








Partly cloudy with a chance of mosquitoes: Developing a flexible approach to forecasting mosquito populations

Travis McDevitt-Galles¹  | Arthur T. Degaetano² | Sarah C. Elmendorf³  |
John R. Foster⁴  | Howard S. Ginsberg^{5,6}  | Mevin B. Hooten⁷ |
Shannon LaDeau⁸ | Katherine M. McClure⁹  | Sara Paull¹⁰ |
Erin Posthumus¹¹ | Ilia Rochlin¹²  | Daniel Grear¹ 

¹U.S. Geological Survey, National Wildlife Health Center, Madison, Wisconsin, USA

²Northeast Regional Climate Center, Cornell University, Ithaca, New York, USA

³Institute of Arctic and Alpine Research, University of Colorado Boulder, Boulder, Colorado, USA

⁴Department of Earth and Environment, Boston University, Boston, Massachusetts, USA

⁵U.S. Geological Survey, Eastern Ecological Science Center, Laurel, Maryland, USA

⁶Department of Plant Sciences and Entomology, University of Rhode Island, Kingston, Rhode Island, USA

⁷Department of Statistics and Data Sciences, The University of Texas at Austin, Austin, Texas, USA

⁸Cary Institute of Ecosystem Studies, Millbrook, New York, USA

⁹U.S. Geological Survey, Pacific Island Ecosystems Research Center, Hawaii National Park, Hawaii, USA

¹⁰Battelle, National Ecological Observatory Network, Boulder, Colorado, USA

¹¹USA National Phenology Network, University of Arizona, Tucson, Arizona, USA

¹²Center for Infectious Diseases, Department of Microbiology and Immunology, Stony Brook University, Stony Brook, New York, USA

Correspondence

Travis McDevitt-Galles

Email: tmcdevitt-galles@usgs.gov

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Abstract

Climate-induced shifts in mosquito phenology and population structure have important implications for the health of humans and wildlife. The timing and intensity of mosquito interactions with infected and susceptible hosts are a primary determinant of vector-borne disease dynamics. Like most ectotherms, rates of mosquito development and corresponding phenological patterns are expected to change under shifting climates. However, developing accurate forecasts of mosquito phenology under climate change that can be used to inform management programs remains challenging despite an abundance of available data. As climate change will have variable effects on mosquito demography and phenology across species it is vital that we identify associated traits that may explain the observed variation. Here, we review a suite of modeling approaches that could be applied to generate forecasts of mosquito activity under climate change and evaluate the strengths and weaknesses of the different approaches. We describe four primary life history and physiological traits that can be used to constrain models and demonstrate how this prior

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information can be harnessed to develop a more general understanding of how mosquito activity will shift under changing climates. Combining a trait-based approach with appropriate modeling techniques can allow for the development of actionable, flexible, and multi-scale forecasts of mosquito population dynamics and phenology for diverse stakeholders.

KEYWORDS

climate change, forecasting, macroecology, mosquito, phenology, synthesis

INTRODUCTION

Climate change is affecting biological communities by shifting the average timing and shape of species' seasonal activity patterns (Badeck et al., 2004; Carter et al., 2018; Ibáñez et al., 2010; Parmesan & Yohe, 2003). These changes in the temporal structure of biological activity, also referred to as phenological shifts, can alter biological processes through direct changes in population dynamics via disruption in the temporal or spatial synchrony between species and the resources they interact with (Kudo & Ida, 2013; Walther, 2010). These phenological shifts can have substantial effects on vital ecological processes such as pollination services (Kudo & Ida, 2013), pest control (Damien & Tougeron, 2019), and disease outbreak and spread (Rohr & Cohen, 2020). One ecological system of major concern involves arthropod vectors, in particular mosquitoes that transmit multiple wildlife and human pathogens (Kilpatrick & Randolph, 2012; Mills et al., 2010; U.S. Global Change Research Program, 2018). As small-bodied ectotherms, mosquitoes are expected to be highly sensitive to changing climates (Cohen et al., 2018; Forrest, 2016; Mordecai et al., 2019). Our current understanding regarding the specific effects of changing climate on mosquito phenology and population dynamics is relatively poor (Whittaker et al., 2022). This knowledge gap is concerning because climate-induced shifts in mosquito phenology and population structure can affect disease transmission patterns by altering the timing and intensity of mosquito interactions with infected and susceptible hosts (Iwamura et al., 2020; Rohr & Cohen, 2020) and by shifting the mosquito's ability to transmit pathogens (i.e., alteration in mosquito vectorial capacity; Villena et al., 2022). Thus, predictive understanding of mosquito phenology and population dynamics are critical to effectively adapt management practices to reduce vectorial disease spread to humans and wildlife under future climates (Morissette et al., 2009).

Mosquitoes are a highly diverse and globally distributed taxa, resulting in large spatial gradients in species richness (Foley et al., 2007) and individual species distribution patterns spanning continents and climatic zones

(Liu-Helmersson et al., 2019; Samy et al., 2016). With this broad diversity in taxa and spatial coverage, using both micro- and macroecological perspectives would be beneficial to effectively develop a general framework designed to assess mosquito sensitivities to changing climates (Boser et al., 2021; Chandrasegaran et al., 2020). A microecological approach can provide valuable insight on the mechanistic processes that determine the population and phenological sensitivities to changing climates of a particular species at smaller local scales. This approach, however, may fail to capture the more general responses of the entire mosquito community at local scales or, alternatively, the overall climate sensitivities of a single species across its entire geographical range. We can unify these perspectives by considering modeling approaches that capture mechanistic processes while having the flexibility to scale across species diversity or geographical range. The unification of micro- and macroecological approaches could allow us to simultaneously gain insight on climatic sensitivities of small-scale processes while enabling the detection of general and emergent patterns at macroscales. This flexible approach can provide researchers and managers with an adaptable framework to address concerns regarding climate change and mosquito-borne diseases at the scale of their needs and interests.

In this synthesis, we lay out a concise roadmap for how to expand our understanding of the factors shaping mosquito sensitivity to climate change to generate forecasting capabilities for both demographic processes (i.e., growth rates) and critical elements of mosquito activity (i.e., first, peak, and end dates of seasonal activity). We discuss different modeling approaches and the importance of considering management needs in determining model structure and scale. We also identify primary life history and physiological traits of mosquitoes that are likely to determine interspecific variation in the sensitivity of mosquito species' population dynamics and phenology to environmental change. The trait-based approach can be integrated into mechanistic and phenomenological models of mosquito activity patterns to reduce complexity and improve our ability to scale to a

macroecological theory on how mosquitoes will respond to changing climates. Such information can provide insights into the allocation of limited resources, such as funding or intensified surveillance efforts, for vector control and public health measures (Whittaker et al., 2022).

