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From puddles to planet: modeling approaches to vector-borne diseases at varying resolution and scale

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Since the original Ross–Macdonald formulations of vector-borne disease transmission, there has been a broad proliferation of mathematical models of vector-borne disease, but many of these models retain most to all of the simplifying assumptions of the original formulations. Recently, there has been a new expansion of mathematical frameworks that contain explicit representations of the vector life cycle including aquatic stages, multiple vector species, host heterogeneity in biting rate, realistic vector feeding behavior, and spatial heterogeneity. In particular, there are now multiple frameworks for spatially explicit dynamics with movements of vector, host, or both. These frameworks are flexible and powerful, but require additional data to take advantage of these features. For a given question posed, utilizing a range of models with varying complexity and assumptions can provide a deeper understanding of the answers derived from models.

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Introduction

Modeling mosquito transmission of pathogens has a long history starting with the foundational work of Ross [1] and Macdonald [2,3], who established the mathematical formalisms for modeling the transmission of malaria between a vector and a host population [4]. The Ross–Macdonald model identifies five key quantities: mosquito population density, mosquito survival probabilities, mosquito blood feeding frequency, mosquito host preferences, and parasite development in mosquitoes. This basic model was extended first for modeling the Garki project [5] and later in the cyclical feeding models [6,7]. From 1970 through 2010, there was a rapid proliferation of mathematical models of vector-borne disease, but most of these models retained the basic Ross–Macdonald structures and assumptions, as cataloged and analyzed in the comprehensive review by Reiner *et al.* [8••].

As described in that review [8••], several of the simplifying assumptions of the Ross–Macdonald model structure become important to address including well-mixing of vectors and humans, representation of the aquatic stage ecology, spatial dynamics, multiple vector species, and heterogeneous biting rates. Over the past decade, several new model structures have emerged that build off of the foundation built by Ross and Macdonald but extend modeling of vector transmission to new levels of realism. These are described below, and range from improved representation of larval aquatic habitat driving transmission [9,10] to continental-scale maps for the distribution of important vectors [11,12] or parasite and transmission rates [13]. As analyses range in scale from puddle to planet, one of the biggest challenges has been to model transmission at intermediate spatial scales, and this review examines several new model frameworks that have been recently developed to address this challenge.

Elaborations on Ross–Macdonald

Even though Ross and Macdonald developed their models by 1910 and the 1950s, respectively, recent work has continued to elaborate details and implications of theory based on these established model structures [4]. Work by Smith and McKenzie demonstrated that the effect of adult vector mortality may be even greater than that predicted by Macdonald [14]. Recently published work by Brady *et al.* demonstrates the importance of larval populations and the impacts of adult mortality and combined interventions including larval control on both juvenile and adult populations and ongoing transmission [15]. At much broader spatial scales, transmission rates varying by location can be estimated from mapped estimates of parasite rate using Ross–Macdonald theory [13].

Implicit assumptions in standard Ross–Macdonald theory involve details of the vector life cycle including population densities and simple descriptions of adult feeding behavior. Recent mathematical models have relaxed these assumptions and introduced a new level of detail and realism to vector-population simulations. Depinay *et al.* developed a model framework with exceptional realism in the mosquito life cycle, with full representation of aquatic stages and explicit responsiveness to temperature in both larval and adult life stages [9], with potential to add in spatial structure. Bomblies *et al.* went even further with a detailed, spatially explicit hydrology simulation of puddle and pond formation and volume, with explicit effects of temperature, rainfall, humidity, soil, and slope [10]. Another model framework maintained this explicit aquatic stage and detailed feeding behavior, but added in the ability to track multiple species simultaneously, with the potential for each to have separate larval ecology responses to rainfall and feeding preferences [16].

Detailed feeding behaviors such as feeding location and host preference can also be important details of the transmission system, especially in the context of introducing interventions such as insecticide-treated bednets (ITNs). Host-selection in the presence of alternate hosts was described in a model framework built on a cyclical adaptation of Ross–Macdonald theory [17]. The impact of shifts in vector behavior for feeding location, timing, and host preference on interventions was recently explored in even more depth [18•]. Detailed feeding behavior by species in the contexts of multiple species is explored in [16] and this framework was recently used to explore the effect of feeding behavior on the impact of combined interventions [19]. Competition between species in the larval stage is being studied [20], along with the impact of sugar-feeding behavior [21].

