur for no more than a few hours and larvae may survive these short periods.

Paaijmans et al [81, 96] stressed the importance of temperature fluctuations for larval development. The authors provided a conceptual model of radiation and energy fluxes at the air-water and soil-water interfaces of small, shallow and clear water pools and did field measurements comparing smaller and larger water bodies [81]. In general, the small-sized water pool reacted more dynamically to suddenly changing meteorological variables and experienced larger fluctuations. Several important conclusions follow from these experiments: The top layer (upper 2 mm) of each water pool differed in temperature from the layers underneath, which has important consequences for larval dynamics as anopheline larvae generally live horizontally near the air-water interface of aquatic habitats [66]. There can be large differences (> 10 degrees C) between air and water temperature. Larger pools had larger buffering capacity. Mosquito immatures can be exposed to a wide temperature range under natural conditions and they are apparently evolutionarily adapted to their direct environment. The observed differences between air and water temperature have important consequences and

should be carefully employed for ecological models that use the air temperature as an input parameter for larval development.

3.2. Light

There are species occurring mostly in sun-exposed environments such as *An. gambiae* s.s., *An. albimanus*, *An. pseudopunctipennis*, members of the *An. sudaicus* complex, *An. sinensis*, *An. aconitus* etc., while others seem to prefer shaded water bodies (*An. funestus*, *An. vestitipennis*). The question of whether sun or shade has a direct effect on the development of larvae or impacts them indirectly through the effect of temperature on food source development has not been answered, although some laboratory experiments seem to show that light is not an important direct factor [83, 97]. It is possible that in some instances, larvae are positively correlated with shaded environment only because shade of trees reduces drying speed of the pools [98]. Little is known about the effects of darkness on larval development in *Anopheles* species. It has been shown, however, that light deprivation causes a significant reduction in the development of adult *An. stephensi* when larvae were bred in the absence of light [33]. In the dark treatment group, only about 60% of pupae transformed into adults.

3.3. Salinity

There are large differences in the tolerance of anopheline larvae to water salinity. While the majority of anopheline larvae are found in fresh waters, there are several species that show high salinity tolerance and are associated with coastal malaria transmission. *Anopheles melas* and *An. merus* within the *An. gambiae* complex are examples from Africa [61]. *Anopheles farauti* s.s. and *An. irenicus* (formerly designated *An. farauti* No. 7) in the Farauti Complex are reported to be salinity-tolerant in Australasia [63, 99]. Malaria vectors of the *An. sudaicus* complex in Southeast Asia are well known brackish water breeders [100, 101]. On the American continent an example of salt tolerant species is *An. aquasalis* [48, 102].

A major challenge faced by all mosquito larvae is the tendency for larval habitats to fluctuate widely in salinity due to changes in rainfall and evaporation [13]. Organisms living in brackish and saline environments have evolved various mechanisms of coping with increased salinity, and in order to survive in these conditions, they have to be able to regulate their osmotic potential. Larvae of salinity tolerant mosquito possess cuticles that are less permeable to water than freshwater forms, and their pupae have thickened and sclerotized cuticles that are impermeable to water and ions. Larval survival depends upon the ability to regulate hemolymph osmolarity by absorbing and excreting ions [103]. Osmoregulatory mechanisms vary among various mosquito genera, for example *An. albimanus* larvae osmoregulate through rectal ion excretion and the larvae undergo a dramatic shift in rectal Na⁺/K⁺-ATPase (an enzyme important for ion regulation) localization when reared in freshwater *vs.* saline water [103].

Saltwater tolerance is a trait that involves ionic regulation at the aquatic larval stage, and it appears to have been a factor in the adaptive radiation of the *A. gambiae* complex into diverse larval habitats. A mechanistic understanding of the physiology and genetics of ion regulation

is important because it can open up new classes of larvicide [104]. Additionally, increasing amounts of saltwater pools and puddles associated with natural disasters (tsunami), land subsidence, or sea level rise would facilitate increased breeding of brackish water malaria vectors (e.g., *An. sudaicus*) and may increase the risk of malaria outbreaks [105, 106].

3.4. Hydrology and geomorphology

Hydrology of a region, i.e., distribution and seasonal dynamics of lotic and lentic water bodies is determined by the geomorphology and precipitation patterns [107, 108]. Water quality in these different water bodies is influenced by rock and soil chemistry, vegetation of the surrounding landscape, and human activities. Both hydrology and water chemistry determine the type of aquatic vegetation present in lakes, pools, and streams [42]. Geomorphological parameters such as elevation, slope, aspect, and ruggedness play an important role in malaria transmission as exemplified, e.g., by Atieli [108] who found broad flat-bottomed valleys in Kenya Highlands to have a significantly higher number of *Anopheles* larvae/dip in their habitats than the narrow valleys. Heavy rains in the tropics can be detrimental to larval survival. In particular, rainstorms are known to flush mosquito larvae from their breeding sites [109, 110] – but see Manguin et al. [47] who reported survival of 3rd and 4th instar larvae in clumps of detritus that was stranded in trees and shrubs in the wake of the flood.

3.5. Vegetation

Many shallow water bodies are dominated by aquatic plants – both microphytes (algae and cyanobacteria) and macrophytes.

Aquatic macrophytes, often also called hydrophytes, are key components of aquatic and wetland ecosystems. As primary producers, they are at the base of herbivorous and detritivorous food chains, providing food to invertebrates, fish and birds, and organic carbon for bacteria. Their stems, roots and leaves serve as a substrate for periphyton, and a shelter for numerous invertebrates and different stages of fish, amphibians and reptiles [66, 111]. Biogeochemical processes in the water column and sediments are to a large extent influenced by the presence/absence and type of macrophyte, and macrophytes can also have a profound impact on water movement and sediment dynamics in water bodies [112].

Phytoecological relationships of many species are strong enough to indicate presence or absence of mosquitoes according to presence or absence of associated plants [44]. The effect of aquatic plants on mosquito oviposition and larval survival and development, particularly among the anophelines, has been recognized since the early 1930's [38, 39, 66, 113-115]. Many aquatic plants provide food and protection for mosquito larvae and create favorable conditions for oviposition. Of special importance is the interface of air-plant-water, which has been termed the intersection line [38]. The intersection line is important to anopheline larvae because it is where the larvae find food and shelter and adults find the water surface broken up into numerous quiet cells favorable for ovipositing [19, 66]. A number of studies have documented a positive correlation between larval density and amount of plant cover or intersection line, e.g., [38, 115-118]. Plants provide favorable conditions for anopheline production if they

continuously intersect the water surface during the mosquito breeding season. Collins and Resh [118] present a table showing the evaluation of common wetland plants for habitat suitability including the intersection line value.

Aquatic macrophytes are extremely diverse taxonomically, morphologically and functionally. Thus it is not surprising that different groups of macrophytes provide suitable habitats for different mosquito species (Figure 2). Of the four major macrophyte categories, i.e., freely floating, emergent, submerged, and floating-leaved [112], emergents generally provide the largest number of intersection lines. The positive benefits associated with aquatic macrophyte cover, and dense patches of emergent plants in particular, should result in a strong selective advantage (i.e., increased fitness) to individuals that choose high density macrophyte patches as habitat [66]. Selective pressure for such habitat preferences should operate on both larval and adult stages of *Anopheles* and the strong preferences of larvae and ovipositing adults for higher density patches of *Myriophyllum* were indeed observed by Orr and Resh [66].

