

Species distribution modeling of snail hosts in neglected disease systems: Current limitations and future opportunities

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ABSTRACT

Trematode infections, transmitted broadly via freshwater snails to vertebrate hosts, pose an infection risk to hundreds of millions of people and livestock annually. Species distribution models (SDMs) are commonly used to map snail distributions which can inform host population control measures. However, the scope and quality of SDMs applied to trematode intermediate hosts has not been critically assessed, potentially undermining their utility for disease control. To address this gap, we reviewed existing methods for modeling trematode intermediate host distributions, identified trends and gaps in study focus and methodologies, and determined the adherence of published studies to best practices by using an existing assessment framework. While studies were roughly evenly distributed across major human endemic regions, we found that roughly 80% of studies model *Schistosoma* intermediate hosts, making intermediate hosts of other health-relevant trematodes relatively understudied. We found that recent snail SDM studies predominately use modeling practices that are not up to standard. Further, these practices have not improved over time. Snail SDMs generally exhibit lower levels of adherence compared to other taxa, suggesting that the field may be lagging behind others methodologically. In addition to modeling standards, studies did not generally conform to open access data sharing principles. Notably, only 6% of the studies provide open access to code used for analysis. However, in nearly all cases minimally acceptable practices are attainable with only minor methodological changes. Implementing the targeted recommendations presented here will strengthen future snail SDMs and support the WHO's goal of eliminating trematodiasis as a public health burden.

1. Introduction

Food- and water-borne trematodiasis are a diverse group of diseases caused by trematode parasite infections of vertebrates. These diseases afflict over 200 million people globally and pose an infection risk to over 750 million more (Li et al., 2025; Liu et al., 2024). The chronic symptoms and prolonged burdens of these diseases result in roughly 3.6 million disability-adjusted life years (DALYs) lost per year (WHO, 2022; Montresor et al., 2022). Motivated by this profound burden, the World Health Organization has set an ambitious goal of eliminating trematodiasis as public health issues in endemic regions by 2030 (United Nations, 2015). Trematodiasis also impact animal health, affecting a wide range of economically important ruminant livestock (Kebede et al.,

2023; Mage et al., 2002). In these cases, disease results in reduced economic output, imposing a further strain on developing regions (Megersa et al., 2024; Strydom et al., 2023). Although trematodiasis constitute a substantial public health issue, they remain classified as neglected tropical diseases (NTDs) because they have been historically understudied and predominantly impose a public health burden on developing tropical nations (Chai and Jung, 2024).

Trematode parasites have complex life cycles that require passage through a specific freshwater mollusk intermediate host, followed by development and emergence into freshwater as cercariae (Keiser and Utzinger, 2009; Nelwan, 2019). In some species, cercariae further progress into encysted metacercariae in the water column or a second intermediate host (Poulin and Cribb, 2002). Vertebrate definitive host

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infection then occurs in one of two ways: from the penetration of skin via tailed cercariae in a waterbody, or from the ingestion of encysted metacercariae (from the waterbody or the consumption of an undercooked, infected second intermediate host). Following maturation within the definitive vertebrate host, eggs are produced and passed through urine or feces before hatching into miracidia if they are passed into a suitable freshwater body. Miracidia are the free-swimming life stage infectious to mollusks (Keiser and Utzinger, 2009; Nelwan, 2019). As such, disease prevalence is exacerbated by poor sanitation infrastructure and lack of access to clean water (Grimes et al., 2015). While eggs can hatch into miracidia in any suitable water body, further life cycle progression requires the presence of specific mollusk intermediate hosts. Thus, sustained transmission is typically limited to areas where suitable intermediate hosts and environmental conditions allow for the completion of the trematode life cycle.

As a result of this complex life cycle, the control of some trematodiasis has focused on the control of snail intermediate host populations. In standard practice, these methods include competitive exclusion, predation, molluscicide application, and the reduction of snail habitat (Ohmae et al., 2003; Pointier and Jourdan, 2000; Rohr et al., 2023; Yang et al., 2012). As current drug treatments for trematodiasis do not prevent reinfection, and no vaccines exist, reducing persistent trematodiasis transmission is reliant on the control of intermediate hosts, human behavioral adaptation, and the improvement of water and sanitation infrastructure (Grimes et al., 2015; Torres-Vitolas et al., 2023). Better understanding the current and future distribution of snail intermediate hosts is therefore necessary to effectively guide future control practices and identify areas at risk of increased trematode burden.

One of many approaches to better understand and project snail intermediate host distributions is through the use of species distribution models (SDMs), which are a broad suite of statistical and mathematical tools used to relate species presence to the environment (Elith & Leathwick, 2009a). While SDM approaches are varied, they all use spatiotemporally explicit records of species occurrence as the response variable, with associated environmental conditions being used to predict those occurrences. Appropriate use of SDMs involves making decisions regarding model building (e.g. parameter selection) and evaluation (e.g. cross-validation). The use of SDMs is increasingly common in disease macro-ecology, particularly in mapping vector-borne disease risk and in quantifying the influence of environmental variables on pathogens and their hosts (Johnson et al., 2019).

