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Species distribution models applied to mosquitoes: Use, quality assessment, and recommendations for best practice

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ABSTRACT

Mosquito borne diseases (MBD) are a major global health concern. To aid MBD management efforts, the distribution of mosquito species is frequently investigated through species distribution models (SDMs). However, the quality these SDMs for management use has not been examined. We evaluated 127 publications of mosquito SDMs published between 1998 and 2020 and assessed each against a set of recently-developed, best-practice standards pertaining to quality of the response variable, predictor variables, model building, and model evaluation aspects. Mosquito SDMs were predominantly trained with presence-background response variables (77% of studies), bioclimatic predictor variables (39-63%), maximum entropy algorithm (54%), and evaluated by area under the receiver operating curve (36%) or confusion matrix metrics (34%). Aedes were the best-studied genus (70 studies). Pan-African (20%) and global (16%) distribution studies dominated. All published studies had one or more unacceptable standards within considered aspects, but no aspect observed unacceptable standards in all publications. The highest proportion of unacceptable standards were observed within predictor variables (60%), followed by model building (53%), model evaluation (34%), and response variable (17%). Response variable and model building demonstrated 8% and 0.2% increases in quality over time, but predictor variables and model evaluation exhibited 6% and 2% decreases in quality, respectively. Quality of mosquito SDMs has not changed since introduction of best practice standards. Quality of mosquito SDMs can be improved by ensuring known species temperature and precipitation thresholds are represented within the response variable. Resolution of predictor variables must be justified from ecological knowledge or statistically approximated. SDMs of mosquitoes require improved evaluation against independent data or creation of geographically-structured data. We encourage future mosquito SDM applications to utilize the most recent SDM standards and recommendations to improve applicability.

1. Introduction

Transmission of diseases by mosquitoes is of global health importance. Mosquito-borne diseases (MBD) cause over one million deaths and suffering for hundreds of millions more people annually (Caraballo and King, 2014). MBDs include dengue, zika, yellow fever, and chikungunya vectored by *Aedes aegypti* and *Aedes albopictus,* malaria vectored by *Anopheles spp.* and Japanese encephalitis and West Nile fever by *Culex spp*. (Calvo et al., 2016; Yang et al., 2018). Estimates suggest that half of the world's population will be at risk of MBD by 2050 (Kraemer et al., 2019). Reducing the public health burden of MBD mainly focuses on understanding and determining areas vulnerable to mosquito colonization (Jones et al., 2021). Species distribution models (SDMs) - also known as ecological niche models - have been widely implemented to anticipate disease introduction and spread (Escobar, 2020). SDMs relate the presence, absence, or abundance of a species or disease with environmental conditions to generate hypotheses about a species' potential distribution, thereby improving traditional disease risk maps (Escobar and Craft, 2016).

Despite their popularity, SDMs have been criticized owing to their assumptions, sensitivity to input data, and methodology choices (Araújo and Peterson, 2012; Sofaer et al., 2019). These sensitivities relate to the response variable selected, predictor variables used, model building, or model evaluation considerations (Jarnevich et al., 2015; Araújo et al.,

Abbreviations: MBD, Mosquito-borne diseases; SDM, Species distribution model.

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2019). The response variable is the primary building block of SDMs, defining the geographic, environmental, and temporal conditions in which species are presumed present or absent (i.e. occurrence records) (Guisan and Zimmermann, 2000). Predictor variables considered in SDMs dictate the species-environment relationships considered to explain, predict, or project a species' distribution. Model building details fitting a statistical relationship between the response variable and predictor variables. Model evaluation details the criteria for assessing SDM realism, accuracy, and generality. For example, response variables are often limited to publicly accessible areas, introducing sampling bias (Champan et al., 2019; Jarnevich et al., 2015); . Bystriakova et al. (2012) calibrated SDMs for five fern species with and without accounting for sampling bias. SDMs that did not account for sampling bias poorly estimated species occurrence with broader environmental niches (Bystriakova et al., 2012).

Previous authors sought to address these concerns by providing a step-by-step guide (Sillero et al., 2021), reproducibility methodology checklists (Feng et al., 2019; Zurell et al., 2020), and assessment frameworks (Araújo et al., 2019; Sofaer et al. 2019) for SDMs. Recently there has been an increase in deterring limitations of specific SDM applications (e.g. Silva et al., 2019). However, current research has not identified SDM limitations on public health, epidemiology, or MBD. Given the interest and application of SDMs to mosquitoes, an assessment of constraints and suggested best practices is warranted. The general application and limitations of SDMs concerning epidemiology have been reviewed (Johnson et al., 2019; Escobar, 2020). Response data represented by vector occurrence is preferred over disease occurrence to minimize spatial uncertainty (Johnson et al., 2019). However, lattices often represent vector or disease responses. Lattice responses detail a landscape that has been divided into equal (i.e. UTM grid) or unequal-sized subunits (i.e. geopolitical region; Saveliev et al., 2007).

Interpreting ecological characteristics within a lattice may bias results by failing to sufficiently represent the species-environment response (Moudrý et al., 2019; Cheng et al., 2021). A species' natural dispersal range provides an approximate scale of the species-environment responses (Jackson and Fahrig, 2015). Verdonschot and Besse-Lotoskaya (2014) reviewed mosquito flight literature. They found that 91 mosquito species demonstrated average flight ranges of less than 2 km, except for three *Culiseta* species and *Culex annulirostris*, which could fly 4.5 and 6.2 km, respectively (Verdonschot and Besse--Lotoskaya, 2014). Predictor resolution must match the size of each corresponding lattice cell to limit spatial uncertainty (Vergara et al., 2016). Yet, accounting for the lattices risks additional statistical bias to the model (Openshaw, 1981) unless it reflects ecologically important ecological zones or the interested level of effect (e.g. García-Carrasco et al., 2021). For example, Johnson et al. (2017) applied contiguous United States county latticed responses and environmental averages to predict county-level suitability of *A. aegypti* and *A. albopictus* distributions. Though counties in the United States are vastly more extensive than the natural dispersal range of mosquitoes, the occurrences were appropriately considered within the objective and SDM methodology. Further, use of lattice scales allowed Johnson et al. (2017) to assess the dispersal capacity of *A. aegypti* and *A. albopictus* populations as opposed to individuals. In contrast, Miller et al. (2012) estimated the distribution of Japanese Encephalitis in Asia given administrative district *Culex tritaeniorhynchus* occurrences with 1 km^2 resolution predictors. Their selected resolution more closely reflected the expected species-environment response, but the resulting SDMs did not account for the spatial accuracy of each occurrence. Consequently, the interpreted species-environmental response was calibrated from inaccurate values, limiting model reliability, the results, and the application.

Although mosquito response variables have been investigated, consideration of other SDM aspects of predictor variables, model building, and model evaluation are limited. These aspects have not been examined or reviewed for mosquito SDMs. Instead, methodology decisions rely on more general SDM reviews (e.g. Elith et al., 2006). Recently, Araújo et al. (2019) and Sofaer et al. (2019) proposed assessment frameworks of SDMs' applicability and utility, respectively. Both focused on SDM aspects of response variable, predictor variables, model building, and model evaluation procedures to guide higher-quality SDMs and corresponding applications. However, Araújo et al. (2019) provided a more in-depth assessment framework which evaluated SDMs concerning their objective and use(s); explanation, prediction, or projection. The standards by Araújo et al. (2019) reflect 15 issues across the four SDM aspects per use. Each issue and use was scored regarding quality: gold, silver, bronze, or deficient. Araújo et al. (2019) applied these standards to assess 400 SDM publications between 1995 and 2015 and reported that most aspects of SDMs had improved over time. Arthropods - including mosquitoes - accounted for approximately 5% of studied cases (Araújo et al., 2019). Assessing published mosquito SDMs against these standards allows for an examination of their adherence to these quality standards. It is important to note that an SDM's validity is evaluated for its designed purpose and is not universally valid or invalid (Araújo et al., 2019).