MOSQUITO PHENOLOGY AND FORECASTING MODELS

A forecast is a type of prediction with the goals of predicting an ecological outcome at future points in time with utility for decision-making (Dietze et al., 2018; Petchey et al., 2015). Other forms of prediction serve explanatory purposes, such as hypothesis testing or constructing models to explain previously observed phenomena. However, our focus is on forecasting, which includes making predictions into inherently unknown system states and covariate values (Yates et al., 2018). Forecasting presents several technical challenges related to modeling approaches, data needs, and sources of uncertainty (addressed in subsequent sections). Before we tackle these challenges, we first need to determine the specific forecast target and relevant spatial and temporal scales for the resultant mosquito forecast. For mosquitoes, changing climate can affect both long-term phenological trends (i.e., shifts in the timing of emergence, senescence, and duration of seasonal activity over decades) and near-term population growth rates (i.e., altering the within-season population abundance patterns). Vector control agencies, public health practitioners, and natural resource managers may each require specific insight into multiple aspects of mosquito responses to changing climates, or on multiple timescales, to respond adequately to emerging threats (Aryaprema et al., 2023; Colón-González et al., 2021). Forecasting models can produce a variety of products including estimates of future adult abundances or near-term, relative growth rates (i.e., days to weeks out) or estimates of trends in desired phenometrics such as first dates or adult seasonal activity duration under varying climate scenarios (years out). However, to some end users it may be of limited value if models only offer insight into a specific aspect of mosquito's population dynamics such as how temperature changes will affect seasonal growth rates but not into relevant phenometrics such as how these changes will affect the specific timing of first flight dates or peaks of abundance.

The specific needs of a given stakeholder should thus guide the structure and scale of the forecast model (Mozelewski & Scheller, 2021; Tulloch et al., 2020) (Figure 1). For example, if a mosquito control agency wishes to know when to switch from larval to adult control practices for a given location, the forecast, ideally,

would estimate a particular phenometric related to this transition period at the relevant scale such as site-specific estimates of first flight date. This forecast will likely utilize models that focus on discrete phenometrics instead of forecasting models that describe seasonal patterns of population growth rates. Phenometric-based forecasting products are widely used to inform decision-making for pest application in forestry and agriculture (Crimmins et al., 2020) to forecast general events such as the start of seasonal green up (Gerst et al., 2021). However, phenometric-focused forecast models may not always be useful for all management agencies. Public health departments may need a weekly forecast of mosquito abundance to project mosquito-borne disease transmission risk, likely needing a process-based population forecast model that projects mosquito populations levels at larger regional scales (i.e., across counties or entire states) for specific time periods (Keyel et al., 2021). Developing forecast models to address the breadth of stakeholder needs across the diversity of species and habitats is thus not a one-size-fits-all type of venture. To aid analytical choice, we discuss the tools researchers have at their disposal regarding developing descriptive models to enhance our understanding of climate change and mosquito dynamics and how to adapt those models to make probabilistic forecasts.

Demography as phenology versus direct modeling of phenometrics

Whether the forecasting goal is to predict a particular demographic parameter, such as population growth rate or a discrete phenometric, such as first, end, or peak dates, it is important to recognize that the core biological processes structuring population dynamics are inherently hierarchical with overarching phenology and specific phenometrics being descriptors of the seasonal population dynamics, which are determined by population vital rates (Iler et al., 2021; Ramula et al., 2015) (Figure 2A). Not all analytical approaches are equally suited to address the demographic and phenological aspects of how mosquitoes will respond to changing climates. One of the most frequently used approaches for evaluating how abiotic factors, like temperature, influence demographic parameters is process-based population modeling. This approach is often viewed as the gold standard when quantifying climate change effects on mosquito populations and developing predictive models at local scales (Drake et al., 2020). Process-based population models integrate mathematical equations that represent a theoretical understanding of population processes (e.g., growth, survival, carrying capacity) and can capture