While the majority of anopheline species are rather generalists and not very selective for a particular type of vegetation, there are others with tighter phytoecological associations. *Anopheles gambiae* is an example of a generalist whose larval habitats are shallow temporary water bodies with algae or short grasses but also devoid of any vegetation [61], see Figure 2H and papers of Mutuku et al. [119] and Ndenga et al. [89] for illustrations. Among examples of an extremely close association are the larval habitats of *An. pseudopunctipennis*, which are typically sun-exposed streams with abundant filamentous algae [42, 94, 120-124], see Figure 2E. The selection of filamentous algae by *An. pseudopunctipennis* has been confirmed by oviposition experiments [125, 126]. Similarly, the presence and abundance of *An. farauti* larvae was positively associated with filamentous algae in Solomon Islands [99]. Another species whose habitat can be clearly defined by vegetation presence is *An. vestitipennis*. Numerous reports confirm its association with tall dense macrophytes and/or flooded swamp forest [127-130] see Figure 2A. It is perhaps the preference of *An. vestitipennis* for a shaded environment generally that results in it being associated with these two types of habitats [129]. Preferred habitats for *An. darlingi* are patches of detritus often accumulated behind a fallen stump, or vegetation at the shady edges in slowly running streams and rivers [26, 42, 47, 73, 82] see Figure 2F. Barros et al [82] call these habitats "microdams" and they found the presence of microdams to be the most important parameter determining spatial distribution of *An. darlingi* larvae in northern Brazilian Amazon. Achee et al [73] experimentally evaluated the importance of floating detritus patches and overhanging bamboo for *An. darlingi* habitat selection using floating screened enclosures placed in a river at a location with documented presence of both larval and adult *An. darlingi* populations. The detritus treatment had a significantly higher average count of *An. darlingi* larvae documenting that females preferentially oviposited in this habitat.

Even with these tight associations, there are often exceptions, e.g., *An. pseudopunctipennis* found in tall dense macrophytes (*Schoenoplectus californicus*) in the coastal zones of Peru (DR, ER unpublished data), or even without vegetation [124], but these snapshot observations on larval presence don't really provide information about survival and adult fitness.

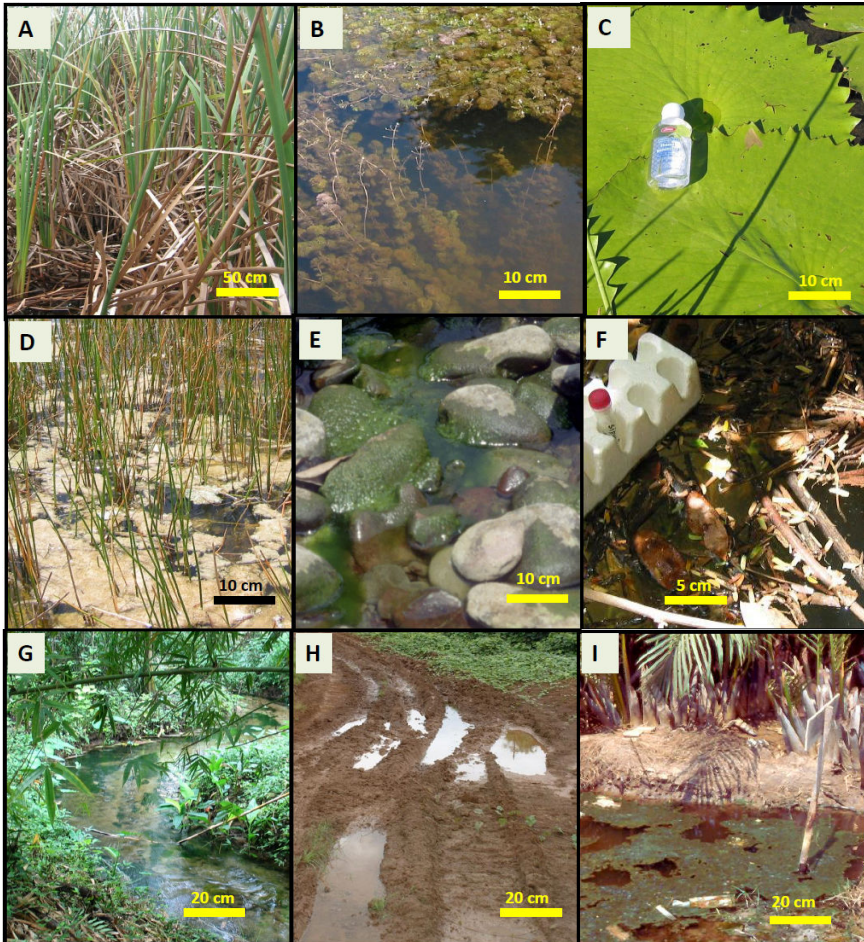


Figure 2. Examples of various larval habitat types as defined by vegetation. A: Freshwater marsh with tall dense macrophyte, *Typha domingensis*, a typical habitat for *Anopheles vestitipennis*; B: River edge vegetation dominated by a dense submersed macrophyte *Cabomba aquatica*, a potential habitat of *An. darlingi*; C: Marsh dominated by floating-leaved macrophyte, *Nymphaea ampla*, an example of an environment where larvae are typically not found; D: Marsh with sparse emergent macrophyte, *Eleocharis cellulosa*, interspersed with floating mats of cyanobacteria, a typical habitat of *An. albimanus*; E: A stream with filamentous green algae, a typical habitat for *An. pseudopunctipennis*; F: Detritus in a protected riverine environment, a typical habitat of *An. darlingi*; G: Small, partially shaded stream with vegetated margins, a typical habitat for *An. minimus*; H: *An. gambiae* habitat from Equatorial Guinea (Malabo region); I: Stagnant pool of water with floating mats of algae, a habitat of *An. epiroticus* (Sundaicus complex) from southern Vietnam. Note the different scale bars. (Photo G & I courtesy of Sylvie Manguin; photo H courtesy of Pierre Carnevale).

3.6. Rice fields

Considering the large extent of rice fields in the areas with endemic malaria, they deserve their own subchapter. The changing crop practices, such as the shift to irrigated wetland rice affect

Anopheles vector populations, increasing the extent of larval habitats and transmission of malaria [131]. Irrigated rice cultivation extends the time in which vectors breed and in countries with two crops of rice per year, anopheline breeding and biting rates extend well beyond their usual seasons [131, 132].

The aquatic community in rice fields is a dynamic system related closely to rice plant growth, rice cultivation practices, and seasonal climatic changes [133-135]. Each mosquito species often has a preference for a particular phase in rice field development, which may result in an orderly succession of species as the rice plants develop and mature [136]. The pioneer colonizers are typically sun-preferring species, such as *An. gambiae* (Africa), *An. albimanus* (Central America), and *An. fluviatilis* and *An. culicifacies* (Oriental region); but when the rice grows taller it shades the water and shade-preferring species, such as *An. funestus* (Africa), *An. umbrosus* (India), *An. hyrcanus* group (Asia), *An. leucosphyrus* complex (Malaysia), *An. freeborni* (North America), *An. punctimacula* (South America) usually become more abundant [131, 136]. The abundance of aquatic macroinvertebrates, including predators, also changes during the growth of a single rice crop [76, 135, 137]. Compared to Asia and Africa there is less documentation of linkages between rice cultivation and disease in Latin America, although in parts of Mexico and Venezuela rice appears to be associated with seasonal increases in malaria incidence [138].