Here, we investigate mosquito SDM quality based on the four SDM aspects identified by Araújo et al. (2019). From our literature review, we sought to i) determine the uses of SDMs applied to mosquitoes; ii) assess areas of MBD concern; iii) assess mosquito SDMs against the four aspects outlined by Araújo et al.'s (2019) standards; iv) assess mosquito SDM quality over time; and v) propose recommendations for best practice. We do not intend to reiterate caveats and guidelines standards across SDM literature but focus on those specific to mosquito applications. We compare our results to Araújo et al. (2019) to identify which issues are particularly problematic to mosquito SDMs.

2. Methods

2.1. Literature review

We searched the literature to identify SDM publications applied to mosquito species published between 1995 and 2020. Specifically, we queried Web of Science (apps.webofknowledge.com), Scopus (www.elsevier.com/solutions/scopus), Pubmed (www.ncbi.nlm.nih.gov/pubmed/), and Scientific Electronic Library Online (www.scielo.org) with the search terms "species distribut*" OR "habitat distribut*" OR "climat* envelope" OR bioclimat* OR "habitat suitab*" OR niche OR "resource selection" OR SDM OR ENM OR BEM OR BCM OR HSM OR RSF AND model* AND vector OR disease (last accessed May 16, 2021). This search returned 4,441 unique publications. We refined the initial publications to focus on only those that applied or investigated SDMs of mosquitoes and omitted mechanistic models or application of MBD rather than species occurrence, resulting in 127 retained publications.

2.2. Assessment of SDM standards

We reviewed the selected publications according to the best-practice standards for models in biodiversity assessments (Araújo et al., 2019). We provide a summary of the standards below, though full details are found in Araújo et al. (2019). The standards consist of four quality levels: gold, silver, bronze, and deficient. Gold represents aspirational methods that usually require ideal data and next-generation modeling approaches which are seldom available and remain under development, respectively. Silver corresponds to cutting-edge techniques, typically involving imperfect but best available data. Bronze standards represent the minimum acceptable practices for SDMs. Finally, deficient standards indicate unacceptable practices to drive policy and practice (Araújo et al., 2019).

SDMs may be applied to investigate a wide range of ecological situations (Aguirre-Gutiérrez et al., 2013; Sillero et al. 2021). We reviewed and evaluated SDMs to determine their use and objectives. For example, prediction of disease prevalence to aid public health initiatives (Dicko et al., 2014), determining areas suitable for species conservation (Regos

et al., 2021), or analyzing invasive species niche conservation (Medley 2010). Therefore, we assessed SDM quality for the general uses of explanation, prediction, and projection for consistency and simplicity. Standards scoring reflected three to five issues per SDM aspect: response variable, predictor variables, model building, and model evaluation (Table 1)

Response variable quality was strongly related to human effort, specifically sampling effort. The sampling effort reflected the depth of survey design to encompass all locations and environmental conditions within the taxon range, identification of taxon, and quantification of spatial accuracy of resulting occurrence records for the study objective (Araújo et al., 2019). Inaccuracies or bias within any part of the sampling effort can potentially limit SDM ability (Anderson, 2012). Though primary field surveys provide more reliable and accurate occurrence records, many rely on records from heterogeneous sources, such as occurrence repositories (i.e. Global Biodiversity Information Facility, www.gbif.org). Response variable quality also considered the depth that studies cleaned heterogeneous data to remove records within justified unreasonable locations, conditions, positional accuracy, and taxonomic identification (Araújo et al., 2019). We characterized the spatial accuracy of responses as assumed or known to represent a precise location (i.e. latitude and longitude from field survey), latticed points, or a combination thereof.

The quality of predictor variables corresponded to the depth that the predictors were identified, acquired, prepared, and selected related to study objectives and species' biology. We assessed the evidence or justification for predictor selection and preparation concerning biological response and spatial and temporal resolution of the response variable (Araújo et al., 2019). Ideally, predictors represent conditions that the response variable is dependent at a relevant spatial and temporal resolution with any uncertainty (i.e. measurement error) quantifiable in the final SDM. Further, SDMs are applied to determine which predictor limit a species' distribution, often referred to as variable importance (Bardie and Leung, 2017). If SDMs identified variables of importance - also referred to as high contributing or demonstrated a significant effect – we recorded the corresponding variables identified as important per species. As variable importance estimates vary by algorithm and assessment method (Smith and Santos, 2020; Harisena et al., 2021), whether a variable was considered important or not was based on the original authors' interpretation. Given the various predictors applied, we grouped similar and less common predictors when considering overall importance. For example, temperature may be represented by minimum, maximum, mean, or median air or land surface temperature per month(s). If less than three publications applied a specific predictor, it was considered an "other" predictor (i.e. other temperature).

Model building quality represents the degree of SDM techniques that addressed issues of model complexity, bias, noise, collinearity, and uncertainty with respect to the study's objective (Araújo et al., 2019). Proper model building consisted of evaluating sequences of all choices, including algorithm, hyper-parameters, and the number of predictors to prevent overfitting and adjust for characteristics of response data. Comparison of all sequences allows for quantification and mapping uncertainty among model building choices. Failure to properly account for bias, noise, or collinearity can cause erroneous results (Dormann et al., 2013; Bailey et al., 2014).

Model evaluation was related to the quality of the methodology used to assess the realism, accuracy, and generality of model outputs per model use for an objective (Araújo et al., 2019). SDMs are expected to approximate ecological reality and should be evaluated against data representative of the response variable's spatial, temporal, and environmental distributions. Model evaluation assessment included considering the depth to which authors assessed theoretical and statistical assumptions of SDMs, the selection of evaluation data, and the meaningful evaluation metrics used. Ideally, SDMs were evaluated against multiple lines of evidence with no assumptions violated (Araújo et al., 2019). Unreliable or inflated results are possible if SDMs violate assumptions or are evaluated against biased data (Guisan and Zimmermann, 2000; Hijmans, 2012).

Reproducibility remains an issue across science (Baker, 2006). The lack of transparent methodology within SDM publications may have inhibited quality assessments. To address this, we evaluated the reproducibility of mosquito SDMs according to Feng et al. (2021) to complement the quality assessment. Feng et al. (2019) outlined a checklist of the minimum information essential for SDM reproducibility. This checklist reflects the framework of Araújo et al. (2019), with nine, four, seven, and 12 necessary information related to the response variable, predictor variables, model building, and model evaluation, respectively (Feng et al., 2019). SDMs were assigned a binary score if the reproducible element was provided or not. Full details on the checklist are available in Feng et al. (2019).

Table 1.
Standards for distribution models in biodiversity assessments from Araújo et al. (2019) and percent of observed quality levels per issue and aspect across 127 publications. Total percentages indicate the percent of each quality level for all issues per aspect. Standards levels of deficient, bronze, silver, and gold represent unacceptable, acceptable, cutting-edge, and aspiration quality, respectively.