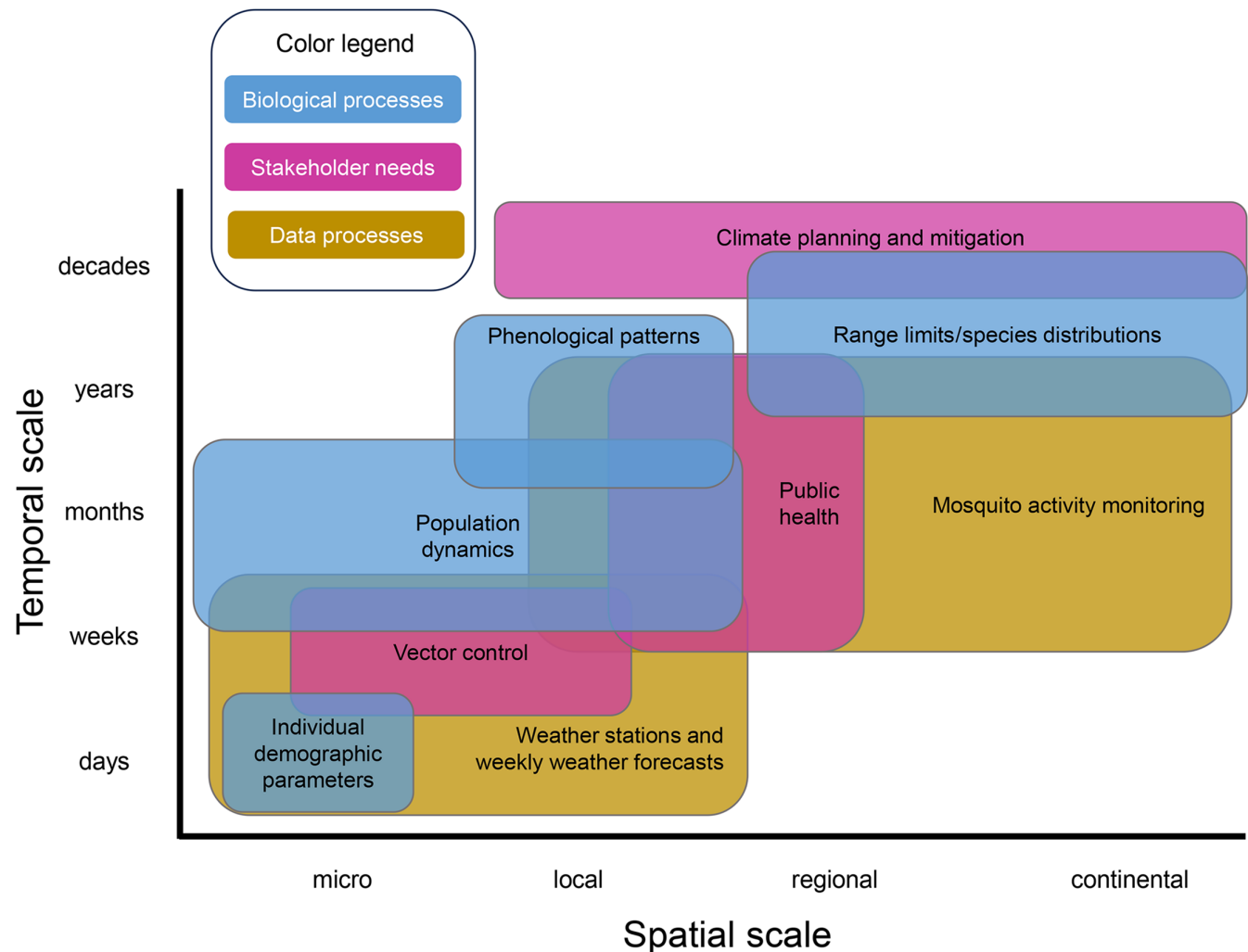


FIGURE 1 Integrating models of the biological processes with data to meet stakeholder needs (magenta area) requires an understanding of the spatial and temporal scales of each process. Our ability to address these needs will determine what biological processes to consider (blue area) and what data (gold area) are available to us. Effectively synchronizing across scales of these distinct aspects of the forecasting problem is important for addressing rising mosquito risk with climate change.

the hierarchical structure and nonlinear patterns of seasonal population dynamics. Parameters in the model equations reflect current understanding of how biotic and abiotic factors shape these population processes. This allows researchers to directly test how different factors such as temperature or precipitation shape demographic parameters (i.e., growth rates or carrying capacity; Figure 2C). For example, Marini et al. (2016) demonstrated that *Culex pipiens* growth rates were largely driven by changes in environmental temperature, whereas carrying capacity was determined by precipitation patterns. One of the biggest strengths of process-based models is that they provide mechanistic insight into the specific factors that influence how and when mosquito populations grow (Briscoe et al., 2022; Munch et al., 2023). An added benefit of this approach is that once fitted, any number of phenometrics, such as

first or last activity dates, can be easily estimated from the fitted population trends (Edwards & Crone, 2021) (Figure 2D,E). However, process-based approaches require large amounts of data, present challenges when estimating numerous parameters (Bolker et al., 2013), and thus often have high computational demand (Xia et al., 2020). For example, a stage-structured demographic model describing insect phenological shifts in response to temperature change required 21 fitted parameters to be estimated from laboratory experiments as inputs to the model (Scranton & Amarasekare, 2017). Mechanistically determining how a diverse group of mosquitoes respond to climate change across space can, accordingly, be challenging and time-consuming. If a primary goal is to rapidly produce probabilistic forecasts, then initially developing simple mechanistic models or utilizing alternative approaches may be more appropriate and effective