3.7. Food sources

Aquatic plants (both micro- and macrophytes) provide protection from predators and, together with trees and shrubs, contribute detritus that supports the bacterial community, which, in turn, serves as food for larvae [139]. An understanding of the spatial and temporal distribution of the dietary resources available to larval mosquitoes in their natural habitats could clarify the relationships among food availability, vector competence, and mosquito fitness [19, 140, 141]. Yet, the quantity and quality of food sources available to larvae is often ignored in the study of larval growth and development [9]. Natural food assemblages of larval mosquitoes are extremely diverse biochemically [142]. Generally, bacteria have been considered the most important of the microorganisms that comprise the food of mosquito larvae [19, 24], and mosquito growth can occur on cultures of bacteria alone [19]. In the water column of aquatic ecosystems, bacteria are the major decomposers of organic matter and the presence of particulate heterotrophic bacterial biomass represents an important link between detritus, dissolved organic matter, and higher trophic levels [143]. This bacterial production is controlled by or directly related to the supply of decomposable organic material. Thus, larval habitats with ample supplies of autochthonous and/or allochthonous detritus are capable of providing sufficient supplies of larval food resources. Experiments with diets also demonstrated that mosquito larvae can develop solely by drinking dissolved nutrients [19]. Larval food sources are not distributed homogeneously throughout the water column. The surface microlayer contains relatively high amounts of nutrients, organic material both particulate and dissolved, and various microorganisms as compared to subsurface water [144]. Anopheline larvae are well suited to utilize food sources from the enriched surface layer as they typically feed at the surface of the water where they engage in interfacial feeding behavior [13, 144].

Microalgae and/or small cyanobacteria can also serve as an important food source [19, 53, 93, 145]. Gimnig's et al [10] study demonstrated that larval grazing reduced algal abundances and biomass by an order of magnitude, and changed microeukaryote community structure. Changes in this algal food resource due to larval consumption almost certainly led to the observed density-dependent responses in larval development. Kaufman et al [145] conducted experiments to investigate the importance of algal food resources for larval growth and adult emergence of *An. gambiae* in simulated larval habitats in Kenya. Their results confirmed the importance of algal biomass in the surface microlayers of larval habitats to larval development and production of *An. gambiae* adults. They also showed that soil quality in these ephemeral larval habitats is important as the growth of algae depends on nutrient availability, particularly phosphorus (P). Thus soils releasing more P after flooding would support more algae that can feed more larvae.

While some microalgae are an important food source, other algae can be harmful to anopheline larvae. Marten's [146] review concludes that many species of green algae in the order Chlorococcales are resistant to digestion by mosquito larvae. Larvae are unable to complete their development if indigestible algae are numerous enough in the aquatic habitat to prevent the larvae ingesting enough other food to satisfy their nutritional needs. In addition, cyanobacteria (blue-green algae) can potentially kill larvae by toxins they produce [53].

3.8. Essential fatty acids

Lipids are an important food component for mosquito larvae because they provide a concentrated form of energy storage and a source of essential biochemical nutrients. Fatty acid (FA) constituents of lipids are present in a great structural variety, and are increasingly being used as chemical markers of biogeochemical processes and trophic relationships [147]. While the saturated palmitic acid (16:0) is often one of the most abundant fatty acids in lipid extracts, the interest of nutritional studies has concentrated on polyunsaturated fatty acids (PUFA) with two or more double bonds [148]. Some of these PUFAs are essential to the normal function of cells and they or their corresponding precursors have to be obtained in animal diets. In most animals, the 18-carbon chain, 18C, PUFAs can be converted to the longer-chain essential PUFAs, specifically arachidonic acid, ARA, eicosapentaenoic acid, EPA, and docosahexaenoic acid, DHA. Mosquitoes seem to be an exception because their dietary FA requirements cannot be satisfied by the C-18 PUFAs [149, 150]. They require some 20- and 22-C polyunsaturated fatty acids, EPA, ARA and DHA and without an adequate supply of these PUFAs they are not able to fly [149, 150]. Adult females may get these from a blood meal [151] but these PUFAs are believed essential in the larval stage for flight muscle development. The understanding of the spatial and temporal distribution of dietary resources available to mosquito larvae is needed in order to clarify the relationship among food availability, vector competence, and mosquito fitness. Not only does the nutrient availability within the habitat have to meet a minimum dietary requirement for proper larval development, but the food consumed in the larval stage is critical for a number of physiological processes that impact adult performance [152].

Kominkova et al. [153], in order to reveal the importance of feeding habitats for the nutrition of anopheline larvae, analyzed the FA composition of larvae of three malaria transmitting mosquito

species *An. albimanus*, *An. vestitipennis* and *An. darlingi* and their corresponding habitats. They found that habitats were generally low in essential PUFAs and there were no significant differences among the FA composition of habitat samples. However, there were significant differences in FA composition of larvae. *Anopheles darlingi* contained significantly higher amounts of FA, specifically the linoleic acid. Large differences in PUFA content were found between field collected and laboratory-reared *An. vestitipennis* larvae, however, there were no differences in the total dry weight of the 4th stage larvae between the wild vs. laboratory-reared populations. Total FA in both larvae and samples of habitats of *An. albimanus* and *An. darlingi* were positively correlated with the concentration of particulate organic carbon and nitrogen (POC, PON) in their respective habitats, but no such correlation was found for *An. vestitipennis*. This study revealed that PUFA are a good indicator of nutritional quality although factors controlling the success of anopheline development in larval habitats are likely to be more complex and include, among others, the presence of predators, pathogens and toxins.

3.9. Species interactions (predation and competition)

Understanding species interactions such as competition and predation, across environmental gradients provides insight into how assemblages of mosquitoes are structured. This information is then critical for proper application of biological control [154]. The topic of competition and predation is a good example of the dichotomy in the approach to studying larval stages of mosquitoes. Many papers focus on use of predators for larval control [155-157]. There is a lack of studies focusing on larval competition and predation in the ecological context such as habitat size and temporal stability. But it is what influences the prevalence, pattern, and effects of species interactions across freshwater communities [158-160]. Spatial variation in biotic interactions can explain spatial variation in larval mosquito densities and ultimately the abundance of adult mosquitoes [78, 158]. Studies on predators of mosquito larvae go way back into history. Hinman [161] in his summary of predators on mosquito larvae lists over 100 references. Competition on the other hand is less studied even though interspecific competition for limited resources can be quite important and has been shown to have large effects on mosquito larvae. Mosquitoes compete with tadpoles [162, 163], other species of mosquitoes [164] and cladocerans [165].

Relative impacts of competition and predation change across a gradient of habitat size and permanence [159]. Bodies of water that may serve as larval habitats form a gradient from small and highly ephemeral to large and permanent. At the small, ephemeral end of this gradient, large long-lived predatory organisms (namely fish) are often absent, and aquatic organisms need to develop quickly. These conditions favor rapid growth and development, active foraging, movement, and competitive ability. As water bodies become larger and temporally more stable they can support more diverse community of larger, longer-lived predators. This increase of diversity, number, and voracity of predators favors refuge use, inconspicuousness, predator deterrence, and slow growth and development [159]. Organization of mosquito communities can be viewed in the same way. Interspecific competition among mosquitoes can be more important as a determinant of community structure in small ephemeral habitats, whereas predation can be more important in large permanent habitats [159]. Limited evidence

suggests interspecific competition and cannibalism among mosquitoes is common in small pools [70], but comprehensive review of the ecology of competitive interactions of mosquitoes is lacking.