Aspect	Code	Issue	Deficient	Bronze	Silver	Gold
1. Response variable	1.A	Sampling of response variables	14	62	22	2
	1.B	Identification of taxa	28	57	13	2
	1.C	Spatial accuracy of response variable	13	37	24	26
	1.D	Environmental extent across which response variable is sampled	20	79	1	0
	1.E	Geographic extent across which response variable is sampled (included occurrence data and absence, pseudo-absence, or background data)	9	46	44	1
	Total		17	56	21	6
2. Predictor variables	2.A	Selection of candidate variables	24	62	12	2
	2.B	Spatial and temporal resolution of predictor variables	76	24	2	0
	2.C	Uncertainty in predictor variables (both under current and projected conditions)	83	14	4	0
	Total		60	33	6	1
3. Model building	3.A	Model complexity	59	20	21	0
	3.B	Treatment of bias and noise in response variables	48	31	21	0
	3.C	Treatment of collinearity	53	45	1	1
	3.D	Dealing with modelling and parameter uncertainty	51	48	1	0
	Total		53	36	11	0
4. Model evaluation	4.A	Evaluation of model assumptions	68	31	1	0
	4.B	Evaluation of model outputs	17	74	5	3
	4.C	Measure of model performance	16	76	8	0
	Total		34	61	5	1
All aspects	Total		38	47	12	3

2.3. Analysis

We assessed the geographic areas investigated per mosquito genus to determine regions of MBD concern. To do this, we considered the country or countries in which each publication applied an SDM. We presented genera at the continent level, excluding global applications. Total publications per country were mapped in ArcGIS 10.8.1 (Environmental Systems Research Institute (Esri) 2018).

We evaluated SDM quality scores concerning 50% and 90% quantile scores per issue. The 50% and 90% quantiles represent the 50% and 90% levels on an ascending list of quality, respectively. We quantified overall performance per aspect (Table 1) by the 'area inside the line' measure, a metric that reaches 100% if all standard issues reach gold for all studies at or above the given quantile (Araújo et al., 2019). Area inside the line was determined for each quantile line per aspect within a polar coordinate system such that area increased with higher quality scores (Fig. 3).

We fitted an ordinal regression with a Bayesian approach to determine the change in mosquito SDM quality over time rstanarm package in R v4.1.1 (Goodrich et al., 2020; R Core Team, 2021). We calibrated the ordinal regression with a warm-up of 1000 iterations followed by four chains with 5000 iterations sampled with an assumed prior distribution between -1000 and 1000. Regression models were fitted against an interaction of year and aspect. Additionally, a similar model fitted with an interaction of year and issue was determined (Table 1). We interpreted the estimates obtained by this analysis as the change in the quality over time.

We determined the presence of temporal trends since the establishment of Araújo et al.'s (2019) standards by comparing quality up to and including 2019 (before, 114 publications) to 2020 onwards (after, 13 publications). We evaluated the independence of scores before and after the release of standards by Fisher's exact test of independence on the expected proportion of each score per issue published before or after SDM standards (Table 2). Expected proportions reflect the average count of each score across all 15 issues per period.

3. Results

3.1. Literature review

A total of 116 species from *Aedes, Anopheles, Culex, Ochlerotatus, Culiseta, Haemagogus,* and *Psorophora* genera were investigated using SDMs. Species of most interest included *A. aegypti, A. albopictus, Culex pipiens, Anopheles gambie,* and *Anopheles aradiensis* were investigated by 44, 36, 19, 15, and 14 publications, respectively (Supplementary material 1: Table S1). Prediction and explanation were the most common uses of SDMs (40% of cases), followed by prediction only (27%) (Fig. 1a). Seventy-four percent of studies used presence-background as the response variable, while a further 4%, 17%, and 6% utilized presence-only, presence-absence, or species abundance data, respectively. Assumed precise locations provided the response variable for 61% of cases, while latticed or a combination of occurrence types were used by 15% and 17%, respectively (Fig. 1b). The response variable was represented by primary field collections for 39% of publications, while 61% relied on information from the literature, occurrence repositories, or multiple sources.

Bioclimatic variables (Supplementary material 1: Table S2) were the most applied predictors (39-63%), followed by elevation (59%) and urban land cover (35%) (Fig. 1c). Slope, elevation, and agricultural land were the most important predictors in 53% or more of SDMs, though findings varied by mosquito species and genus (Supplementary material 2). Most SDMs, 56%, were fit with predictors at a 1 km^2 or finer resolution, followed by 35% with scales between 10 and 1000 km^2 (Supplementary material 1: Fig. S1).

The selected studies examined mosquito distributions with 23 SDM (Fig. 1d). Maximum entropy (MaxEnt) was most popular with 68 publications, while generalized linear models, genetic algorithm for rule-set production, and generalized boosting methods were next and applied by 18, 15, and 11 studies, respectively. Under ten publications applied the remaining 19 algorithms, with 12 algorithms used by a single publication each (Fig. 1d). Model complexity was addressed within 40% of studies, particularly when MaxEnt (50% of cases) or ensemble (55%) were considered.

Previous studies evaluated SDMs using various metrics, though 10% of publications did not provide any evaluation (Fig. 1e). Area under the receiver operating curve and subsampling of training data were applied by 60% and 73% to evaluate SDMs. Subsampled data relied on confusion matrix metrics (i.e. sensitivity, specificity) for 34% of all studies. Random hold-out methods (i.e. random split, cross-validation), independent, re-substitution, and geographically structured data were reported by 79%, 8%, 2%, and 1% of studies, respectively (Fig. 1e).

3.2. Regions of SDM application

Mosquito SDM literature focused on African (20% collectively), global (16%), the contiguous United States (12%), Italy (8%), and China (7%) forecasts. Within Africa, Kenya (12%) and Tanzania (10%) were the most-covered countries (Fig. 2a). The genera investigated varied by continent. *Aedes spp.* were studied extensively in the Americas, Europe, and globally, while *Anopheles spp.* models were confined mainly to African and Asian studies. Oceania had equal representation of *Aedes* and *Anopheles spp.* investigations (Fig. 2a). SDMs investigating *Aedes spp.* have increased rapidly in recent years, while those addressing *Anopheles* and *Culex spp.* remained relatively constant over time (Supplementary material 1: Fig. S2).

3.3. Assessment of SDM standards

All 127 publications observed at least one deficient standard (i.e. unacceptable practice) within a single aspect, but no aspect consistently implemented deficient practices in all publications. Accordingly, SDMs predominantly demonstrated deficient (38% of assessments) or bronze (47%) practices. Only 12% and 3% of SDMs applied silver and gold practices, respectively. Response variable, model building, and predictor variables observed higher proportions of silver or gold practices (Table 1). Specifically, 26% of SDMs applied gold standard spatial accuracy of the response variable, while sampling, taxonomic identification, and geographic extent of the response variable considerations were 22%, 13%, and 44% silver quality, respectively. Within model building, examination of model complexity demonstrated silver quality by 21% of SDMs, and treatment of bias and noise by 21%. The selection of predictor variables improved to silver and gold for 12% and 2% of all SDMs, respectively. Issues related to model evaluation observed silver or gold quality in less than 8% of SDMs.

Overall performance - as defined by the area inside the curve (see methods) - revealed that response variables demonstrated the highest quality, with 16% and 52% of possible scores achieved by 50% and 90% quantiles, respectively (Fig. 3). Both predictor selection and model building were poor overall for 50% quantiles with only 4% area inside

Table 2.
Change in the average count of observed SDM qualities across all issues before and after the publication of best-practice standards in 2019. SDM quality was not dependent on time by Fischer's exact test (p=0.88). Observed quality percentages per issue before and after are available in Supplementary material 1: Table S3.