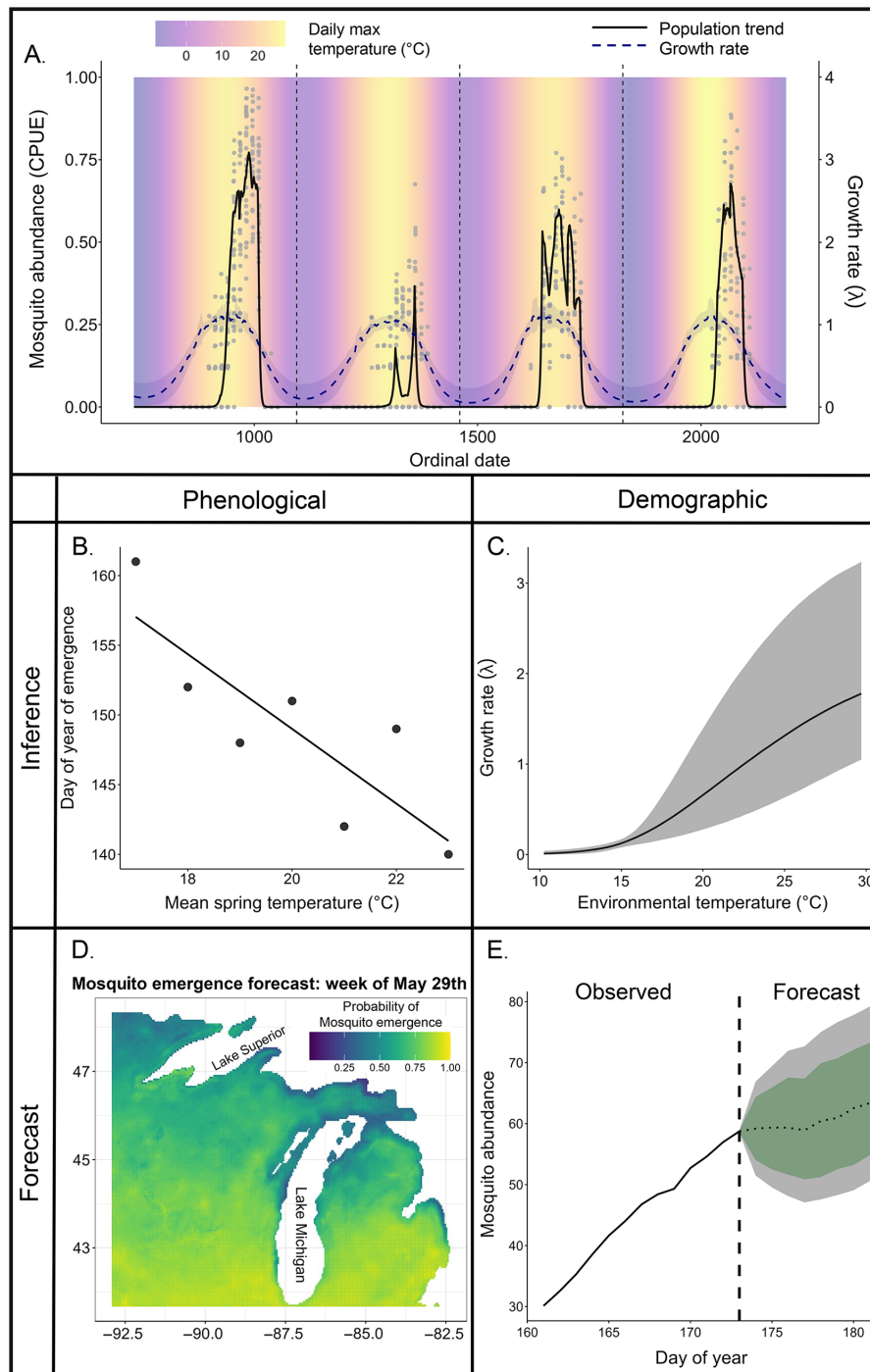


FIGURE 2 Utilizing a hierarchical modeling approach to develop predictive forecasting models can allow us to simultaneously make inferences and forecasts related to both phenological and demographic processes. (A) By developing process-based models on hypothetical mosquito capture per unit effort (CPUE) data (gray circles), we can obtain multiple derived quantities of interest such as seasonal population trends (black line) and latent mosquito growth rates (blue dashed line; the gray area represents uncertainty in latent growth rates [λ]). We can make various inferences from these derived quantities. (B) From a phenological perspective, we can statistically test the relationship between relative temperature and the day of the year of first emergence, a derived quantity from the seasonal population trend. (C) From a demographic perspective, we can assess the relative relationship between the latent growth rate and environmental temperature, an important component of the climate sensitivity of mosquitoes. Building upon these inferences, we can expand to a forecast framework. (D) From a phenological perspective, we estimate the likelihood of emergence based on forecasted weekly temperature. (E) From a demographic perspective, we can estimate future mosquito abundance (dashed line; colored areas represent uncertainty at different confidence levels) based on forecasted temperature and previous mosquito abundance data (solid line).

in assessing the general impact of changing climate across species and locations in a timely manner.

Alternatively, phenological sensitivities to changing climate (i.e., changes in phenometrics such as first and end dates) can be directly estimated by identifying and quantifying the phenometrics of interest utilizing available data (e.g., estimating annual date of first sighting, or peak activity from weekly trap data), and then build statistical models with climate-related covariates to predict annual timing of these events across years phenomenologically (Inouye et al., 2019). This approach can generate predictions that are analogous to the mechanistic approach we described above: forecasts of relevant phenometrics with associated uncertainty while requiring less analytical and computational demand. Although raw data often show bias in terms of observed first or peak events due to inconsistent sampling effort over space and time (Schwob et al., 2023), a range of parametric models (e.g., 2nd-order polynomial regression; quantile regression; Weibull models; Inouye et al., 2019) and non-parametric (e.g., generalized additive models; Stemkovski et al., 2020) have been used to harmonize disparate datasets into unbiased phenometric estimators (Belitz et al., 2020; Youngflesh et al., 2021). Some disadvantages of these phenomenological approaches are that they are descriptive rather than mechanistic and are not as amenable to simultaneously using predictive validation to learn about process components. For example, using the phenomenological approach can demonstrate how changing climates will influence timing of phenometrics only, but cannot determine the specific demographic patterns, such as growth rate, behind the shifts in timing. The lack of mechanistic processes in phenomenological approaches also limits our ability to accurately develop forecasts for novel geographical areas or species (Heilman et al., 2022; Taylor & White, 2020). For addressing mosquito forecasting goals, phenomenological approaches are best utilized for assessing the variation in phenometrics across space and taxa and determining the relative sensitivities of the timing of these metrics to shifts in abiotic factors (Chmura et al., 2019; Inouye et al., 2019; Figure 2A). The efficiency of this approach allows researchers to derive phenometrics from a large combination of locations, species, and years, thus capturing macroecological spatiotemporal-scale processes that are important metrics of populations' response to changing climate (Figure 2D). Although this approach has yet to be utilized widely for mosquitoes, it has been applied in other systems to assess how different taxa's phenologies are responding to changing climates (Hällfors et al., 2021; Youngflesh et al., 2021).

Data availability and structure

Regardless of the modeling approach, one of the primary challenges in any forecast endeavor is determining the volume, quality, and consistency of data needed for model building, fitting, and inference. Ongoing efforts to produce and publish widespread seasonal data on mosquito activity have greatly improved our ability to develop better descriptive and predictive models of seasonal mosquito activity at local and regional scales (Whittaker et al., 2022). Efforts from organizations such as the National Ecological Observatory Network (Hoekman et al., 2016), VectorBase (Giraldo-Calderón et al., 2021), and the extensive, multi-decadal VectorSurv and Iowa Mosquito Surveillance programs (Sucaet et al., 2008) offer researchers the mosquito surveillance data that are needed to address both local and macroscale questions on mosquito sensitivities to changing climates (Lippi et al., 2023). Additional online databases such as VectorByte (<https://www.vectorbyte.org>) and VectorMap (<https://vectormap.si.edu>) provide data on mosquito vectorial traits and blood meal analysis enabling inclusion of disease transmission potential in forecast models. Data collection at these broad scales often comes with limitations that warrant consideration when deciding on modeling approaches. For example, most monitoring programs record only adult mosquito activity, and data on egg and/or larval abundances are often lacking, making the development of a stage-structured demographic model difficult. Furthermore, inconsistencies across data collecting agencies in data format and associated meta-data can introduce additional challenges in being able to link disparate datasets to address macroscale questions (Rund, Braak, et al., 2019; Rund, Moise, et al., 2019). Even with compatible datasets, the sampling protocols vary widely across most publicly available mosquito monitoring programs (Engler et al., 2013; Pernat et al., 2021). Differences include variation in the type of traps used, when traps are set, trap deployment duration, type of baits or lures used, and sampling processing techniques including variation in taxonomical resolution (Pernat et al., 2021). Analytical approaches would need to account for these heterogeneous sampling protocols to produce robust, unbiased parameter estimates and forecasts.