Natural predators of mosquito larvae are quite diverse and include the tadpole stages of amphibians [166], planktivorous fishes [165] and aquatic insects (Coleoptera, adult Heteroptera and larval Odonata). There is a range of papers reviewing predators on mosquito larvae and their potential use in biological control. Kumar and Hwang [167] provided an excellent review of larvicidal efficiency of amphibian tadpoles, larvivorous fish, cyclopoid copepods and aquatic insects. Mogi [168] reviewed insects and invertebrate predation on different life stages of mosquito. Quiroz-Martinez and Rodriguez-Castro [169] summarized the information on arthropods (insects, mites and spiders) that prey on mosquito larvae and discussed the potential of these predators in mosquitoes' biological control programs. Shaalan and Canyon's [156] review covered the predation of different insect species on mosquito larvae, predator prey-habitat relationships, co-habitation developmental issues, survival and abundance, oviposition avoidance, predatorial capacity and integrated vector control. Rozendaal [170] and Chandra et al [171] reviewed information on different larvivorous fish species and the present status of their use in mosquito control.

Despite thorough reviews and much information on different types of predators, there is a paucity of well-designed experimental studies verifying the long term effect of predators on mosquito populations. Although predation has been suggested as one of the important regulation mechanisms for malaria vectors in long lasting aquatic habitats, the predatory efficiency of potential predators is largely unknown [22, 157]. Research on predation of mosquito larvae has relied partly on the identification of larvae in the predators' gut – serological methods [172, 173], partly on correlative field observations evaluating the abundance of larvae and predators in the habitats [52, 174], and partly on laboratory feeding studies [157]. However, many predators that have been shown to be highly successful in eliminating target prey in the laboratory do not show a similar response in their natural habitats [75, 155]. The most basic question is whether predators have an important impact on mosquito populations in the field in the presence of alternative prey. Collins and Resh [118] listed the ecological factors affecting predation that should be considered when designing predation experiments: 1) dietary preference for mosquitoes, 2) abundance of alternative prey; 3) degree of congruity between habitats of the predator and target mosquito; 4) density of predators within habitat; 5) density of mosquito population; 6) quality of habitat as a refuge from predator. Among examples of well-designed experimental studies on multiple predator impacts we can cite Kumar et al [155] who compared the control potential of three larvivorous predators commonly co-occurring in the wetlands of tropical and subtropical regions, the mosquito fish *Gambusia affinis*, the cyclopoid copepod *Mesocyclops aspericornis*, and naiads of the dragonfly *Zyxomma petiolatum*, against the larvae of *An. stephensi* in the presence of alternative cladoceran prey. The presence of the alternative prey significantly reduced larval consumption by all three predators. Kumar et al [155] also discuss the issues related to using non-native mosquito fish considering its potential negative impacts on native assemblages and its lower selectivity for mosquito larvae.

Mosquito control using fish has focused on a limited number of species, primarily *Gambusia affinis* and *Poecilia reticulata* that have traditionally been used for controlling mosquito larvae [175, 176]. One of the most important concerns when introducing exotic fish for mosquito control is their impact on native species [177] and thus information on the predation role of native species is desirable. Louca et al [175] evaluated the role of larval predation by native fishes in Gambia River and they pointed out that the major impact on larvae was actually exerted by a detritivorous *Tilapia*, which is a prevailing species in the system that feeds on larvae only opportunistically in small aquatic habitats.

Blaustein [134] documented an unefficient control of anopheline larvae in the rice fields in California. He pointed out that contrary to what a good system should be composed of, i.e., a relatively permanent habitat, a specialist control agent and a relatively abundant pest species, the fish-mosquito-rice field system does not have any of these attributes. In addition, mosquito fish may have indirect positive effects on mosquito abundance; they also feed on invertebrates which are either natural predators (see [178]) or potential competitors of mosquito immatures [165]. Thus, this strategy attempts to control a relatively rare prey species with a generalist predator. The underlying mechanisms of predator-prey relationships need to be more clearly defined in order to use this biological control agent more effectively. There is a general need for field experiments on competition, predation, and mutualism, and on their context dependence across species and habitats [159].

Predation at larval stages can have important evolutionary consequences for mosquitoes [179]. For example, the predation of aquatic immature stages has been identified as a major evolutionary force driving habitat segregation and niche partitioning in the malaria mosquito *An. gambiae* in humid savannahs of West Africa [160, 180]. These studies explored behavioral responses to the presence of a predator in wild populations of the M and S molecular forms that typically breed in permanent (e.g., rice field paddies) and temporary (e.g., road ruts) water collections. The experiments showed that the M and S forms modify their behavior in the presence of a natural predator by becoming less active and positioning themselves at the wall of the container. These behavioral modifications suggest that mosquitoes are able to detect a predator's presence, through as yet unknown mechanisms which deserve further investigation.

4. Habitat selection

Habitat selection, defined as a process in which individuals preferentially choose and occupy a nonrandom set of available habitats, is of major importance for interpretation of spatial and temporal distributions of populations [139, 181]. The choice for suitable places for female mosquitoes to lay eggs is a key-factor for the survival of immature stages (eggs and larvae). Oviposition site selection has been recognized as critical both for the survival and population dynamics of mosquitoes. It is influenced by several environmental factors [182], including the salinity and turbidity of the water, the size and degree of permanence of the water body, the amount of sunlight, the presence of emergent/floating vegetation and shade, presence of predators, and distance to human habitation [8, 66]. In general, larvae of anopheline mosquitoes prefer clean rather than polluted water [8, 183], although in urban areas in parts of Africa *An. gambiae* appears to be adapting to new habitats such as rubbish-filled pools, sometimes

containing sewage [182, 184]. Larvae of several Asian species (*An. dirus*, *An. punctulatus*, *An. subpictus*) have been reported from muddy and/or polluted waters [63].

In choosing sites for oviposition, females have to consider multiple—and possibly conflicting—factors to arrive at a site selection strategy that will optimize their reproductive success [185]. As many other oviparous species, mosquitoes also avoid oviposition in habitats with high risk of predation to their larvae [154, 186]. Females perceive these different characteristics of their habitats through a set of various cues both positive and negative. Among positive cues, volatile substances released from larval habitats have been implicated as potential olfactory cues mediating oviposition [54, 126, 139]. Experimental verification of dose response confirmed that low concentrations of volatile materials extracted from species-specific larval habitat materials increased oviposition, while there was a shift to reduced oviposition at high volatile concentrations. Rejmankova et al [139] also confirmed through reciprocal treatment tests that volatile effect was strongly habitat/species-specific.

Different mosquito species may rely on distinct chemical cues to avoid predators [187]. Mosquitoes that can detect aquatic predators often do so by sensing predator-released kairomones [187], see also review in Vonesh and Blaustein [188]. This was confirmed by preferential oviposition of *An. gambiae* in containers with clean water rather than water conditioned with predators (backswimmers, *Notonecta* sp. and tadpoles, *Xenopus* sp.) [72]. The experiment with *Notonecta* was later successfully repeated on other strains of *An. gambiae* by Warburg et al [187].

After oviposition, the main factors determining larval survival are food availability and refuge from predators. Orr and Resh [66] documented microhabitat selection by larvae of *An. freeborni*. They found that larval distribution throughout the habitat (an emergent macrophyte, *Myriophyllum aquaticum*) was not random, but that the larvae tended to congregate in denser patches of macrophytes. Observational data confirmed an active mechanism of selection, i.e., larvae actively choose patches with higher plant densities.