Filling in the intermediate spatial scales

Between the scales of the very short spatial-scale aquatic habitats modeled in mechanistic detail [10] and the global patterns of mosquito species habitat [11,12] lie many spatial scales containing important dynamics. Two generalized model concepts that facilitate questions at scales between puddles and the planet are patch models [22] and continuous space models (Figure 1). Patch models function as metapopulations dividing landscapes into smaller subareas, or 'patches.' Hosts and vectors within the same single patch can interact strongly, and connectivity on the landscape is determined by weaker interactions among patches occurring through time spent at risk by hosts, or migration of hosts, vectors, or both [23]. Other frameworks utilize a continuous space in which feeding and oviposition locations are single points. The relationship between continuous space and patch models can be seen in Figure 2.

Successfully extending beyond non-spatial or single-patch dynamics, in which all vectors and hosts in the model are able to interact, to higher-spatial resolution or

Figure 1

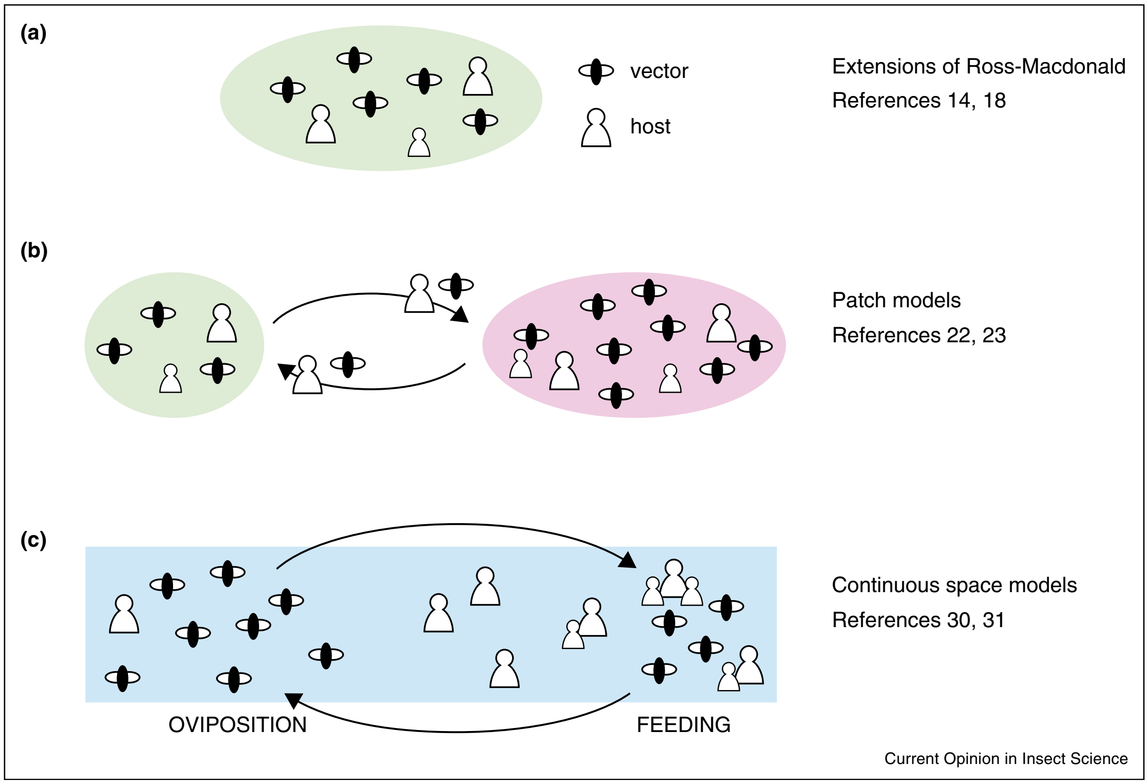

Illustration of single-mixed population extensions of Ross–Macdonald, patch models, and continuous space models.