Generating forecasts also presents challenges when utilizing environmental data to make predictions into future states (Dietze et al., 2018; Yates et al., 2018). Environmental data (e.g., temperature, moisture, precipitation) are widely available and are useful covariates for mosquito forecasting, as we discuss in subsequent sections. The temporal and spatial scales of such data sources do not necessarily integrate seamlessly with each

other or with the response data of interest (mosquitoes in our case). The challenge to developing effective predictive models is in synthesizing the relative importance of such factors across scales and developing the corresponding data requirements (Bütikofer et al., 2020). Including temporally varying environmental covariates, such as temperature or precipitation, in forecast models introduces new sources uncertainty (Dietze et al., 2018). Forecast models that project near-term mosquito dynamics will need to include the forecasted changes in the corresponding environmental covariates (i.e., expected changes in weekly temperature), which will have its own projected uncertainties. Reconciling data sources, scales, and covariate uncertainties to meet the technical and decision space needs of an ecological forecast will remain an important and complex issue when building a forecast model. Efforts to standardize the construction, use, and forecasting outputs will foster better understanding and comparison between forecasts (e.g., the Ecological Forecasting Initiative; Dietze et al., 2023). Nonetheless, building a forecast model will always require consideration of complex data issues, much of which is beyond the scope of this synthesis but common to many forecast applications, to best serve accuracy and usefulness (Luo et al., 2011; Petchey et al., 2015; Wander et al., 2024).

Challenges in forecasting uncertainties

Developing forecast models and approaches requires embracing uncertainties. Forecast products that only produce predictions without associated uncertainties are of limited value to most stakeholders and can reduce overall trust if the forecast is perceived to perform poorly. The quantification and representation of uncertainty not only properly reflects our current understanding of the given process of interest, but also helps to identify primary gaps in our knowledge by quantifying the different sources of uncertainty (Lewis et al., 2023). Uncertainty can arise from numerous sources including variation inherent in biological systems (i.e., mechanistic processes), data collection, initial conditions, parameters, and covariate uncertainties (Dietze et al., 2018). Each different analytical approach we have outlined will likely need to handle different sources of uncertainty in distinct ways (Heilman et al., 2022). For mechanistic models, one of the core sources of uncertainty is process uncertainty, because to construct these models we need to clearly define the biological mechanism or process in terms of form and functional shape (Ward et al., 2014). This uncertainty is further expanded when we attempt to utilize a mechanistic-based model to forecast at novel spatial locations, or for additional species because a well-understood

biological process for a species at a given location is not always compatible with a new species or location (Heilman et al., 2022; Taylor & White, 2020). Capturing this type of uncertainty would require careful consideration regarding how we model the mechanistic processes and how likely that process will vary across species and sites. Phenology-focused forecasts using phenomological approaches that rely on derived annual events (phenometrics) ideally would properly handle parameter uncertainty as well as propagate the uncertainties in the estimated derived products in downstream analyses (Zylstra & Zipkin, 2021). Treating the derived phenometrics as known quantities can result in overconfidence in model prediction and inference, reducing the quality and performance of any forecasting products (Youngflesh et al., 2021). Many analytical forecasting approaches will warrant the fusion of multiple data sources to ensure that the empirical data spans both the appropriate time scale and spatial extent (Pau et al., 2011). This fusion of data sources presents the analytical challenge of reconciling variation in measurement procedures and data quality. Incorporating multiple data sources often requires that forecasting models properly account for observation-level variation and uncertainties (Heilman et al., 2022). By accounting for and identifying the sources of uncertainty in our models, we can begin to reduce the uncertainty of mosquito forecasts, resulting in more accurate and precise predictions that can then be communicated properly to relevant resource managers.

REDUCING COMPLEXITY THROUGH A TRAIT-BASED PERSPECTIVE

Trait-based approaches characterize organisms based on their biological attributes such as variation in physiology, morphology, and life history strategies and quantify how those traits interact with environmental gradients to influence fitness and interaction outcomes (Messier et al., 2010) (Figure 3A,B). With over 3500 species worldwide, even taxonomically similar mosquitoes vary greatly in their traits, such as diet breadth, diurnal activity patterns, and habitat specificity (Chandrasegaran et al., 2020; Crans, 2004; Pratt, 1959). Trait-based approaches can help reduce complexity in systems by collapsing species identity into specific trait-based categories that can explain and predict variation in biological performance along environmental gradients, as opposed to taking a species-by-species or population-by-population approach (Crans, 2004). Utilizing a trait-based approach to facilitate forecasting and prediction has been well established