Larval habitats of the main malaria vectors in Belize are associated with three distinctly different aquatic environments: marshes with sparse macrophytes and cyanobacterial mats (*An. albimanus*), tall dense macrophyte marshes (*An. vestitipennis*), and floating detritus assemblages within freshwater rivers (*An. darlingi*). To assess species specific habitat suitability, we conducted mosquito transplant experiments [74]. First instar larvae of *An. albimanus*, *An. vestitipennis* and *An. darlingi* were placed in floating containers in the respective habitats of each species. Response of mosquito species to environmental conditions of its own and transplanted habitats clearly showed that each species was performing best in its own habitat. Survivorship of *An. vestitipennis* and *An. darlingi* in the *An. albimanus* habitat was extremely low or none.

5. Landscape context, remote sensing, GIS

Larval habitats are not located in a vacuum, they are an integral part of a broader landscape and their environmental requirements should be studied in this context. The landscape level

approach gained momentum when technologies such as remote sensing (RS) and GIS became widely used in 1990's [55, 57, 59, 60, 189-191] and it has continued improving with the progress in RS technology (see review in Machault and coauthors [192, 193]. Direct measurements of the Earth's hydrological and biophysical characteristics, its geological features and its climate from space have provided new data layers with spatial and temporal resolutions relevant to landscape-scale habitat characteristics and ecological processes [194, 195]. The landscape, vegetation, and ecosystem attributes derived from the applied remote sensing data contribute significantly to defining habitat characteristics and help discern patterns and gradients that may exist even within seemingly homogeneous environments.

The use of RS may involve various degree of complexity. The simplest case is when larval habitats are large enough to be directly identified within spatial resolution of remote sensors as, e.g., in Wood et al [55] study from irrigated rice in northern and central California. This study [55] provided a model of rice field mosquito population dynamics using spectral and spatial information. Analysis of field data revealed that rice fields with rapid early season vegetation canopy development, located near livestock pastures (i.e. bloodmeal sources), had greater mosquito larval populations than fields with more slowly developing vegetation canopies located further from pastures. Remote sensing reflectance measurements of early season rice canopy development and GIS measurements of distance to livestock pasture were combined to distinguish between high and low mosquito-producing rice fields. These distinctions were made with 90% accuracy nearly two months before anopheline larval populations peaked.

A more complex approach is needed in situations where larval habitats are spatially below the detection limit of RS data. As an example, a hierarchical approach was used to link larval habitat-types with larger land cover units in an integrated RS, GIS and field study in the Pacific coastal plain of Chiapas, Mexico [57]. Using this approach, villages with high *vs.* low risk for malaria transmission were identified and it was demonstrated that remote sensing-based models generated for one area can be used successfully in another, comparable area [59, 60]. Similarly, RS generated maps of larval habitats in Madagascar rice fields and urban areas were used for predictions of adult densities and definitions of areas that may require indoor insecticide spraying [196, 197]. The landscape determinants of anopheline mosquito larval habitats in Kenya highlands and lowlands and their temporal changes were assessed by Mushinzimana et al. [198], Jacob et al [199], Munga et al [200], Mutuku et al [201], from elsewhere in Central and west Africa by Dambach [193] and Clennon et al [202], and from Malaysia by Ahmad et al [203]. The use of RS as a predictive tool to locate larval habitats has not always been successful as demonstrated by Achee et al [204]. Their results indicated that remotely sensed land cover is not a valuable indicator of the location in which *An. darlingi* larval habitats will form. High-resolution satellite imagery could be used to detect homes along river systems and potentially predict general areas at risk for *An. darlingi* breeding habitat formation based on distances from houses to waterways (Figure 3). The basic idea behind the remotely sensed assessment of larval habitats is to define environmental parameters that can be used to identify areas with increased risk of malaria transmission [193]. Yet, as already stated by

Roberts et al [205], the successful use of RS and GIS technologies to predict potential or actual malaria trouble spots is dependent on clear understandings of environmental factors that determine the presence of malaria vectors.

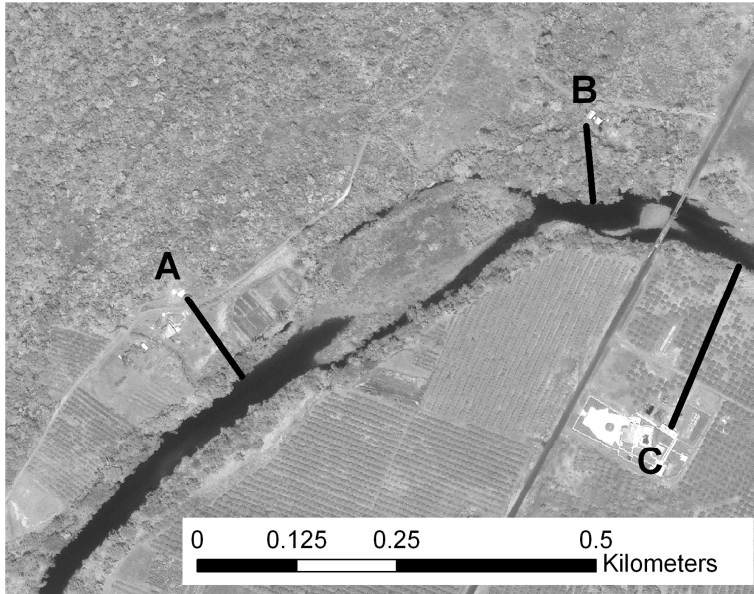


Figure 3. IKONOS 1m-resolution panchromatic image showing three houses (A-C) along a section of the Sibun River. Distance from the river to houses (black lines) was predictive for presence and abundance of *An. darlingi*, the primary malaria vector in Belize.

5.1. Ecological niche models

Populations of mosquito larvae are ideally suited to GIS and remote sensing applications due to their close association with their microenvironment. Specifically, larval mosquitoes have three distinct ecological characteristics that are directly related to predictive risk-modeling: 1) specific habitat preferences, 2) microclimate requirements and 3) vegetation-dependent associations to include plant height and density. Spatial-temporal interactions of mosquito larvae with their natural environment are critical to understanding the risk of contact between the vectors and their human hosts. Due to the fact that mosquitoes spend a substantial portion of their life cycle in the larval stage, population structure and vector survival is greatly influenced by the environmental surroundings. One area that is increasingly being applied to disease ecology which takes advantage of these environmental associations is the use ecological niche models [206]. An ecological niche model is an estimate of the distribution of a species and requires two input data sets: the known locations of a species and environmental data in an image format (such as larval habitats, climate data, elevation data, land cover, etc.). The ecological niche modeling program examines the environmental data at the locations where

the species occurs to infer the environmental requirements of the species across a much larger area. The requirements of the species are then used to create a map of the predicted distribution of the species. Any species affected by environmental conditions such as climate can be modeled including disease vectors, disease hosts and pathogens. Models of monthly predictions of dengue fever in Mexico have been created based on mosquito activity [207]. Niche models of malaria vectors in the *An. gambiae* complex have been developed for under-sampled regions of Africa [208]. The benefit of niche modeling is the development of maps showing predicted distribution of an organism based on current and projected vector ecology and environmental data.

6. Human impact land use/global change

Natural ecosystems throughout the world are being severely altered by human intervention. Population pressure results in transformation of natural ecosystems to agriculture, construction of roads and hydroelectric dams, irrigation projects, open pit mines, and uncontrolled human colonization [209, 210]. Anthropogenic modification of the ecosystems also contributes to global climate change represented by an increase in temperature and accompanied by extremes of the hydrologic cycle (e.g., floods and droughts) [211, 212]. The global rate of tropical deforestation continues with nearly 2% to 3% of global forests lost each year and land use change for agriculture represents the largest driver of land cover change across the earth [85, 209, 213]. Arthropod vectors in general, and insect vectors in particular are very sensitive to their environment, which determines their presence, development and behavior. As a consequence, climatic, as well as landscape and land cover factors greatly influence the spatial distribution of vectors and the diseases they transmit [214].