Quality	Before	After
Deficient	6	4
Bronze	7	9
Silver	2	2
Gold	0	0

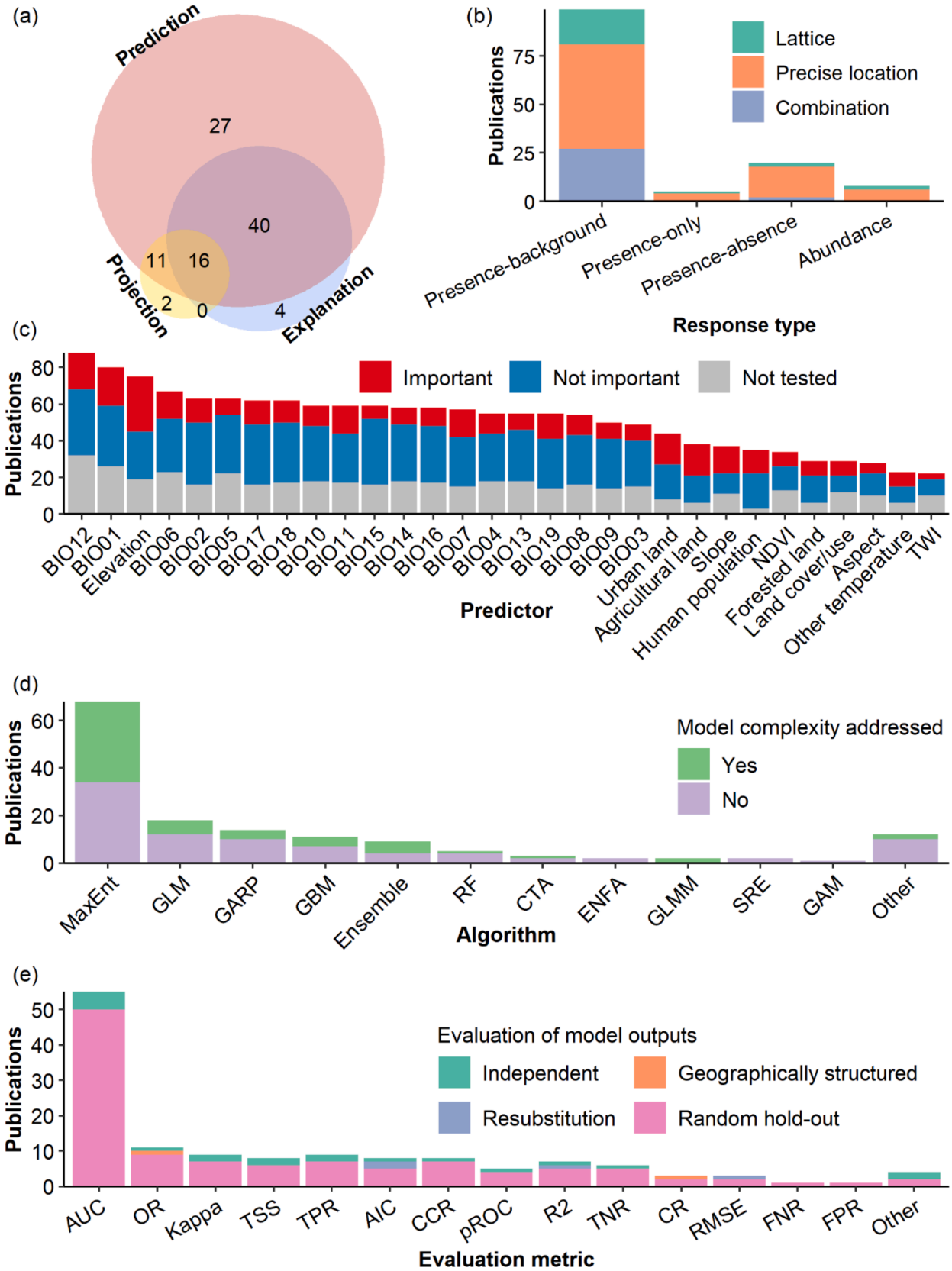

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Fig. 1. Overview of mosquito SDM aspects across the literature. Summary of literature review including the purpose of study (a), response data type and reference of assumed or known precise location (i.e. latitude and longitude from field survey), latticed (i.e. records on a grid), or a combination of both (b), top 30 predictors considered and identified as important (c), algorithm considered with or without consideration of complexity (d), and evaluations considered (e). Numbers in (a) represent the percent of publications that considered each single or combined study purpose. Predictor abbreviations: NDVI= normalized difference vegetation index, TWI = topographical wetness index. SDM algorithm abbreviations; MaxEnt = Maximum entropy, GLM = generalized linear model, GARP = Genetic algorithm for rule-set production, GBM = generalized boosting method, RF = random forest, CTA = classification tree analysis, ENFA = ecological niche factor analysis, GLMM = generalized linear mixed model, SRE = surface range envelope, GAM = general additive model. Other algorithms included Similarity search, alpha-shapes, learning approach for one-class classification, niche of occurrence, proportional, artificial neural networks, support vector machines, MaxLike, multiple adaptive regression splines, and undefined models. Evaluation metric abbreviations: AUC = area under the receiver operating curve, OR = omission rate, TSS = true skill statistic, TPR = true positive rate (sensitivity), AIC = Akaike information criterion, CCR = correct classification rate, pROC = partial area under the receiver operating curve, R2 = correlation, TNR = true negative rate (specificity), CR = commission error, RMSE = root mean square error, AVI = absolute validation index, CVI = contrast validation index, FNR = false-negative rate, FPR = false positive rate. Other evaluation metrics included Bernoulli deviance, error rate, and point biserial correlation.

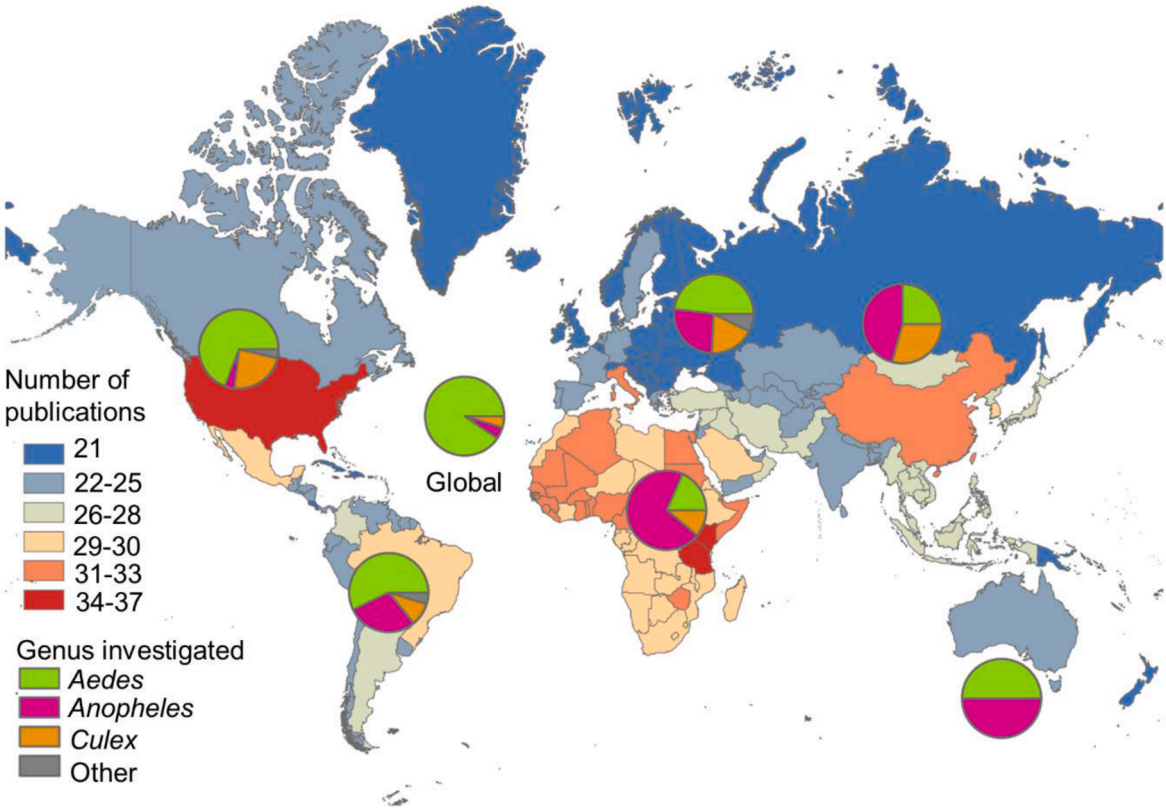

Fig. 2. Spatial publication trends. The number of publications investigating mosquito distribution through SDMs per country and genus representation (proportion) by continent. Publications that considered global distribution are shown by global proportion in the center.

the curve. Yet, at the 90% quantile predictor selection and model building increased to 19% and 29%, respectively. Model evaluation remained relatively similar between 50% and 90% quantiles, with overall scores of 8% and 12%, respectively (Fig. 3).