As SDMs increasingly guide costly and consequential control efforts, ensuring accurate outputs is crucial (Hollings et al., 2017; Sofaer et al., 2019). Achieving ecologically and statistically robust SDM projections requires sound decisions regarding 1) response data, 2) predictor data, 3) model building, and 4) model evaluation (Araújo et al., 2019; Soley-Guardia et al., 2024). To encourage effective use of SDM methodologies, Araújo et al. (2019) devised a general set of “best practices” for improving SDM rigor and transparency. The study also presented a scoring framework, hereafter referred to as the “best practices framework,” to determine how well studies adhere to modeling standards. While the ability to adhere to some of these practices may be limited in some systems by, for example, data limitations or funding availability, striving to adhere to these standards increases model validity and reproducibility, with minimally acceptable adherence being feasible in the majority of cases. For example, while conformation to current best practices regarding statistical or theoretical assumptions may be out of reach due to data limitations, achieving an acceptable level of adherence requires only testing for conformity and discussing the potential impact of any violations on model inference. This structured framework was made with the intent of improving accountability and transparency in ecological modeling, and has been employed with the goal of improving studies across a diverse range of taxa (Barker and MacIsaac, 2022; Bowden et al., 2021; Paulukonis et al., 2021).

Despite this, available evidence indicates that broad adherence to

best practices has not necessarily improved over time (Vasconcelos et al., 2024). For SDMs of snail intermediate hosts, this suggests that the ability of models to provide robust guidance for disease control policy may not necessarily be improving, despite the large body of literature detailing the impact of poor modeling practices on model utility. For example, overly complex models may be overfit to their input data, resulting in areas suitable for snail hosts being deemed unsuitable (or vice versa). Likewise, if biased input data are not corrected, then model outputs will reflect the same bias, resulting in potentially misleading projections and erroneous application of snail management.

Given the high burden of trematodiasis and limited understanding of how SDMs have been applied to snail intermediate hosts, a synthesis of existing studies is timely. Taken further, as the utility of these studies to inform snail control can be compromised by decisions made in the modeling process, analyzing previous adherence to best modeling practices and open access principles is crucial. The intention of this analysis is not to undermine prior studies, as they comprise the baseline set of models in the field and have all shed light on neglected disease systems that predominantly impact impoverished communities; rather, the aim is to facilitate methodological improvements. In assessing adherence to best practices using the published criteria mentioned above, we do not construe “gold standard” studies as “gold standard” science, as one could use other approaches to make rigorous inference, but rather to identify where future snail SDM studies can improve model utility via a framework applicable across diverse fields (Barker and MacIsaac, 2022; Bowden et al., 2021). Synthesizing and analyzing current studies will aid in creating more rigorous and transparent distribution projections across a greater range of understudied snail intermediate hosts. These qualities will improve the ability of models to inform the attainment of the WHO's trematodiasis eradication goal by lending a macro-ecology perspective to control efforts, which is a vital but often missing component (see Acharya et al., 2022). While we are mindful of the challenges associated with this goal (see Adenle, 2012), better informed control efforts will lower the public health burden, which in this instance is disproportionately borne by populations already impacted by economic stress, food insecurity, and climate change (King, 2010; Ngcamu, 2023).

To this end, we systematically reviewed the published literature on SDMs applied to snail intermediate hosts of trematode parasites of human and veterinary importance and assessed studies methodologically using a published best practices framework. By reviewing the current body of literature on snail SDMs, we aimed to: i) synthesize how SDMs have been applied to snail intermediate hosts, ii) identify current geographic and disease system gaps, iii) identify current adherence to open access practices and global taxonomic standards, iv) evaluate current adherence to modeling best practices and compare compliance to other study systems, and v) highlight opportunities to improve future research efforts.

2. Methods

2.1. Literature review

We conducted a literature search on Web of Science and PubMed using terms related to distribution modeling and snail intermediate hosts of trematodes (see Supplementary Method S1 for list of search terms). This search yielded 84 and 89 results from Web of Science and PubMed, respectively. Genera were included in the search terms if they were identified as major hosts of human or livestock trematodiasis. Taxonomic names used in the search terms and throughout this manuscript are based on those used in the World Register of Marine Species (WoRMS) global taxonomy (Ahyong et al., 2025; WoRMS Editorial Board, 2026) (Supplementary Table S1). From the initial search, 35 duplicate publications were removed and a further 84 were removed after title and abstract screening, if they did not both 1) utilize SDM methodologies and 2) focus on snail intermediate hosts. Studies were

classified as using SDM methodologies if they used numerical approaches to relate species occurrence or abundance to environmental conditions (Elith & Leathwick, 2009b). These filtering steps resulted in 53 studies selected for full-text screening (Fig. S1). We only retained studies which focused on modeling the snail intermediate host of the trematode, rather than modeling trematode disease occurrence, resulting in a final inclusion of 48 peer-reviewed articles published in 28 unique journals. Studies focused on modeling trematode disease occurrence were excluded because they fall beyond the scope of the best practices framework used here: models informed by disease cases require a different set of assessment standards (Johnson et al., 2019).

For the retained studies, we then extracted information regarding study focus (e.g. snail species modeled, spatial extent of the study, region of the study), methodologies (e.g. SDM algorithms used, evaluation metrics calculated, source of predictor variables), and data availability (e.g. open access to data and code used for analyses) to synthesize the current state and replicability of SDMs applied to snail intermediate hosts (Supplementary File 1). Studies were also screened for inclusion of a globally accepted taxonomic identifier (e.g. taxonomic serial numbers from the Integrated Taxonomic Information System), to identify whether studies use taxonomies that align with globally recognized taxonomic databases (Supplementary File 1). Species names used in the screened literature were further cross-referenced to the WoRMS taxonomic database to identify whether the names used align with currently accepted taxonomies (Table S2).