Mosquitoes are among the most sensitive insects to environmental change; their survival, density, and distribution are dramatically influenced by small changes in environmental conditions, such as temperature, humidity, and the availability of suitable larval habitats [48, 88, 215-219]. All these changes can alter the incidence, seasonality and intensity of transmission, and geographic range of diseases such as malaria. Changes in the distribution of malaria cases and intensities of malaria transmission have been documented by many historical examples. As described by Hackett [220], malaria increased in Malaya as jungle was cleared for rubber plantations. Where forest was removed the sun penetrated and populations of *Anopheles maculatus* mosquitoes proliferated, greatly increasing the incidence of human malaria. The better we are able to assess and explain the distribution and dynamics of vector species in relation to fluctuations in their environments, the more accurate prediction can be made of malaria in the context of ongoing environmental change [221, 222]. This will allow us to evaluate the risks associated with current practices, better explain the patterns of increasing and decreasing disease, better identify measures to mitigate the likelihood and impact of disease emergence, and eventually improve its control [213]. Below are specific examples of changes related to important human activities.

6.1. Deforestation

Deforestation is one of the most important factors driving emerging and re-emerging infectious diseases. Through the process of clearing forests and subsequent agricultural development, deforestation changes almost every attribute of local ecosystems such as microclimate, soil, and aquatic conditions, and most significantly, the ecology of local flora and fauna, including human disease vectors. Numerous country and area studies have described the influence of deforestation and subsequent land use on the density of local mosquito vectors [223]. One of the most thorough evaluations of the impact of deforestation combined with the prediction of future changes has been presented by Yasuoka and Levins [224] who conducted a meta-analysis of 60 published studies of changes in ecology of 31 anopheline species and malaria incidence as a consequence of deforestation. In comprehensive tables they summarized density changes by land cover, and for larval habitats the niche-width and sun-preference indices of each species. The conclusion was that mechanisms linking deforestation and agricultural development with mosquito ecology and malaria epidemiology are extremely complex. The impacts of deforestation on mosquito density and malaria incidence are influenced by both the nature of the agricultural development and the ecological characteristics of the local vector mosquitoes. Some species were directly affected by deforestation, some favored or could adapt to the different environmental conditions, and some invaded and/or replaced other species in the process of development and cultivation. The results of the statistical analyses showed that deforestation and agricultural development are favorable for sun-loving species, allowing them to increase in or invade deforested areas where water bodies become exposed to sunlight.

As a specific example of the complexity of a malaria vector to deforestation we present the case of *An. darlingi* in the Amazon region. Vittor et al [225] examined the larval breeding habitat of a major South American malaria vector, *An. darlingi*, in areas with varying degrees of ecologic alteration in the Peruvian Amazon and concluded that deforestation and associated ecologic alterations are conducive to *An. darlingi* larval presence, and thereby increase malaria risk. According to Barros et al [82], deforestation and human presence creates a new habitat, a forest fringe ecosystem, by promoting three changes in *An. darlingi* bionomics: (i) increasing contact with humans; (ii) increasing the number of microdams (small river obstruction causing the accumulation of debris), which increases the number of potential larval habitats as well as the breeding season; and (iii) reducing the number of shaded breeding sites in a given geographical area, which results in a concentration of larvae in remaining shaded areas. The ideal breeding site occurs in the forest fringe, where the three factors, shade, microdams and human blood meals, are located close to each other.

Environmental changes caused by deforestation often lead to vector replacement (for examples referenced in older papers see Service [136]). Conn et al. [226] conducted entomological surveys in malaria areas of Macapá, northeastern Amazonia, and found *An. marajoara* replacing *An. darlingi* as the primary vector. It is hypothesized that the observed change in mosquito population densities was caused by deforestation for agriculture that resulted in newly created ground pools favoring *An. marajoara* larvae. For many regions in the Amazon Basin, populations of *An. darlingi* have increased because road construction in the forest has considerably expanded the breeding sites—large areas of neutral, partially shaded and unpolluted water.

These characteristics also attract human inhabitants. Subsequently, clearing of forests and water pollution reduce the suitability of these for *An. darlingi* breeding. However, these sites, and newly created ponds for agricultural use, attract other mosquito species such as *An. marajoara*. In addition, humans have colonized land near extensive marshy areas, another preferred breeding habitat of *An. marajoara*.

6.2. Dam construction

Water reservoirs have long been recognized to be a risk factor for malaria transmission [227-231]. Hydroelectric or irrigation dam construction increases the habitat availability by the formation of lakes. Shallow parts of these lakes are typically overgrown with macrophytes that provide excellent breeding sites for anopheline mosquitoes [227]. However, compared to the number of studies on land use change due to deforestation and agricultural expansion, research related to the entomological and ecological determinants of the rising malaria burden in the vicinity of large dams is rather limited [232]. There are historical examples, such as that of Tennessee Valley Authority ([35], see also p. 3) of well executed environmental management measures to control malaria vectors [21, 35]. These successfully executed environmental measures can be adapted to control malaria associated with dam construction in sub-Saharan Africa and elsewhere in malaria endemic regions. Construction of new reservoirs under the tropical, sub-humid climatic conditions should therefore be accompanied by entomologic studies to predict the risk of malaria epidemics [233]. Keiser et al [231] calls for institutionalization of health impact assessments for future water development projects analogous to environmental impact assessments as well as the employment of monitoring and surveillance systems that would facilitate systematic evaluation of the impact of these ecosystem interventions over time. The reality is that more dams will be built and thus mitigation strategies to alleviate potential negative health effects are mandatory to reduce the current burden of malaria in settings near irrigation or dam projects.

6.3. Wetland destruction

Draining wetlands has been extensively practiced and promoted as the easiest solution to localized public health threats posed by malaria vectors [21, 234]. Unfortunately, this practice has not always worked. Among many cases of increasing malaria transmission after destruction of natural wetlands are the examples from African papyrus swamps [64]. As stated already by Goma [32, 235] and confirmed recently by others [72, 88, 236], the interior of a papyrus swamp is unsuitable for anophelines, while the swamp periphery and cultivation of natural swamps provides productive larval habitats for *An. gambiae* and consequently, increase the risks of malaria transmission to the human population. Many natural wetlands have been destroyed and changed to brick-making pits – the most abundant habitat type containing *An. gambiae* larvae in Africa [237].

What has not been taken into account when manipulating wetlands for health benefits is the loss of valuable ecosystem services provided by these wetlands, such as water purification, flood control, or provision of food and fiber, and their contributions to human health. This aspect was emphasized by the 2008 Conference of the Contracting Parties to the Ramsar

Convention on Wetlands, whose resolution stated among others: "Those concerned with wetland conservation and management should encourage new and ongoing research regarding the links between wetlands and human health and to bring information on the scientifically proven contributions that functioning wetland ecosystems make to good health to the attention of national ministries and agencies responsible for health, sanitation, and water supply. The human health sector, and all relevant stakeholders should collaborate in assessing the consequences of wetland management linked with human health, and vice versa the consequences for the ecological character of wetlands of current practices which seek to maintain or improve human health, including the identification of appropriate trade-offs in decision-making."