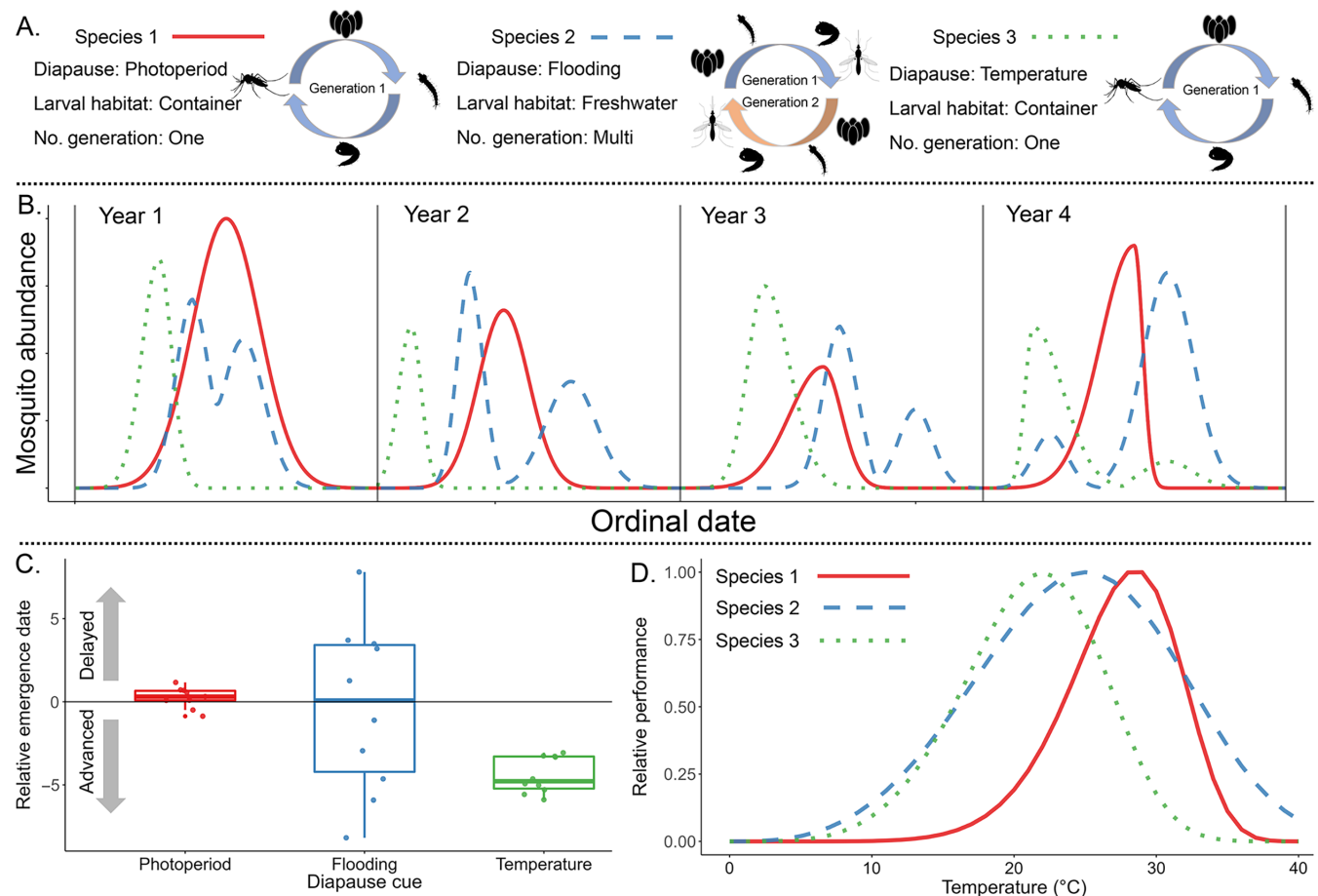


FIGURE 3 Mosquito life history traits can strongly determine the variation in the timing of phenological events and shape seasonal abundance patterns across species. These same traits can be used to predict how species' phenology and seasonal population trends will respond to future climate conditions. (A) Here, we present hypothetical examples of three mosquito species with distinct life histories and physiological traits and their corresponding seasonal population dynamics. Species 1 (red solid line) is an obligate univoltine taxon that relies on photoperiod to trigger exit from diapause and uses small containers as larval habitat. Species 2 (blue dashed line) is an obligate multivoltine taxon that only uses inundation in water as a cue to exit diapause and uses a large breadth of freshwater bodies as larval habitats. Species 3 (green dotted line) is a univoltine taxon that uses temperature as its primary cue to exit diapause, and uses containers as larval habitats. (B) The three species have distinct phenologies and seasonal abundance patterns. Species 3 is an early-season mosquito, typically with a single peak early in the season. Species 2 is more variable in its emergence date and has two peaks during a given year due to its multivoltine life history strategies. Species 1 is consistently a midseason species with a single peak during the middle of the season. (C) The variation in these mosquito taxa's emergence date can largely be attributed to specific abiotic cues used to exit diapause. Species 1 (red) uses only photoperiod to exit diapause, so we would expect little variation or directional shift in its emergence date. Species 2 (blue) uses flooding to exit diapause, and although the unidirectional shift is limited, we might expect high variation in emergence date as precipitation patterns become more variable under future climate scenarios. Species 3 (green) relies on temperature to exit diapause, and with expected general warming, we would expect earlier emergence dates for these taxa. Each point represents a hypothetical annual emergence date relative to a baseline date. (D) By extracting the temperature dependency of each species' relative growth rate, we can further assess when we expect to see relative changes in growth for each species across a season. By combining a trait-based approach with a forecasting framework, we can simultaneously improve our understanding of the mechanisms driving variation in mosquito sensitivities to changing climates while developing an informative predictive model.

in numerous disciplines and has been used at both local and global scales (Green et al., 2022; Webb et al., 2010). Recent efforts have utilized a multi-trait approach to develop a predictive framework to understand how changing temperatures will alter mosquito-borne disease transmission and risk (Ryan et al., 2019;

Shocket et al., 2020). This work compiles numerous temperature-sensitive vectorial capacity traits such as biting rates and mosquito lifespan to generate predictions of transmission rates under future climate scenarios (Mordecai et al., 2019). Similar approaches have yet to be developed to forecast mosquito population

dynamics and phenology under changing climates. Before we can incorporate a trait-based framework into forecast models of mosquito population dynamics and phenology we need to clearly define what are the relevant biological traits. Then, we will be able to synthesize the relationship between these trait values and their effects on mosquito responses to changing climate. Leveraging a focused trait-based approach in conjunction with seasonal trapping data, which are both readily available from public data sources, can improve our ability to develop flexible, multi-scale mosquito forecasts under climate change through increased data coverage and simplified generalized modeling approaches.

In the following sections, we highlight four primary life history and physiological traits that are expected to be sensitive to changing climate, and propose how they are likely to drive changes in vital rates and phenological response to altered climates: (1) Cues used to enter into and exit diapause, (2) thermal performances of demographic rates, (3) larval developmental habitats, and (4) the number of generations per year (voltinism). Although these four characteristics will not fully characterize how life history and physiological variation shape sensitivities to climate change, they capture major axes of variation across mosquito taxa (Crans, 2004). By exploring the variation across these four traits we establish how to best incorporate trait-based generalization into forecasting frameworks to enable generalizable predictions across scales (Figure 3).

Diapause

Diapause is an evolved life history strategy found in many invertebrates to temporarily pause or slow down development due to suboptimal environmental conditions (Ragland et al., 2019). Many mosquito taxa diapause through winter or dry seasons (Denlinger & Armbruster, 2014). These taxa often require specific combinations of abiotic cues to trigger both the entry to and exit from diapause, which can, in turn, determine the mosquito species' relative sensitivities to changing climates. Variation in these abiotic cues can alter the timing of particular phenometrics such as emergence, senescence, and duration of activity (Armbruster, 2016; Peffers et al., 2021). One of the primary abiotic cues used across multiple taxa is photoperiod (Denlinger & Armbruster, 2014). The seasonal variation in photoperiod or daylight is fixed at a given latitude and is thus a reliable cue of the onset of more favorable environments with longer day lengths occurring in the warmer months. Since photoperiod alone cannot fully predict the specific timing of favorable