2.2. Assessment of best practice adherence

Following the literature search and screening, we scored the methodological rigor of the retained studies according to the guidelines outlined in the best practices framework. These guidelines allowed us to assess model adequacy—how appropriate modeling decisions are given the model objective—which is an essential consideration given the potential for snail intermediate host SDMs to inform public health planning. Following Araújo et al. (2019), adherence scores were assigned across four ascending ranks: deficient, bronze, silver, and gold. These designations are used purely to remain consistent with previous assessments (e.g. Barker and MacIsaac, 2022), and are not intended to suggest that studies utilizing ‘deficient’ practices are without merit or that studies utilizing ‘gold’ practices are perfect. Broadly, ‘deficient’ scores represent unacceptable modeling practices; ‘bronze’ represents current minimally acceptable practices; ‘silver’ represents current best practices, and; ‘gold’ represents current aspirational practices. Studies were scored across four major modeling aspects: response variable, predictor variables, model building, and model evaluation. Each modeling aspect is made up of three to five specific modeling issues, which pertain to major methodological decisions that have to be made within that aspect. Below we outline the scoring criteria and adherence implications within each modeling aspect; detailed criteria can be found in Supplementary Methods S2–5.

Response variable assessment focused on decisions regarding occurrence records, such as species identification, sampling effort, and the use of heterogeneous data sources. Best practice in this area entails utilizing a systematic survey approach across the entire environmental and geographic extent available to the species, with high spatial accuracy and multiple lines of evidence for species identification. Employing unacceptable practices in this aspect, such as improper species identification, the use of imprecise location estimates, and failure to sample across the full environmental and geographic extent available to the species, limit the ability of SDMs to accurately predict species' distributions (Costa et al., 2015; Graham et al., 2008; Tassarolo et al., 2014). Ensuring adherence to response variable best practices helps ensure that models use data representative of the spatial and environmental distribution of the focal taxa.

Best practice adherence regarding predictor variables relates to the selection and processing of variables to describe the species-

environment relationship. Adhering to gold standard practices in this area entails training models with predictors that are known to be causally related to the species distribution at the same spatio-temporal scale as the response variable, then conducting post-hoc analyses to quantify predictor-based uncertainty. Utilizing deficient practices regarding variable selection, spatiotemporal scale matching, and uncertainty estimation can result in misleading suitability projections (Beale and Lennon, 2012; Fournier et al., 2017; Pennino et al., 2019). Adhering to predictor variable best practices increases the generalization of the SDMs employed, increases transferability, and improves confidence in suitability estimates.

Best practice assessment for model building addresses the degree to which models account for complexity, bias, collinearity, and parameter uncertainty. Gold-standard practices in this context involve the assessment of model complexity and over-fitting, treatment of response variable bias and predictor collinearity, and the comprehensive characterization of model and parameter uncertainty. Utilizing deficient practices regarding model complexity and predictor variable collinearity could result in the presentation of spurious correlations in model outputs (Dormann et al., 2013; Merow et al., 2013), while failing to address bias in the response variable results in that bias being similarly reflected in model outputs (Syfert et al., 2013). Further, failure to characterize and present output uncertainty produces overconfident suitability estimates (Buisson et al., 2010). Adhering to best practices regarding model building makes suitability estimates more reflective of the true species-environment relationship, and presents a more comprehensive picture of where models are most confident.

The final scored modeling aspect, model evaluation, concerns how models are validated. Gold standard practices involve proving conformity to modeling assumptions and evaluating model outputs against statistically independent data to quantify multiple aspects of model performance. Deficiencies regarding these practices, such as the use of non-independent data for evaluation or the presentation of only one evaluation metric, can result in an overconfident perception of how realistic, accurate, and generalizable model outputs are (Lobo et al., 2008). Ensuring that models are evaluated in the most rigorous way possible, given the available data, allows for a more comprehensive presentation of model performance and calibration.

2.3. Analysis

To identify any spatial and temporal trends in the publication of snail SDMs, we first collected counts of publications per year and counts of what continent(s) studies focused on. To determine whether the number of publications per year has increased over time, we conducted a linear Poisson regression analysis. We tested for evenness of publications across the three major continents where human trematodiasis and their snail hosts are endemic (Africa, Asia, South America) using a chi-square goodness-of-fit test.

To assess snail SDM adherence to best practices we calculated a composite quality score based on the proportion of criteria met within each modeling aspect. To do this, we followed Araújo et al. (2019) and calculated an “area inside the line” metric in polar space, where a score of 100% represents reaching gold for all issues within an aspect; a score of bronze across all modeling issues within a modeling aspect would result in an area inside the line metric of 33.3%.

To capture any temporal trends in snail SDM quality, we conducted a Bayesian ordinal regression analysis to identify whether adherence has changed as modeling approaches and philosophies broadly evolved (*rstanarm* package; Gabry and Goodrich, 2016). Model priors and settings were based on those used in the analysis of mosquito SDM quality conducted by Barker and MacIsaac (2022), wherein the score was fitted against an interaction of year and modeling issue. Following this, we utilized a cumulative link mixed model, with study as a random effect, to determine whether there were differences in adherence to best practices before and after the publication of the best practices framework (*ordinal*

package; Christensen, 2010).

To compare adherence to best practices across different study systems, we calculated the difference in adherence at the 50% and 90% quantile of snail studies with SDM studies focused on mosquitoes (Barker and MacIsaac, 2022) and on biodiversity assessments irrespective of taxa (Araújo et al., 2019). These studies were selected to allow for comparison to standard adherence with another common disease vector and with broader SDM modeling efforts, respectively. Comparing in this way allowed us to identify how well the median and most adhered studies performed between fields, as sorted by overall adherence within each modeling aspect. Details of all code and model components relevant to the above-mentioned analyses can be found in the data availability statement.