6.4. Wetland creation and restoration

In addition to rice fields, which are the most extensive human made wetlands and their significance as larval habitat has been already described previously, the use of constructed wetlands for wastewater treatment is expanding [236, 238, 239]. Constructed wetland technology has broad applications for the treatment of many types of wastewaters and provides an ecological approach to mitigate the release of nutrients and toxic materials into the environment [240]. However, design features, maintenance activities and the characteristics of the wastewater undergoing treatment contribute differentially to potential levels of mosquito production and, consequently, to threats to human and animal health from mosquito-borne pathogens. Nutrients (nitrogen and phosphorus), and the configuration and maintenance of emergent vegetation can have strong effects on mosquito production. As loading rates of organic matter and nutrients decline, the diversity of mosquitoes produced by treatment wetlands tends to increase and the relative abundance of *Anopheles* species increases in temperate man-made wetlands [239, 241]. A proper design, e.g. subsurface rather than surface flow or flow-through rather than pond-type wetland [242] can help local mosquito problems. Surface-flow wetlands can also be designed to minimize mosquito breeding by increasing macro-invertebrate predators [243]. Greenway [243] concluded that a marsh with a diversity of macrophytes appears optimal for macro-invertebrate biodiversity and the control of mosquito larvae by predation. The key to mosquito management is to ensure a well-balanced ecosystem supporting a diversity of aquatic organisms [240]. A general conclusion from those areas that contain both treatment wetlands and unimpacted natural wetlands is that adequately designed and appropriately managed treatment wetlands do not pose any greater mosquito threat than the existing natural wetlands [244].

To compensate for a large loss of wetlands in the past, we are now witnessing many projects attempting to restore, rehabilitate, or create various types of wetland habitats. The resulting restored wetland areas provide flood control, improve water quality, and provide habitat for wildlife, especially bird species. However, they create great mosquito habitat and only a few restoration project address this issue properly [234] and there is a need for a better coordination between wetland restoration design and management and mosquito larval management.

6.5. Eutrophication

Freshwaters are among the most extensively and rapidly altered ecosystems on the planet [213]. Increased use of fertilizers in agriculture and destruction of natural buffer zones leads to runoff of excessive nutrients, specifically nitrogen and phosphorus to lakes, rivers and reservoirs [245-250]. Nutrient increase is generally responsible for plant production resulting in potential changes in other trophic levels. Several studies have shown positive correlations between concentrations of inorganic nutrients in surface waters and larval abundance for *Anopheles* [43, 251]. Nutrient enriched waters are easily invaded by aggressive aquatic weeds such as water hyacinth (*Eichhornia crassipes*), which are known to be very productive anopheline habitats [37, 44, 252].

The authors' research in Belize [56, 86] provided data in support of the hypothesis that eutrophication causes changes in freshwater communities. The Central American country of Belize contains large wetland areas that used to be dominated by phosphorus limited sparse macrophyte communities interspersed with floating mats of cyanobacteria – a typical *An. albimanus* habitat (Figure 4).

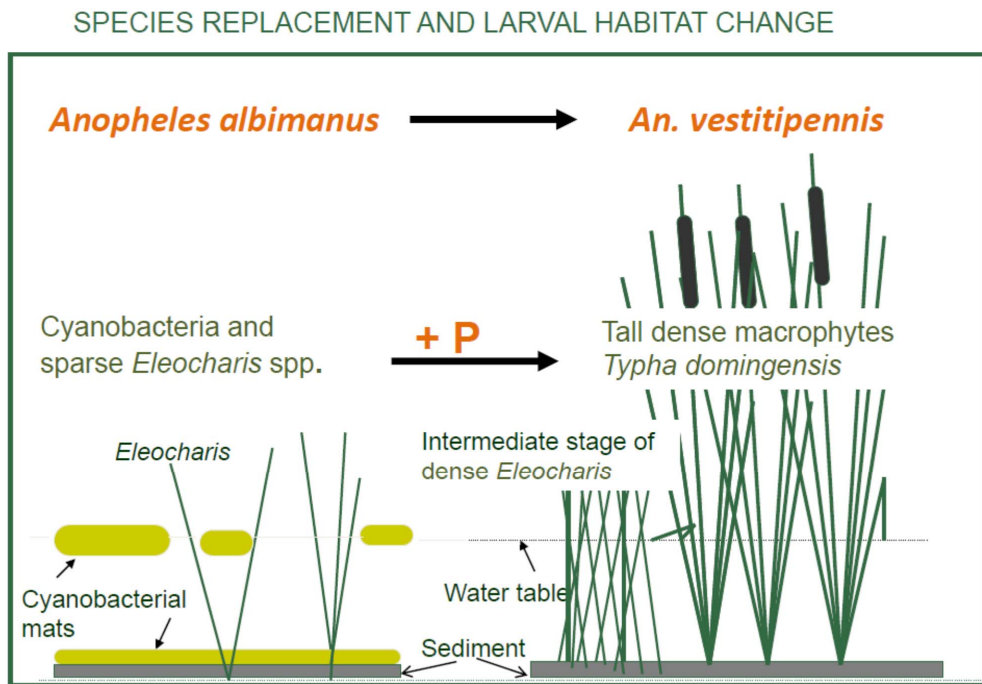


Figure 4. Schematic representation of the change of plant communities in marshes of Belize caused by increased eutrophication by phosphorus. This change is accompanied by the replacement of *An. albimanus* habitat with *An. vestitipennis* habitat.

Anthropogenically mediated P enrichment of wetland plant communities through introduction of fertilizer runoff from expanding sugar cane fields is causing a switch from sparse macrophytes to tall dense macrophytes represented mostly by *Typha domingensis*. Tall dense macrophytes provide favorable habitat for *An. vestitipennis*, which appears to be a more efficient vector of malaria. Thus human-caused nutrient enrichment of marshes may lead to increased risk of malaria transmission in human settlements in proximity to the impacted marshes.

6.6. Temperature and precipitation changes

Malaria transmission is very sensitive to both temperature and precipitation, which makes the issue of change in risk due to past and projected warming trends one of the most important climate change-health questions to follow [253, 254]. Large malaria epidemics in the East African highlands during the mid and late 1990s initiated research on the role that global warming might have on malaria transmission. Historically, these highlands have been used as a shelter against malaria because malaria has been naturally absent due to conditions that limit the biology of the parasite [255]. Several authors proposed that spread of malaria into areas that rarely saw malaria transmission could be related to the impacts of small increases in temperature [253, 256]. The issue became hotly debated [255]. Recently, Chaves et al [257] assessed conclusions from both sides of the argument and found that evidence for the role of climate is robust but they also found a large heterogeneity in malaria trends. They argued that over-emphasizing the importance of climate is misleading for setting a research agenda to understand climate change impacts on emerging malaria patterns. The global change is expected to influence rainfall patterns both seasonal rainfall totals and inter-annual variability in malaria endemic regions, and these events will impact larval habitats availability and thus mosquito population dynamics [258].

6.7. Sea level rise

Along with warming temperatures, any increase in sea levels will affect the extent of saline (>30 ppt) or brackish (0.5-30 ppt) water bodies in coastal areas. These include coastal estuaries, lagoons, marshes and mangroves [106]. An expansion of brackish and saline water bodies in coastal areas, associated with rising sea levels, can increase densities of salinity-tolerant vector mosquitoes and lead to the adaptation of freshwater vectors to breed in brackish and saline waters. Higher vector densities can increase transmission of vector-borne infectious diseases in coastal localities, which can then spread to other areas [106].