When examining temporal quality change (via ordinal regression), we observed predominantly yearly quality deterioration (Fig. 4). Notably, procedures of predictor variables indicated a 6% yearly decrease in quality and 2% within model evaluation. Nevertheless, model evaluation indicated higher uncertainty within the 95% confidence interval. In contrast, response variables procedures indicated an 8% yearly quality improvement. Model building showed a low tendency for improvement (0.2%) with high uncertainty.

General trends of SDM aspects were inconsistent across issues, except within predictor variables (Fig. 4). Temporal trends of predictor variables issues were consistently deteriorative but suggested improvement within the 95% confidence interval. The remaining SDM aspects indicated a near 50% split between yearly improvement and deterioration among issues. Response variable sampling and consideration of environmental and geographic extents improved yearly, but taxa identification and spatial accuracy decreased. Model building procedures related to collinearly, model and parameter uncertainty enhanced over time. However, addressing model complexity, bias and noise deteriorated. Lastly, evaluation of model assumptions indicated a yearly increase in quality, but evaluation of model outputs and performance decreased (Fig. 4). All issues revealed wide intervals overlapping zero, indicating high uncertainty. Yet, the quality of mosquito SDMs was independent of the publication of the standards (p=0.88; Table 2).

3.4. Reproducibility

Mosquito SDMs consistently reported the algorithm and source of the response variable (98% of studies each), modeling domain (97%), source of predictor variables (96%), resolution of predictor variables (91%), and temporal range of predictor variables applied for projection (85%) (Fig. 5). Elements with the least consistent reporting included download date or version of predictor variables used for projection (3%), methods to account for spatial autocorrelation (10%), sampling bias (15%), spatial/environmental outliers (17%) in response variables, the threshold of evaluation index (23%), and spatial resolution of predictor variables used for projection (23%). Overall, no paper provided

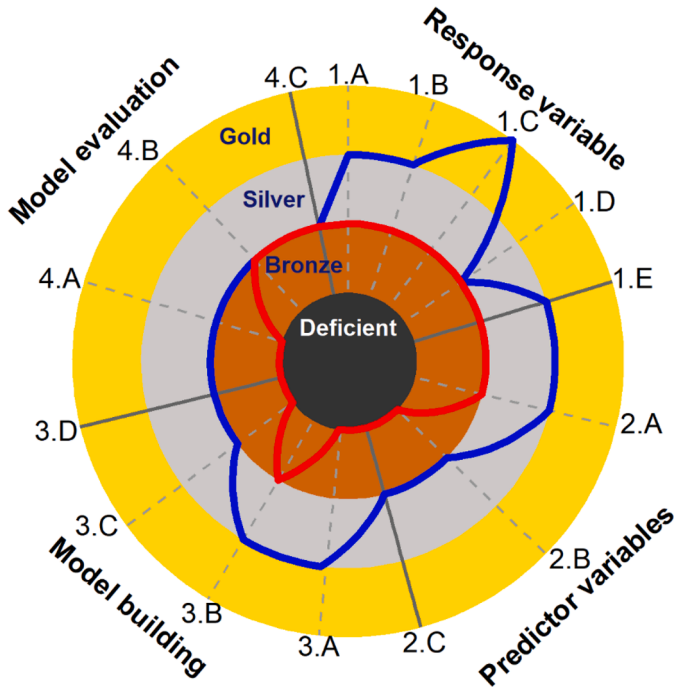

Fig. 3. Best-practice standards achieved by 127 mosquito SDMs publications (1998-2020). Lines indicate 50% (red) and 90% (blue) quantiles scores for each issue. Coloured rings indicate the level of quality: gold, silver, bronze, and deficient, such that the intersection of the quantile line at the outer-most point of the ring indicates quality per issue. The area inside each respective polygon, defined by either quantile line, represents an overall measure of model quality. For definitions of standards, see Araújo et al. (2019). Issue codes are defined in Table 1. Raw standard qualities are available in Table 1.

all or no reproducible methods. SDMs of mosquitoes tended only to report 15 of 33 reproducible elements (45±13%; mean ± standard deviation; Supplementary material 1; Fig. S7). Reporting of reproducibility was particularly limited within elements of the response variable and model evaluation, 39% and 35%, respectively. Predictor variables and model building indicated higher reproducibility with 66% and 60% of elements reported on average, respectively.

4. Discussion

Given the global importance of MBDs, it is essential to develop quality SDMs to aid mosquito and disease management. Most SDMs surveyed here demonstrated unacceptable or minimally acceptable practices, with aspirational or current best practices applied by 12% of studies. Compared to Araujo et al.'s (2019) assessment of SDMs covering all taxa, we found that mosquito SDMs applied lower quality response variable, predictor variables, and model evaluation but better model building considerations (Supplementary material 1: Table S4). We focus on detailing how mosquito SDMs can enhance their quality in the SDM aspects of decreased quality above and highlight how mosquito SDMs achieved higher levels of model building quality relative to Araújo et al. (2019).

4.1. Response variable

Mosquito SDMs indicated a lower quality of environmental extent consideration among the top 90% of SDMs compared to Araújo et al. (2019). We observed that 84% of mosquito SDMs were applied to specific regions, potentially limiting the environmental extent and causing excess generalization. Studies failed to provide evidence of species' environmental tolerance within these areas. Instead, studies calibrated SDMs with the best available mosquito occurrences for the study region (e.g. Dickens et al., 2018). A select few SDMs addressed environmental extent by removing records in unreasonable environmental conditions (e.g. Gomes et al., 2016) or provided a single line of evidence indicating occurrences occur across all major environments within study area (e.g. Fossog et al., 2015). Future studies should design sampling efforts to include all regions within the species' environmental tolerances. However, this is not necessarily feasible owing to accessibility (i.e. private property) and large geographic extents required. Alternatively, Gogol--Prokurat (2011) demonstrated that expanding the environmental extent by considering more predictors to train SDMs of rare plant species improved habitat suitability predictions and field applications. Calibrating SDMs to a greater environmental extent improves model fit