3. Results

3.1. Literature review

Snail intermediate hosts from 20 genera have been analyzed using SDM methodologies, with 96% of studies identifying all modeled species down to the species level (Table S2). The majority of articles focused on intermediate hosts of *Schistosoma* spp., which represented 81% of all publications screened. Accordingly, the genera most modeled were *Biomphalaria* and *Bulinus*, representing 56% and 29% of all articles, respectively. Species most featured include *Bu. globosus*, *Bi. pfeifferi*, and *Bi. straminea*, each of which were the focus of ≥ 10 studies. Over two thirds of the included studies (73%) utilized self-collected or

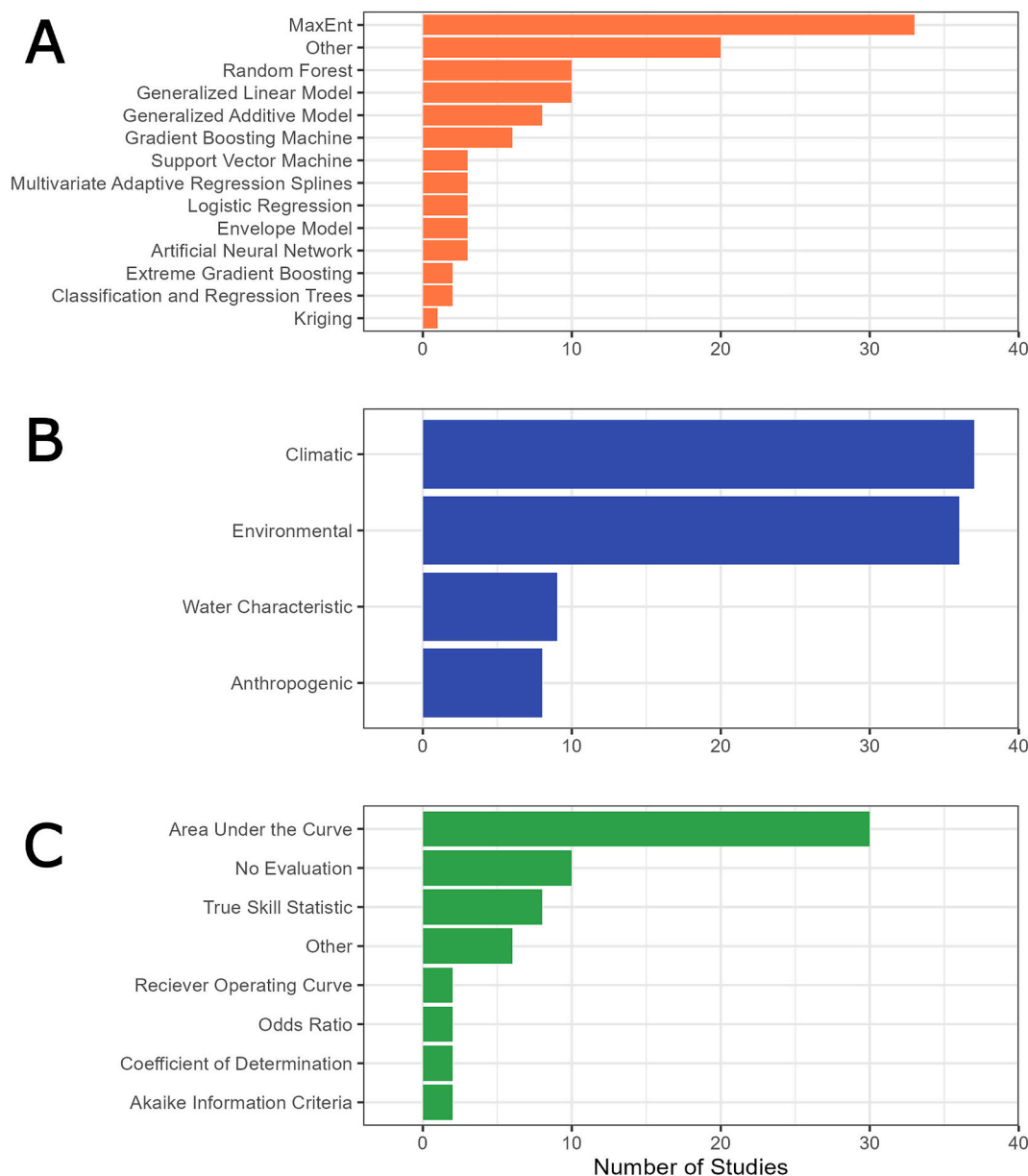


Fig. 1. A) Number of publications which used a given model type. While 48 studies were screened, some studies employed more than one model type, and thus $N = 117$. The other category is comprised of the Pesenko index of species-habitat association, derived algebraic formulas of habitat suitability, flexible tree analysis, surface range envelope, genetic algorithms, basic decision trees, Bayesian inference, flexible discriminant analysis, and niche factor analysis. B) Number of publications which used a given predictor variable type. While 48 studies were screened, some studies employed more than one predictor type, and thus $N = 92$. See Supplemental Fig. S2 for an UpSet plot displaying the frequency of unique combinations of predictor variable categories. C) Number of publications which used a given evaluation method. While 48 studies were screened, some studies employed more than one evaluation metric, and thus $N = 63$. Metric abbreviations: The other category is comprised of sensitivity, specificity, spearman rank correlation coefficient, pROC, consistency rate, and the continuous Boyce Index. See Supplemental Fig. S3 for an UpSet plot displaying the frequency of unique combinations of evaluation criteria.

governmental systematic surveys to source records of intermediate host occurrence or abundance.