climates, many taxa utilize or require secondary cues such as hydrological dynamics or the accumulation of warmer ambient temperatures (Armbruster, 2016). For example, numerous taxa in the genus *Aedes* undergo diapause as desiccation-resistant eggs on dried banks and require repeated inundation from water as the primary cue to exit diapause and begin development (Khatchikian et al., 2010; Sota & Mogi, 1992). Thus, for these taxa, water availability is a necessary factor that determines the start of the developmental period. Variation in the timing of inundation due to climatic factors such as drought, snowmelt, and or water release patterns will largely determine the end of diapause. Alterations in these factors can result in shifts in the specific timing of mosquito emergence (i.e., shifting mosquito emergence phenology; Lega et al., 2017). Coupled with inundation in water, seasonal temperature patterns can be a primary or secondary factor in determining the specific time that mosquitoes enter or exit diapause. Mosquito taxa often utilize a combination of different abiotic cues to ensure they do not enter or exit diapause too early or late (Lega et al., 2017). For instance, exiting diapause when inundated with water often requires temperatures to be above a particular threshold to ensure suitable temperature for larval development (Vinogradova, 2007). Temperature can further be a primary trigger to enter diapause if there are prolonged periods of cold days and/or persistently decreasing air temperatures (Mushegian et al., 2021). Because diapause largely controls the timing of emergence and senescence of mosquito taxa, incorporating the specific environmental cue used by mosquito taxa into forecast models, we can begin to predict the likely change in these phenometrics based on estimated shifts in the associated environmental variables (Figure 3C).

Thermal response

As mosquitoes are ectothermic, all species and developmental stages are highly sensitive to the ambient temperature in their environment (Angilletta et al., 2004; Huey & Kingsolver, 2019; Mushegian et al., 2021) through thermally dependent vital rates and thermal thresholds for survival. Mosquito vital rates such as reproduction, development, emergence, and mortality often respond nonlinearly to thermal changes with an optimal temperature range spanning between 25 and 30°C (El Moustaid & Johnson, 2019; Shapiro et al., 2017). Specific mosquito population responses to temperature are thus the result of integrated thermal performance over multiple axes of life history traits each with a potentially unique thermal-dependent response (Mordecai et al., 2019; Sternberg & Thomas, 2014). The specific response to

warmer seasonal temperatures depends on how the changing temperature, including mean and variability, corresponds to the species' particular thermal performance curves (Mordecai et al., 2019). By coupling species-specific thermal performance profiles and location-specific forecasted temperature changes, we can derive forecasts of population dynamics and phenology for various mosquito species under future temperature profiles (Wagner et al., 2023; Figure 3D). Utilizing these biophysical models is a powerful tool in developing mechanistically based forecasts for how species will respond to changing temperatures (Briscoe et al., 2022). However, as stated above, the response of a mosquito species to altered temperatures will be an aggregate of numerous thermally sensitive demographic rates (i.e., egg laying, development, and mortality), making specific predictions regarding population abundance nontrivial. To add further complexities, the magnitude of the daily fluctuation in temperature can have strong effects on mosquito population dynamics (Bernhardt et al., 2018; Lambrechts et al., 2011; Paaijmans et al., 2013) as well as the underlying alteration to the phenological patterns (Scranton & Amarasekare, 2017). Secondary abiotic and biotic factors such as humidity (Brown et al., 2023) and food availability and larval competition (Huxley et al., 2021) can further influence the mosquito thermal response curves. Nevertheless, variation in the relationship between mosquito growth rates and temperature can provide initial insight into which taxa are likely to experience favorable future environments and how thermal changes are likely to affect resulting population dynamics and phenology.

Larval developmental habitat requirements

Developing mosquito larvae require aquatic habitats to complete development and emerge as adults. Mosquito larvae occupy a diverse array of habitats ranging from small containers such as tree holes to lentic and lotic wetlands to coastal marshes (Getachew et al., 2020). Habitat type will influence how changing climate may affect mosquito larval development and survival rates. For instance, mosquito species that rely on ephemeral breeding habitats such as containers or tree holes may be more sensitive to the timing and intensity of precipitation events (Townroe & Callaghan, 2014). Frequent rain events can provide longer developmental and adult activity periods (Lega et al., 2017; Rochlin et al., 2013), whereas infrequent or highly aggregated rain events can limit the temporal availability of larval habitats constricting the adult activity period (Valdez et al., 2017). Mosquito taxa that

rely on larger aquatic habitats with long hydroperiods might be more sensitive to changes in longer-term trends in precipitation, such as longer periods of drought, that may shape both the number and types of available breeding habitats (Wellborn et al., 1996). Alternatively, periods of high water availability can result in ephemeral and semipermanent wetlands habitats, which support a high density of competitors and predators of mosquito larvae such as other Dipteran larvae, zooplankton, additional mosquito species larvae, dragonfly naiads, and predaceous beetles (Chase & Knight, 2003). Competition and predation can reduce survival and alter the development time and abundance of mosquito larvae (Chase & Knight, 2003; DeSiervo et al., 2021). Collectively, these factors can influence mosquito phenology by altering the timing of peak emergence and the relative symmetry of the seasonal population patterns.

Finally, the volume, persistence, and source of water can greatly affect how sensitive mosquitoes are to changing ambient temperature (Afrane et al., 2012; Kweka et al., 2016). For instance, large spring-fed pools in shaded forests may have a less variable thermal profile across the season, whereas, small pockets of water in an urban landscape are likely to experience high temperature fluctuations (Munga et al., 2007). This contrasting thermal regime has consequences for larval development rates such as growth and survival, resulting in differing patterns of emergence and phenology even if the two habitats experience the same seasonal temperature pattern (Munga et al., 2009). Thus, mosquito taxa that utilize smaller breeding sites across diverse environments might be more responsive to warmer temperatures than taxa that inhabit larger aquatic habitats.

Voltinism

Voltinism or the number of generations per year has been identified as an important trait in determining how insect taxa respond to changing climates (Stoeckli et al., 2012; Tobin et al., 2008). Mosquito species and/or populations can either be univoltine (single generation per year) or multivoltine (multiple generations per year). Both types of voltinism can have their own unique associated climate sensitivities. For multivoltine taxa, warmer late-season weather may result in a more successful second generation, resulting in higher overall abundance and a more prolonged seasonal activity period for these taxa (Tobin et al., 2008). Multivoltine taxa can utilize distinct cues to trigger egg hatching for the initial generation (i.e., flooding events or temperature change) and use secondary cues for corresponding additional generations (i.e., photoperiod or temperature), necessitating

conditional approaches to assess abiotic drivers of population dynamics and resulting phenology in these species (Kong et al., 2019). Although some univoltine mosquitoes are obligate single generation taxa, others have a more plastic response and use a combination of temperature and photoperiod to guide diapause and initiation of a potential second generation (Crans, 2004). With overall increases in the length in the growing season it is likely to become more beneficial for plastic univoltine mosquitoes to have a second generation under favorable late season conditions. Shifting from a primarily univoltine to multivoltine population will have important implications for overall mosquito abundance and total duration of seasonal activity patterns for these species. Understanding both the intrinsic and extrinsic factors that drive when and where mosquitoes shift to more multivoltine life history strategies represents an important research avenue that could improve our ability to forecast mosquito population dynamics and phenology under changing climates.