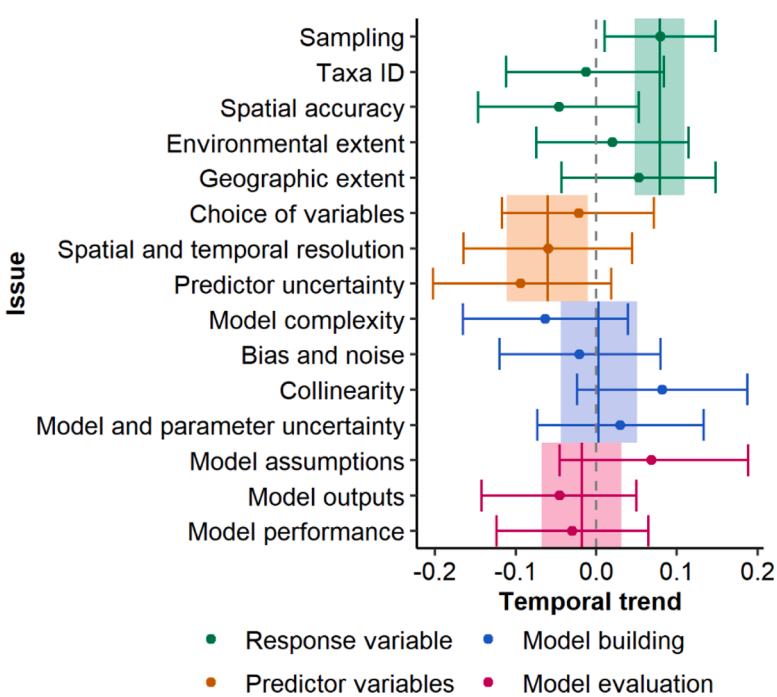

Fig. 4. Temporal trends in best-practice standards from Bayesian ordinal regression across all years. Temporal trends near zero represent no change in standards over time. Solid vertical bars and shading indicate temporal trend (Bayesian coefficient) and 95% confidence intervals of each aspect, respectively. Standard specific temporal trends and 95% confidence intervals of each issue are shown by points and error bars, respectively. Raw proportions over time are shown in Supplementary material 1: Figs. S3-6. The four categories considered herein are identified by different colours, within 15 identified problem areas occur (see Table 1 for the former and Araújo et al. (2019) for the latter).

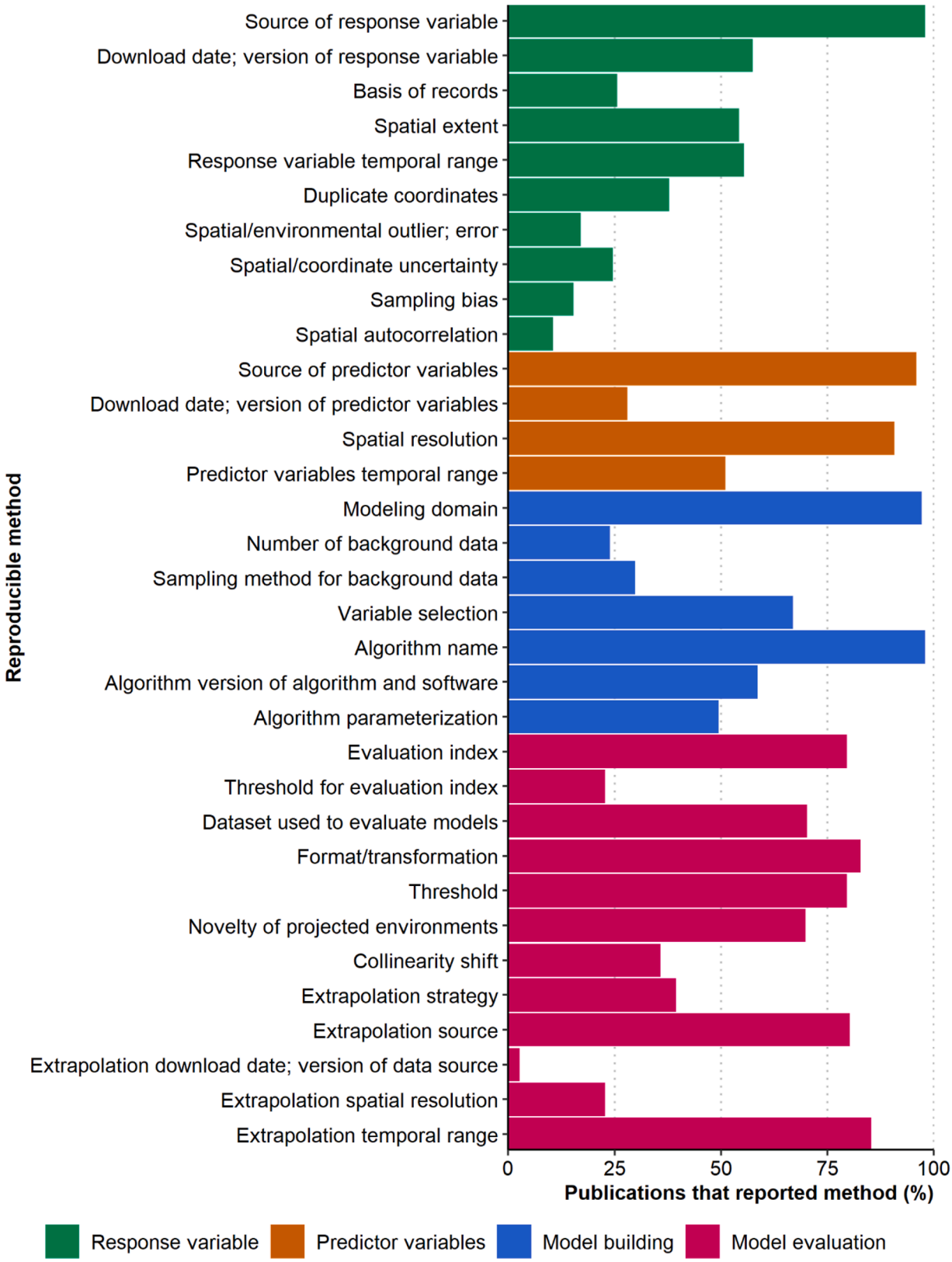

Fig. 5. Assessment of mosquito SDM reproducibility, percent of papers that reported a reproducible element of SDM method with respect to the four aspects of SDM quality. See Feng et al. (2021) for details on reproducible methods of SDMs.

(Thuiller et al., 2004). Additional predictor variables should include a variety of environmental and biotic predictors relevant to the species, geographic extent, and objective (Broennimann and Guisan, 2008; Early and Fox, 2014).

Failure to properly account for environmental extent inhibits SDM applicability for the intended use. Inhibited SDM applicability may cause truncation of response curves and misidentification of important predictors when explaining a distribution. As well as biasing predictions/projections leading to unfounded conclusions and management implications, particularly when projecting into new geographic or temporal ranges (Synes and Osborne, 2011; Harisena et al., 2021). Many mosquito species are considered invasive and demonstrate rapid evolution (i.e. *A. albopictus*) (Egizi et al., 2015). Accordingly, considering the native or invaded distribution alone may not represent the entire niche (Medley, 2010). Specifically, temperature is a fundamental driver of MBD and mosquito life cycle, followed by precipitation or water availability (depending on species) (Wegbreit and Reisen, 2000; Shragai et al., 2017; Mordecai et al., 2019; Franklinos et al., 2019). Therefore, as a minimum, temperature thresholds must be satisfied within the environmental extent and followed by precipitation. When spatially and temporally explicit records are unavailable to demonstrate total environmental tolerance as described by physiological studies of a single predictor, the corresponding predictor should not be applied in model building and the effects discussed (Thuiller et al., 2004).

Those wishing to investigate mosquito distributions are encouraged to consider multiple lines of evidence to infer environmental extent, such as historical and current distributions. For example, Metcalf et al. (2014) combined responses from spatial-temporal fossil data, ancient DNA, and palaeoclimatological reconstructions for the American bison, *Bison bison*, to determine the entire environmental extent. Mosquito response variables are available from literature and museum records as early as 1947 to account for the historical environmental extents of some species (Peach and Matthews, 2020). Alternatively, SDMs considered over large geographic areas, or more predictor variables may capture the environmental extent without including additional records. Nevertheless, future studies must provide evidence of environmental tolerance from global, historical ranges, or physiological studies (Kearney et al., 2009; Varela et al., 2009; Barbet-Massin et al., 2010).