The purpose of modeling within the screened studies fell into three categories: 1) to *explain* the relationship of snail distributions with the environment, 2) to spatially *predict* snail distributions, or 3) to spatially *project* snail distributions (Araújo et al., 2019). Here, *prediction* refers to interpolation within the spatial and temporal conditions of the input data, whereas *projection* refers to extrapolation into novel spatial or temporal conditions. Of the 48 reviewed studies, nine were explanatory, 29 were predictive, and 10 were projections; as such, the majority of studies reviewed here made inference at the pixel-level. Regardless of study purpose, we found that most studies used a single modeling approach (73%), while only a fraction used ensemble (15%) or mixed (17%) modeling approaches, where outcomes across multiple algorithms are combined or independently presented, respectively. All studies focused on non-*Schistosoma* intermediate hosts employed only a single modeling approach. A variety of models were utilized among the total literature screened, though Maximum Entropy (MaxEnt), Random Forest, and Generalized Linear Models were most common (Fig. 1A). These models were trained with species occurrence data (85%) more frequently than abundance data (15%).

Among the screened literature, we found that most studies used

multiple predictor types to inform their model (78%), while the minority only used a single predictor type (22%). The most used predictor types were climatic predictors (e.g., temperature and precipitation), along with other environmental metrics (e.g., elevation and soil characteristics). Meanwhile, freshwater metrics (e.g., acidity and dissolved oxygen) and anthropogenic metrics (e.g., land-use, human population) were less frequently employed (Fig. 1B; Fig. S2). When it came to selecting predictor variables, we found that most articles did not address potential collinearity among candidate variables (65%). Of those that did test for collinearity, 11 did so using correlation coefficients, five used principal component analysis, and two used variance inflation factor.

Among the screened publications, most used evaluation metrics to examine the accuracy of their distribution model predictions (78%), while a smaller number did not evaluate their model results (22%). The most commonly employed methods of evaluation were area under the curve (AUC) and true skill statistics (TSS), which were used in 31 and nine papers, respectively (Fig. 1C; Fig. S3).

Currently, only a small number of snail SDM studies utilize open access data principles regarding the response variable (21%), predictor variable (10%), or code used for statistical analysis (6%; Supplementary File 1). Further, we found that none of the included studies directly reference globally accepted taxonomic identifiers; however, those that