CONCLUSIONS AND FUTURE EXPANSIONS

Over the past century, there has been a massive scientific effort to explore and characterize the abiotic factors shaping mosquito populations. This effort has led to a wealth of knowledge and data (Iwamura et al., 2020; Mordecai et al., 2019; Whittaker et al., 2022). We are currently in the position to improve our forecast accuracy by synthesizing this past work to develop forecasting models that can produce a diversity of predictions ranging from phenological-based estimates, such as first emergence dates, to population dynamic-based predictions of near-term population growth rate. These forecasting advances will be an indispensable tool in combating emerging mosquito-borne disease threats and will provide a better understanding of how climate change is shaping the ecology of vector-borne disease systems. Our road map only captures the beginning steps to building accurate and useful forecasts. As such, we expect the gradual introduction of more complex and intricate ecological and biological processes into forecasting models, improving the accuracy and scope of our forecasting capabilities.

We further suggest that the four life history strategies and the specific traits described herein capture a useful cross-section of the broad variation in how mosquitoes are likely to respond to changing climates. Incorporating these strategies and traits into various modeling approaches may allow for the development of a more general forecasting framework. However, this list is not

exhaustive and other traits may have particular importance for different species, regions, or for other aspects of mosquito biology (i.e., host specificity). For example, if warming temperatures influence phenological shifts of an important disease vector, more information about mosquito blood meal host composition and feeding behavior would be needed to fully assess the effects of the shifting phenology on pathogen transmission. Changes in the vectorial capacity (either through shifts in the experienced temperature profile or shifts in the interaction strength of different hosts) can have implications for disease transmission (Wagner et al., 2023). Thus, trait-based approaches could be a major research avenue to enhance both predictions of under-sampled taxa and predict ecological implications of shifting phenology, particularly for mosquito-borne diseases.

One aspect that we did not fully address in this synthesis is the geographical range expansions of taxa into novel areas with the changing climate (Rochlin et al., 2013; Ryan et al., 2019). Although the approaches described can provide insight into identifying novel geographical areas of suitable habitat, forecasting range expansions requires incorporating additional processes such as rates of spatial spread and factors driving the establishment of a new population (Hill et al., 2011; Leroux et al., 2013). Range expansions and taxa's phenological sensitivities can have critical interactions that can shape the rate of geographical spread and resultant phenology patterns in the novel area (Macgregor et al., 2019; Shuert et al., 2022). For example, taxa that exhibit strong phenological plasticity may be better adapted to track favorable climates, which may result in greater rates of geographic range expansion (Macgregor et al., 2019); however, the generality of this pattern is still debated (refer to Zettlemoyer & Peterson, 2021). Currently few studies have simultaneously assessed how variation in the phenological sensitivities of mosquito taxa can determine the rate of range expansion and how mosquito phenological patterns change when populations colonize novel geographical areas (Bartlow et al., 2019). Understanding these complex spatiotemporal dynamics of mosquito populations, especially at the front of range expansion, would be a highly valuable tool in not only predicting where these taxa are likely to be under future climate scenarios but also forecasting the seasonal patterns of vector-borne risk in novel habitats (Chaine, 2010). Incorporating spatiotemporal dynamics is highly complex both from a conceptual and computational perspective (Eshel, 2011), and is currently an active area of research for numerous large forecasting projects (Hefley et al., 2017; Peng et al., 2020; Williams et al., 2018).

An important assumption behind forecasting models is that the relationship between climate and focal species

response (i.e., phenology or population dynamics) is static in time and does not differ across populations (DeMarche et al., 2019). This assumption ignores the critical role local adaptation and phenotypic plasticity play in both shaping the focal taxa relationship to the climate variable, and perhaps more importantly how these taxa are likely to respond to novel climates (Zettlemoyer & Peterson, 2021). For mosquito taxa, it is likely that local adaptation plays a critical role in how species respond to changing climate (Bennett et al., 2021; Couper et al., 2021), specifically temperature (Sternberg & Thomas, 2014). This variation in local thermal adaptation may result in disparate responses to general warming across populations that span a large latitudinal or elevational gradient, with response to warming temperatures diverging between cool- and warm-adapted populations of the same species (Atkins & Travis, 2010). Furthermore, properly understanding the role local adaptation plays in shaping the response to climate change could be of critical importance in forecasting species that are expanding their geographical range (Dennington et al., 2024). Taxa at the peripheral versus core of the range will likely vary in their adaptation to their local abiotic factors. The inclusion of local adaptation in ecological forecasting models could simultaneously improve our ability to identify climate-sensitive species and populations while producing more accurate forecasts.

Developing accurate forecasts of mosquito population dynamics will fundamentally be an iterative process. Models will constantly need to be evaluated for accuracy in their prediction and modified, as new information and data become readily available. Furthermore, the development of numerous models that vary in scale, form, complexity, and variables used to produce forecasts would be beneficial. The wider the net we cast the more likely we will identify which processes are more important in predicting mosquito abundance and what techniques are best adapted to handling the data that are available. Finally, we argue that with this wide-net approach, researchers can help by ensuring their analyses are as clear and open as possible, allowing for the ability to seamlessly build upon their work. By utilizing the roadmap presented, researchers can meet the challenge of providing resource managers with the tools needed to combat rising threats of shifts in mosquito populations in response to changing climates.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

No data were collected for this study.

ORCID

Travis McDevitt-Galles  <https://orcid.org/0000-0002-4929-5431>

Sarah C. Elmendorf  <https://orcid.org/0000-0003-1085-8521>

John R. Foster  <https://orcid.org/0000-0002-7526-3177>

Howard S. Ginsberg  <https://orcid.org/0000-0002-4933-2466>

Katherine M. McClure  <https://orcid.org/0000-0001-8595-7677>

Ilia Rochlin  <https://orcid.org/0000-0001-7680-6965>

Daniel Gear  <https://orcid.org/0000-0002-5478-1549>

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