4.2. Predictor variables

Overall performance of predictor variables applied to mosquitoes indicated the most significant deficiency compared to all taxa assessments (Araújo et al., 2019). Though the selection of predictor variables and uncertainty quality were consistent with that identified by Araújo et al. (2019), resolution demonstrated lower quality within both quantiles. Predictors' spatial and temporal resolution must reflect that of the response variable to determine accurate species-environment relationships (Thuiller et al., 2004; Barbet-Massin et al., 2010). The spatial resolution was theoretically justified given response variable sampling design (e.g. Tran et al., 2013) or by a known or estimated spatial error in the response variable (e.g. Johnson et al., 2017). Though more often, predictor resolution depended on the resolutions available for selected predictors. For example, we observed a considerable reliance on pre-calculated bioclimatic variables at 1 km^2 resolution without justification (Supplementary material 1: Fig. S1).

If possible, future applications should estimate an appropriate spatial resolution relative to the ecological, biogeographical knowledge, and study objective. The resolution at which a species interacts with any potential predictor is mainly unknown and limited by the spatial accuracy of the response variable (Hirzel et al., 2001; de Knegt et al., 2010). Previous authors have suggested estimating the resolution through dispersal, home, or perceptual range, body size, or reproduction period (Tyre et al., 2001; Mech and Zollner, 2002; Jackson and Fahrig, 2015). On the other hand, one can statistically approximate the appropriate resolution with sensitivity analysis. Sensitivity analysis involves determining the resolution which observes a high correlation with the response variable, therefore approximating the resolution at which a species responses to the predictor (e.g. Lechner et al., 2012). Additionally, species interact with the environment at different levels, such that relationships identified at one resolution are not necessarily observable at others (Lechner et al., 2012). Therefore, species-environment relationships must be measured at the appropriate resolution per predictor, which requires the consideration of multi-resolution SDMs (Levin, 1992). Previous work has highlighted multi-resolutions enhance understanding of the species-environmental relationship and provided guidelines (Václavík et al., 2012). Researchers may consider multi-resolution SDMs to allow species-environment responses to be evaluated at an appropriate resolution if sufficient response variable accuracy exists.

The consideration of lattice responses further complicated predictor resolution. Lattices are assumed to represent the characteristics of the environment across the geographic ranges they represent (Saveliev et al., 2007). Accordingly, lattices allow for powerful investigations of species distributions if in line with the modeling objective (Openshaw, 1981). However, SDMs must be calibrated with predictors that reflect the size of the lattice. Otherwise, the interpreted values misrepresent the environmental conditions (Moudrý et al., 2019). Lattices with equal-sized grids are more reliable for interpretation than unequal sized grids (i.e. administrative regions) (Saveliev et al., 2007). Unequal or irregular lattices increase statistical bias where environmental correlations can vary from positive to negative depending on the aggregation scale, potentially rendering the results inapplicable (Cheng et al., 2021). Applying lattice response and predictor variables to mosquitoes requires caution and should be used if in line with the objective and predictors are aggregated to lattice size. One may integrate more accurate occurrence sets to limit potential statistical bias. Pacifici et al. (2019) provided a framework for incorporating misaligned occurrences sets at varying spatial accuracy. Many states have widely available mosquito occurrence records within the contiguous United States, but others are latticed to county centroids. Therefore, considering all available data, one can create separate SDMs for each response variable set accuracy with appropriate resolution predictors and ensemble appropriately.

Predictor resolution should support the study objective. Many studies sought to aid fine scale targeted species management initiatives, therefore appropriately applied a 1 km^2 resolution or finer resolution (Landau and van Leeuwen 2012; Attaway et al., 2014). However, considering coarser resolutions is appropriate to approximate the probability of occurrence across a large geographic extent (Kraemer et al., 2015) or across a lattice to explore a specific phenomenon or explore the administrative level probability of occurrence (Johnson et al., 2017; García-Carrasco et al., 2021). Projection of habitat suitability into the past or future is greatly limited by available resolution (Koch et al. 2016), therefore a coarse resolution may be applied and interpreted accordingly. Here, most studies focused on determining the fine-scale habitat suitability or probability of vector occurrence. Therefore, most studies required fine resolutions to satisfy the species' biology and objectives. Though many authors did apply a 1 km^2 resolution, this is not true of all SDM applications (Supplementary material 1: Fig. S1). Therefore, future efforts require greater attention to predictor resolution with justification for predictor resolution.

Similarly, the temporal resolution must reflect the time of the response variable and objective. The reliance on pre-calculated bioclimatic variables limited the temporal resolution to 1970-2000 (Fick and Hijmans 2017), though many authors considered responses and objectives outside this period (e.g. Hesami et al., 2019). A mismatch between or within response, objective, and predictor temporal resolutions results in mis-specified environmental conditions and biased results (Fernandez et al., 2017). When the temporal resolution of the response variable is known, predictor temporal resolution should reflect it exactly (e.g. Arboleda et al., 2012) or with the next closest applicable temporal period of effect available (e.g. Alaniz et al., 2017). Future studies may

consider lagged temporal predictors when there is a lag effect between the predictor and response by the impact it triggers in the ecosystem, including carry-on effects exhibited by different mosquito species (Lebl et al., 2013; Roux et al., 2015; Giraud et al., 2022). Though lag predictors have not been evaluated in mosquito SDMs. Evans et al. (2022) reviewed SDMs of euphausiids and indicated considering lag nutrient and chlorophyll levels, large-scale climate events (i.e. El Niño), wind, and up-welling improved a proportion of model accuracies. Future studies should calculate temporally correct predictors from raw values and test lag values when available. Notably, WorldClim provides raw historical monthly climatic data from 1960 to 2018, such that the corresponding bioclimatic variables can be calculated for the appropriate time by open-source functions to better match responses and objectives (Fick and Hijmans 2017).

4.3. Model building

Mosquito SDMs demonstrated higher overall performance within model building than Araújo et al. (2019), though not consistently across issues. The higher quality observed can be attributed to the 90% quantile in model complexity and treatment of bias and noise in the response variable. Possible explanations for this include more recent publications and smaller sample size, allowing for improved model building considerations to be more prevalent. Regardless, mosquito SDMs provide modern examples of addressing and accounting for complexity and bias. Model complexity is related to the number of predictors applied and fine-tuning of hyper-parameters (Merow et al., 2014). The number of predictors used was considered by assessing collinearity and removing low-importance predictors through iterative selection (e.g. Johnson et al., 2017). This process allows inclusion only of predictors that exhibit a robust statistical relationship with the response variable (Dormann et al., 2013). However, considering all correlated factors allows for biased or erroneous estimates (i.e. inflated or obscured) to be identified (Aragón et al. 2010; Real et al., 2013). Iterative removal of lowest important predictor helps to piece out biased or erroneous estimates (Zeng et al., 2016). Likewise, mosquito SDMs fine-tuned hyper-parameters characteristics for each response variable by manual or automated comparisons within specialized R packages (Muscarella et al., 2014; Cobos et al., 2019) or stepwise Akaike information criteria. For example, the rising popularity of MaxEnt has coincided with the increased availability of software to automatically test a range of hyperparameters, such as included feature classes and regularization multiplier, to determine the best fit against resubstituted or random hold-out of training data. Addressing model complexity in these ways decreases the probability that a model will overfit, providing more valuable predictions and projections (Araújo and Pearson, 2005).