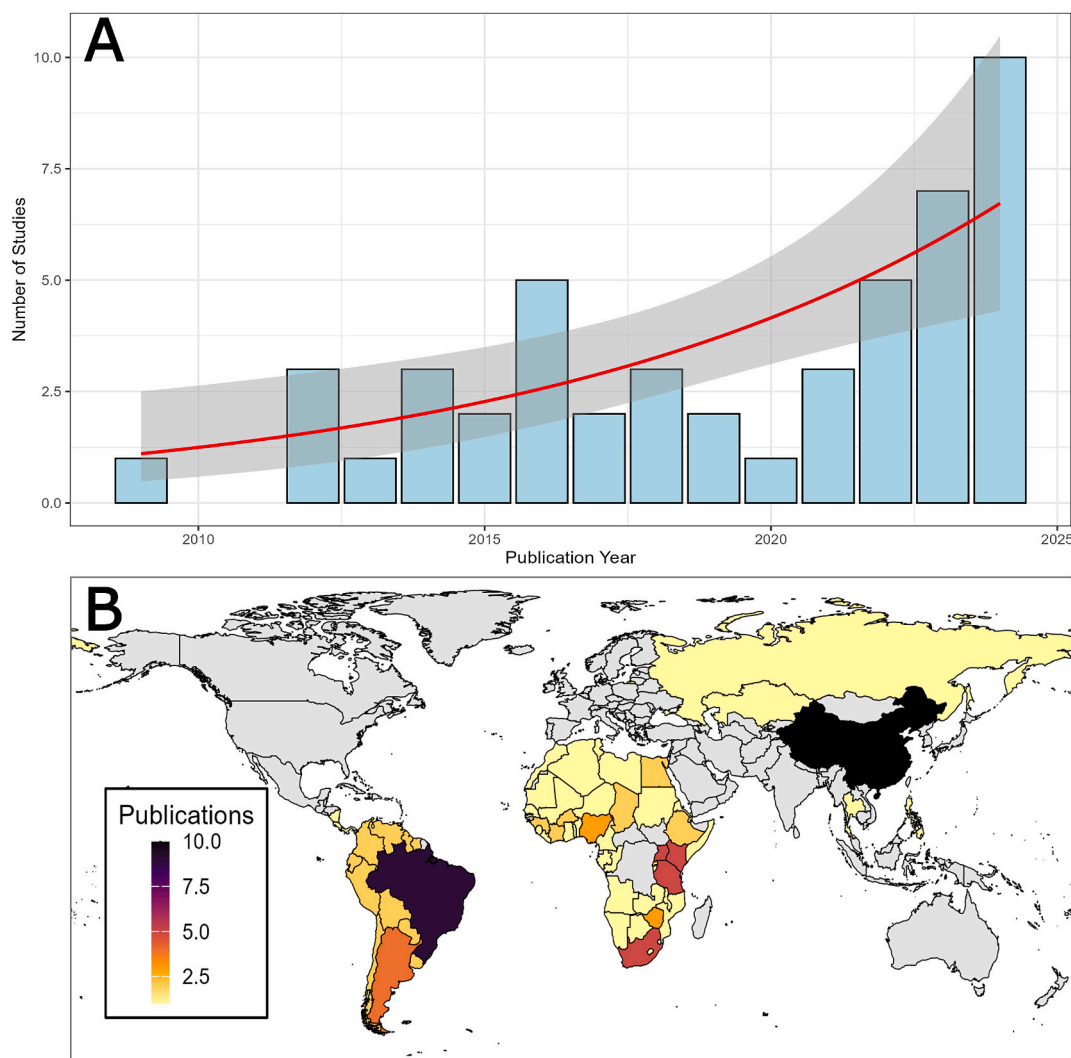


Fig. 2. A) Number of articles published from 2009 to 2024. The number of publications per year significantly increases over time ($\beta = 0.12$, $p = 0.001$). B) Study focus trends. Colors correspond to the number of publications focused on a given country (i.e. if spatial projections or sampling for snails were done in that country for a given publication); the figure does not include global studies ($n = 2$). Studies shown here had extents at regional ($n = 10$), national ($n = 12$), and sub-national scales ($n = 24$).

utilized GBIF (17%) can be assumed to follow the nomenclature presented in the GBIF Taxonomic Backbone (GBIF Secretariat, 2023). The cross-referencing of species names from the reviewed studies with the WoRMS global taxonomy revealed that three referenced names are currently out of date, and that two species designations never existed as accepted taxonomic distinctions in the WoRMS database (Table S2).

3.2. Spatial and temporal trends

Over half of all snail SDM studies were published in the past five years (Fig. 3). Prior to 2020, and the publication of best practices, the number of articles published per year remained roughly consistent, ranging from one to five publications per year. The number of publications increased over time, likely attributable to improvements in computational resources and increased access to necessary data (Fig. 2A; $\beta = 0.12$, $p = 0.001$).

Studies describing snail hosts in Africa (40%) were most common, with roughly equal studies in Asia (29%) and South America (27%; Fig. 2B); studies were evenly distributed across these human endemic continents ($X^2 = 3.06$, $p = 0.22$). Studies in Asia and South America predominantly focused on China and Brazil, respectively. In terms of disease systems, the majority of studies in Africa (95%), Asia (79%), and South America (77%) focused, at least partially, on snail intermediate hosts of *Schistosoma* species (see Supplementary File 1 for a full list of trematode species).

3.3. Adherence to best practices

All screened publications conducted at least one currently unacceptable practice within a single aspect of model quality; however, no single aspect was scored to be deficient across all studies. The studies reviewed here predominantly reflected currently unacceptable (deficient; 57%) or acceptable (bronze; 31%) practices across all measured aspects of model quality, with only 8% and 4% of scores reflecting current best (silver) and aspirational (gold) practices, respectively (Table 1). Decisions made regarding response variables had higher proportions of silver and gold practices compared to the other three aspects of model quality.

We found that response variable and model evaluation achieved 7% and 17% of the total possible score at the 50% quantile, respectively, whereas predictor variable and model building achieved 0%. However, substantial increases were seen in quality among all model aspects when considering the 90% quantile of studies (Fig. 3).

We found no evidence that adherence to best practices have changed over time, as the credible intervals from our ordinal regression analysis were relatively wide and overlap zero for all modeling issues (Fig. 4; Figs. S4–7). Further, we found that there is no difference in best practice adherence pre- and post- publication of best practices ($p = 0.993$).

Snail SDM studies, with the exception of model evaluation, generally exhibited lower levels of best practice adherence compared to studies focused on mosquitoes or across all taxa at the 50% quantile of studies; however, the 90% quantile of studies were more comparable to the other fields across all modeling aspects (Table 2).

4. Discussion

Given the profound global health burden of trematodiasis, it is vital to better understand snail intermediate host distributions. We found that SDM approaches are being increasingly used to accomplish this, with a majority of studies focusing on intermediate hosts of *Schistosoma* species. Despite the increased use of SDMs to model snail intermediate host distributions, we found that snail SDMs generally do not meet currently acceptable practices. Beyond this we found that there are no temporal trends regarding best practice adherence, indicating that models have not been improving over time. While some modeling aspects reflect greater adherence to best practices, notably regarding response

Table 1

Percent of quality scores per issue and model aspect across 48 publications. As defined in Araújo et al., 2019, deficient, bronze, silver, and gold represent currently unacceptable, current acceptable, current best, and aspirational practices, respectively. For definitions of scoring guidelines by issue, refer to Araújo et al., 2019 or Supplementary Methods 2–5.

Model Aspect	Issue	Deficient	Bronze	Silver	Gold
1. Response variable	Sampling of response variables	40	29	29	2
	Identification of taxa	21	21	25	33
	Spatial accuracy of response variable	63	6	10	21
	Environmental extent across which response variable is sampled	75	19	6	0
	Geographic extent across which response variable is sampled	65	31	4	0
	Total	53	21	15	11
2. Predictor variables	Selection of candidate variables	33	58	8	0
	Spatial and temporal resolution of predictor variables	77	6	4	13
	Uncertainty in predictor variables	79	15	6	0
	Total	63	26	6	4
3. Model building	Model complexity	67	23	10	0
	Treatment of bias and noise in response variables	77	17	6	0
	Treatment of collinearity	50	44	4	2
	Dealing with modeling and parameter uncertainty	75	23	2	0
4. Model evaluation	Total	67	27	6	1
	Evaluation of model assumptions	90	4	6	0
	Evaluation of model outputs	25	63	13	0
	Measure of model performance	21	79	0	0
	Total	45	49	6	0
All aspects	Total	57	31	8	4

variables, broad improvements need to be adopted to make future models more robust. Further, we found that snail SDMs generally exhibited lower degrees of best practice adherence than other study systems, which suggests that future improvements in snail modeling efforts are broadly attainable. The following sections outline key study focus and methodological gaps, along with targeted recommendations to improve future models of snail intermediate hosts.