The consequences of human-induced ecological changes provide another set of examples. Large-scale shrimp farming in the Mekong delta of Vietnam locally increased the density of *An. sudaicus* [259]. The greater availability of brackish water bodies can also lead to freshwater breeding mosquitoes such as *An. stephensi* and *An. culicifacies* getting adapted to breed in brackish waters as was observed immediately after the 2004 tsunami in India [260] and some years later in eastern Sri Lanka [261].

6.8. Replacability and adaptability

As already indicated by a few examples in the above text, a change in ecology of a region whether due natural factors or human impact can lead to changes in the quality and quantity of larval habitats. This often leads to changes in mosquito population dynamics and species composition [262]. The original anopheline species can be replaced by species better adapted to new conditions or they can adapt themselves. Mosquito species distributed over broad geographic ranges are more likely to have greater habitat diversity than species distributed over a small range [263] and thus their adaptability can be higher. Except for a few examples, our knowledge on the species adaptability is quite limited. But since at least some species are able to adapt to different environmental conditions, an effort needs to be made to obtain data on anopheline population dynamics before, during, and after ecologic alterations. Furthermore, the long-term effectiveness of any control strategy will depend on whether vectors respond to the evolutionary selection pressure created by intervention [22]. For example, mosquitoes may respond by phenotypic plasticity, or by evolving traits such as insecticide resistance or behavioral avoidance.

7. Implication for vector control

Malaria vector control targeting the larval stages of mosquitoes was applied successfully against many species of *Anopheles* in malarious countries until the mid-20th Century [3, 8, 264-266]. Since the introduction of DDT in the 1940s and the associated development of indoor residual spraying (IRS), which usually has a more powerful impact on vectorial capacity than larval control, the focus of malaria prevention programs shifted to the control of adult vectors [8, 267]. However, when it became clear that this strategy is not working (Service 1983), an integrated disease management approach including control of larval stages of malaria vectors, i.e., Integrated Vector Management (IVM) began to be reconsidered [21, 268]. A great step in that direction was made by Keiser et al [264] who provided a systematic review and a meta-analysis of malaria control programs, emphasizing environmental management as their main feature. Most of the 40 studies (85%) were implemented before the Global Malaria Eradication Campaign (1955–69). The authors concluded that malaria control programs that emphasize environmental management are highly effective in reducing malaria. Lessons learned from these past successful programs can guide sound and sustainable malaria control approaches and strategies. The conclusions of Keiser's et al [231] meta-analysis of past control strategies are in agreement with recently developed malaria transmission models showing that substantial reductions of the entomological inoculation rate are possible when an integrated malaria control program with multiple interventions (e.g., environmental management tools) implemented simultaneously is used [269, 270].

The larval source management (LSM) also termed Environmental management that has been successfully used to control mosquitoes in many developed countries (US, Brazil, Canada) is recently becoming an integral component of malaria control methods in Africa [271]. LSM includes: (1) habitat (or environmental) modification, (2) habitat (environmental) manipulation, (3) biological control and (4) larviciding [236, 264, 271]. **Habitat modification** is designed

to prevent, eliminate, or reduce vector habitat and it involves a permanent change of land and water, including landscaping, drainage of surface water, land reclamation and filling but also coverage of large water storage containers, wells and other potential breeding sites. **Habitat manipulation** refers to activities that reduce larval habitats of the vector mosquito through temporary changes to the aquatic environment in which larvae develop. It is a recurrent activity, such as water-level manipulation, which includes measures such as flushing, drain clearance, shading or exposing habitats to the sun depending on the ecology of the local vector. It may include planting water-intensive tree species such as *Eucalyptus robusta* to reduce standing water in marshy areas. The best strategies are those that are adapted to local vector ecology, epidemiology and resources, guided by operational research and subject to routine monitoring and evaluation [22, 272]. Bond's et al [122, 123] studies can serve as an example of habitat manipulation. They report on how manual algal removal from breeding pools along a river in southern Mexico significantly reduced both larval and adult densities of *An. pseudo-punctipennis*. In a follow up study, the abundance of *An. pseudopunctipennis* larvae + pupae was dramatically reduced by this treatment and remained depressed for two to three months. Algal extraction did not reduce the overall abundance of aquatic insects in river pools. **Biological control** of mosquitoes refers to the introduction of natural enemies into aquatic habitats; these are predatory fish or invertebrates, parasites or disease organisms (see the predator section). *Bacillus thuringiensis israelensis* (Bti) and *Bacillus sphaericus* (Bs) are bacterial species reported to be effective against mosquitoes, and have been widely studied and used as biolarvicides [266, 273, 274]. Recently, researchers have focused on the resident microbiota of insect vectors that can potentially impede transmission of human pathogens. These microbes may prove effective agents for manipulating the vector competence of malaria and other important human pathogens [275-278]. Biological control agents should be evaluated with respect to their climatic compatibility and their capability to maintain very close interactions with target populations [155].

8. What next?

Almost every paper that we reviewed for this chapter ends up with the call for more information on larval stages of malaria vectors, in order to enable a better vector control and more accurate predictions of vector response to changing environment. It is (finally!) becoming clear that understanding the ecology and evolution of mosquito vectors needs to complement epidemiology, genetics and molecular biology in solving malaria problems. Several review papers provide good suggestions for future directions in vector ecology research (see, e.g., Table 2 in Chaves and Koenraadt [255] and Box 3 in Ferguson et al [22]). As stated in the preceding text, almost any factor defining a larval habitat can change as a result of direct human modification (deforestation, agricultural practices, eutrophication) and/or indirectly caused environmental change (temperature, precipitation). In addition, new habitats can be created. All these changes can and will impact the basic environmental determinants of larval habitats – food availability, refuge, predator presence. There are indications that some species will be able to adapt, some will be replaced by other species, and some anophelines that have not traditionally been regarded as vectors may become important ones.

In the context of ecosystem change whether due to nutrient, temperature, precipitation, salinity or vegetation changes, there is a strong need for studies on adaptability of different anopheline species to new conditions. The majority of these studies would be best executed as manipulative field or semi-field experiments focused not only on changing characteristics of species performance but also on interactions with other species (both competition and predation). To be able to accomplish these types of experiments, systems of enclosed, pathogen-free, semi-field mesocosms in which vector populations can be experimentally manipulated will have to be established within environmentally realistic, contained semi-field settings. See, e.g., Ng'habi et al [11] semi-field system of large, netting-enclosed mesocosms, in which vectors can fly freely, feed on natural plant and vertebrate host sources, and access realistic resting and oviposition sites. Ideally, systems of these experimental mesocosms should be established along environmental (temperature, precipitation) gradients or with the capability to experimentally manipulate these variables so that we can conduct the experiments focused on species response to changing environments.

In addition, there is an ongoing need for regular monitoring and good quality long-term dataset on species distributions. High resolution satellite data enable more detailed observations on vegetation changes and regional distribution of precipitations and temperature, which all can results and result in better risk prediction maps [193]. In order to include a temporal component to the risk models, a network of longitudinal population monitoring sites for vector development needs to be established. The ecological niche models [206, 279] mentioned above will undoubtedly play increasingly important role in predictions of disease outbreaks.

Acknowledgements

We thank Stephanie Castle for technical help. Parts of the research referred to in the chapter was supported by the NIH-NSF Ecology of Infectious Diseases program, Grant # R01 AI49726, "Environmental Determinants of Malaria in Belize".

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