We noted that mosquito SDMs were highly dependent on heterogeneous secondary response variables from one or more repositories. These repositories often represented a combination of literature records, citizen science, and organized surveys (Kraemer et al., 2015). Reliance on such heterogeneous sources limits the quality of the response variable and introduces potential bias (Syfert et al., 2013). However, heterogeneous sources can reduce sampling bias if sampling is diverse and widespread (Sardà-Palomera et al., 2012). The appropriate method to account for bias in the response variable will depend on the bias present but is often related to sampling, geographic, or environmental bias (Inman et al., 2021). Accordingly, mosquito SDMs demonstrated a wide range of methods to treat bias and noise, including Mahalanobis distance (e.g. Ducheyne et al., 2018), spatial thinning (e.g. Drake and Beier, 2014), target group sampling (e.g. Wiebe et al., 2017), and bias layers (e.g. Sallam et al., 2016). Also, though not all publications addressed bias and noise, it was acknowledged and described by over half of the studied publications. Model complexity and treatment of bias can continue to improve by quantitative assessments from multiple lines of independent validation to indicate reliability methods (Araújo et al., 2019).

4.4. Model evaluation

Model evaluation of mosquito SDMs reflected those described for all taxa by Araújo et al. (2019), except mosquito SDMs indicated a lower 90% quantile of model outputs. Mosquito SDMs relied heavily on random hold-out evaluations over independent and re-substitution methods. Splitting the response variable into training and testing provides an improved assessment of an SDM's fit and predictive ability over re-substitution but limited assessment compared to independent data (Peterson et al., 2007; Bahn and McGill, 2013). For example, Wenger and Olden (2012) observed that SDMs of Brook trout, *Salvelinus fontinalis,* and Brown trout, *Salmo trutta,* had excellent performance when evaluated with random hold-out methods but poorly predicted independent data in new locations and climates. Independent data can come from an independent systematic survey in a different space or time from training data (Martínez-Meyer et al., 2004; Peterson et al., 2007). Mosquito SDMs applied independent evaluation from updated field surveys from public health or targeted efforts (e.g. Tran et al., 2013; Ibanez-Justicia and Cianci, 2015).

Many workers describe the lack of independent data for evaluation. When an independent evaluation is available, it may be inflated owing to spatial autocorrelation and bias (Hijmans, 2012). Specifically, training and testing datasets may fall within close geographic range to one another, thus being non-independent and inflating evaluation (Peterson and Soberón, 2012). Instead, mosquito SDMs should focus on geographically independent datasets for an unbiased evaluation. Standard practices for geographic structured evaluation data within mosquito SDMs included division by political boundaries (e.g. Levine et al., 2004), latitude, longitude, or quadrants (e.g. Arboleda et al., 2012). Unfortunately, these methods do not directly account for spatial autocorrelation or bias. Instead, one can divide training data into one or more geographically structured datasets to account for spatial autocorrelation. Capinha et al. (2014) estimated the global range of *A. aegypti* and created training and testing sets by accounting for spatial autocorrelation through alpha shapes. Other methods to account for spatial autocorrelation include removing spatial bias by pairwise distance sampling (Hijmans, 2012), automated spatial block cross-validation (Valavi et al., 2019), or spatial "leave one out" method (Le Rest et al., 2014). The appropriate approach to create geographically-structured training and testing sets will depend on the study objective, extent, and response variable.

4.5. Temporal trends

Interest in *Anopheles* and *Culex spp.* remained relatively constant over time, while that of *Aedes spp.* increased. Given the rapid global spread and importance of select *Aedes spp.*, paired with the introduction or resurgence of associated MBD, increased interest in *Aedes spp.* distribution is not unexpected (Lessler et al., 2016; Leta et al., 2018). Likewise, while *Anopheles* and *Culex spp.* have a much lower degree of global spread, distribution was assessed within the proximity of endemic areas (Gangoso et al., 2020; Liu et al., 2020). As such, interest in *Aedes spp.* is expected to increase in future years.

Despite mosquito SDM improvements in some issues compared to all of the taxa studied by Araújo et al. (2019), overall temporal patterns indicated predominantly divergent behavior across issues. The lack of consistent change suggests that most modern mosquito SDMs have not improved on previous models, despite simultaneous SDM research to improve applications over the years. Instead, publications applied the same techniques to new occurrence records or under different conditions. Further, since the development of SDM standards, SDM quality has not changed. This suggests not enough time has passed for the standards to be acknowledged and implemented within mosquito distribution forecasting. The same may not be accurate for all taxonomic groups. Yet these findings must be interpreted with caution as we observed unequal SDM application across years, with no publications in

1999, 2000, and 2003, and only a single year of publications to represent after standard quality.

Response variable and predictor variables observed more consistent increases and decreases in temporal quality change, respectively. These observed patterns were also detailed by Araújo et al. (2019), but mosquito-only SDMs demonstrated more robust trends. Generally, response quality has increased owing to increased biodiversity efforts that allow for occurrence repositories with increased detail (Soberón and Peterson, 2004). Mosquito reporting and surveys are increasing globally to manage MBD through both standardized active and non-standardized passive surveys (Kampen et al., 2015; Kovach and Smith, 2018; Chen et al., 2020). Additionally, increased criticism and technology protocols exist to improve survey efforts (Baldacchino et al., 2015; Parihar et al., 2020; Dormont et al., 2021). Conversely, predictors indicated increasingly haphazard selection limited to bioclimatic variables with little to no justification for selecting predictors, resolution, or consideration of uncertainty. High resolution environmental data is increasingly available via remote sensing efforts but is rarely applied to SDMs (Pinto-Ledezma and Cavender-Bares, 2021). As environmental and other predictors become more accessible, more consideration of predictor variables is required for mosquito SDMs. Authors and reviewers are encouraged to review best practices in SDMs to focus on enhancing their applicability to all SDM aspects and issues.

Finally, it is essential to acknowledge that the applied standards reflect a relative consensus of expert advice and that scientific standards can be challenged and altered accordingly. Other standards for all SDMs applications (Sofaer et al., 2019), reporting (Feng et al., 2019; Zurell et al., 2020), and guides (Sillero et al., 2021) have emerged. As more research on SDMs and mosquito distributions is conducted, the strengths and weaknesses of SDM methods may change (Araújo et al., 2019). We acknowledge that accomplishing gold or silver standards may not be possible in all scenarios due to logistical challenges such as data limitations. The considered assessments here were limited by missing reproducible elements across considered literature (Fig. 5). We recommend that future studies follow reproducibility checklists (Feng et al., 2019; Zurell et al., 2020). Further, the evaluation criteria proposed by Araújo et al. (2019) may be too stringent to meet modern SDM practices. Evaluation against different standards (i.e. Sofaer et al. 2019) may provide a different interpretation. As such, an SDM is not universally valid or invalid but must be evaluated on whether the model is valid for its designed purposes. The recommendations we outline here provide guidelines for mosquito SDM quality improvement. Variation and biases of standard quality interpretation between observers are natural. Here, we assessed SDM quality by a single individual, so uncertainty between assessors could not be quantified or examined. Future standard assessments should apply multiple assessors when possible.

5. Author contributions

JRB and HJM conceived the study, JRB collected, analyzed the data, and drafted the manuscript; HJM edited, revised and approved the manuscript.

Supplementary material

Supplementary material 1: Supplementary tables and figures, Supplementary material 2: Species-specific predictor importance

Declaration of Competing Interest

The authors declare that they have no conflict of interest.

Data availability

Data will be made available on request.

Data accessibility

All supplementary information can be found online for this article

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2022.110073.

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