4.1. Study focus

While we found that SDMs are being increasingly used to model snail intermediate host distributions, this expansion was not reflected in the diversity of study systems. The majority of SDM studies in this review focus on *Biomphalaria*, *Bulinus*, and *Oncomelania*, genera that are prominent intermediate hosts of trematodes in the genus *Schistosoma*. Schistosomiasis, which is caused by these parasites, was responsible for the loss of 1.6 million DALYs in 2019, roughly half of the total burden attributed to all trematodiasis (Montresor et al., 2022). The high burden of schistosomiasis likely explains the focus on intermediate hosts of *Schistosoma*. However, while at the global level we found research effort in *Schistosoma* hosts versus other snail hosts to be roughly proportional to the ratio of human prevalence of schistosomiasis versus other trematodiasis (about 5:1), the focus on *Schistosoma* hosts becomes disproportionate at finer spatial scales in some regions (Liu et al., 2024; Tidman et al., 2023). This is highlighted in studies focused on China,

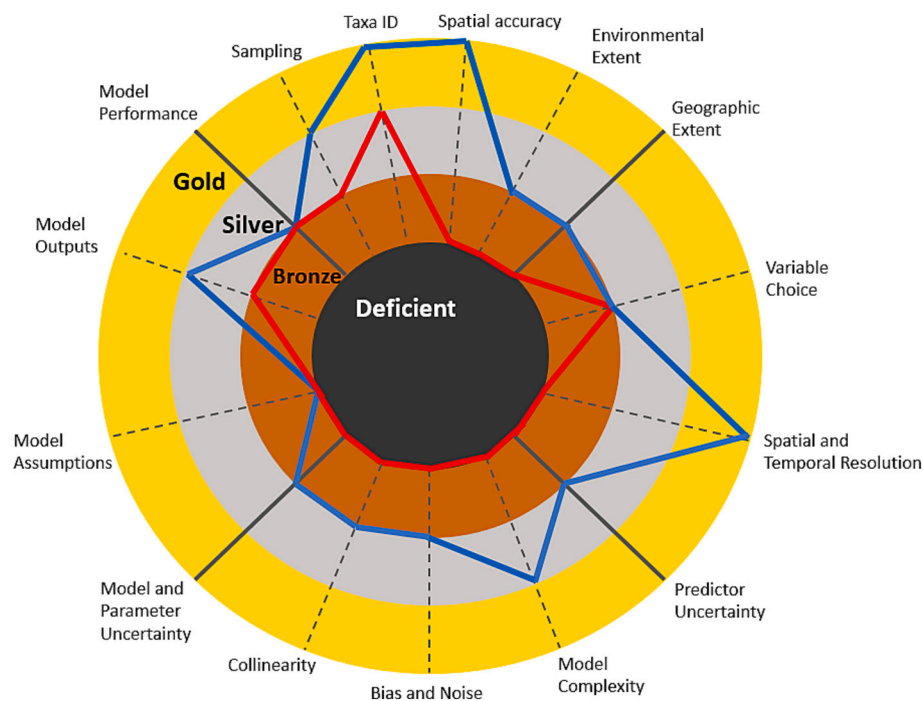


Fig. 3. Best practice adherence achieved by the screened studies. Adherence across issues is illustrated by the red (50% quantile) and blue (90% quantile) lines. The colored rings indicate the quality score, where deficient represents current unacceptable practice, bronze represents current acceptable practice, silver represents current best practice, and gold represents current aspirational practice. For definitions of scoring guidelines by issue, refer to Araújo et al., 2019 or Supplementary Methods 2–5. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

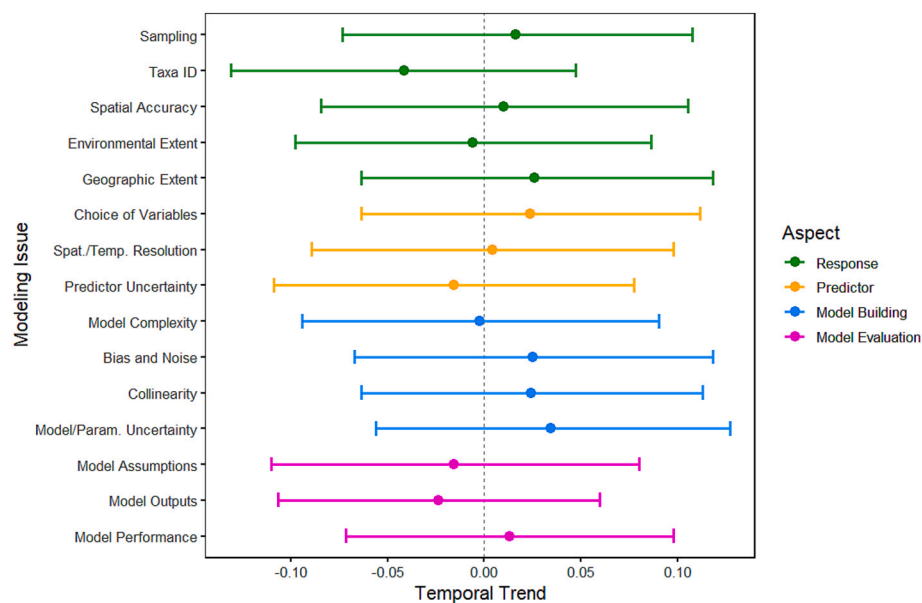


Fig. 4. Temporal trends in SDM quality as estimated from Bayesian ordinal regression across all studies. Issue specific trends and 95% credible intervals are represented as points and error bars, respectively. Temporal trend values closer to zero indicate less change in issue quality over time. Issues are colored by their corresponding model aspect.

where, despite the prevalence of food-borne trematodiasis now being far greater than schistosomiasis due to a highly effective control program, studies still predominantly focus on *Oncomelania hupensis*, the intermediate host of the water-borne trematode *Schistosoma japonicum* (Liu et al., 2024; Wang et al., 2021). In contrast, intermediate hosts of the food-borne trematodes *Clonorchis sinensis* and *Opisthorchis viverrini* were the focus of a single study in this review, despite each causing roughly 13 million disease cases in east Asia, as of 2024 (Qian et al.,

2024). The overwhelming focus on *Schistosoma* intermediate hosts, while vital in better understanding host distributions for the most impactful human trematodiasis, has thus led to hosts of other important trematodes being relatively understudied.

4.2. Best practice adherence

Our analysis indicates that adherence to best practices is highly

Table 2

The relative adherence to best practices achieved across SDM aspects for snail intermediate hosts, compared to those of mosquito SDMs from [Barker and MacIsaac, 2022](#) and to those across all taxa from [Araújo et al., 2019](#). SDM aspect is abbreviated such that 'R.V.' represents 'Response Variable,' 'P.V.' represents 'Predictor Variable,' 'M.B.' represents 'Model Building,' and 'M.E.' represents 'Model Evaluation.'

SDM Aspect	50% Quantile			90% Quantile		
	Snail	Mosquito	All taxa	Snail	Mosquito	All taxa
R.V.	7%	20%	16%	43%	45%	52%
P.V.	0%	4%	12%	19%	19%	25%
M.B.	0%	4%	4%	29%	29%	23%
M.E.	17%	8%	4%	33%	12%	19%

variable, and that significant modeling issues remain pervasive. Further, we found that there were no improvements in best practice adherence among snail SDMs following the publication of the best practices framework, a trend also found in SDMs of mosquitoes ([Barker and MacIsaac, 2022](#)). The predominant methodological issues found here can be grouped into three major categories: 1) assumption violations, 2) response and predictor selection and processing, and 3) the characterization of uncertainty. We summarize each issue, below.

The vast majority of SDM studies scored here (87.5%) reflected currently unacceptable practices by failing to address whether modeling assumptions (both theoretical and statistical) were violated. As currently acceptable practices in this regard do not require meeting assumptions, but merely testing for and discussing the potential limitations on inference, the barriers to achieving acceptable practices are minimal. Given this low barrier to adherence, we encourage all future studies to test for and discuss assumption conformity to make studies more robust and transparent. Meeting this criterion is particularly critical given the potential for SDM studies to inform disease control measures ([Guisan and Zimmermann, 2000](#); [Wiens et al., 2009](#)).

Across screened studies we found that response variables exhibited heterogeneity in source and scale. While over half of all studies used a single source, the remainder relied on heterogeneous sources for their occurrence records (e.g. community science, published scientific literature, systematic government surveys). The use of multiple sources can allow for greater spatiotemporal coverage, while reducing monetary and temporal costs associated with sampling (when accessible open access and for free). However, this introduces response variable bias, due to differences in uncertainty regarding species identification and spatial accuracy; these biases should be carefully considered ([Syfert et al., 2013](#)). Several mitigation approaches are encouraged to limit drawbacks if the use of heterogeneous sources is necessary. First, records that do not align with the known life history of the intermediate host should be removed, followed by spatial/environmental filtering to ensure duplicate records are removed ([Boria et al., 2014](#); [Varela et al., 2014](#)). While the complete removal of misidentified records may be impractical since readily available online repositories seldom have supporting data necessary to evaluate the accuracy of records (e.g. photos, gene sequencing), data cleaning reduces bias and uncertainty in the response variable. Studies utilizing heterogeneous sources are further encouraged to transform or aggregate across sources to ensure matching resolution and extent, which reduces biased point estimates and uncertainty ([Pacifi et al., 2019](#)).

Whether using heterogeneous sources or a single source, we found that the majority of screened studies utilized systematic self-collected (e.g. [Nwoko et al., 2023](#)) or governmental (e.g. [Xue et al., 2023](#)) surveys. The continued use of these surveys, either alone or in conjunction with other sources, is crucial as they improve predictive accuracy and greatly reduce response variable bias relative to records from unsystematic survey approaches ([Tyre et al., 2003](#)); however, future surveys designed for use in SDM frameworks are encouraged to sample across the full environmental and geographic range available to the taxa within the

study extent. This will combat suitability underprediction, wherein areas available and suitable may be projected to have lower suitability than realized ([Thuiller et al., 2004](#)). While these systematic approaches are preferred to using conglomerated occurrence datasets (such as GBIF) or heterogeneous sources, we acknowledge that conducting or utilizing systematic surveys could prove challenging or even prohibitive due to monetary or accessibility limitations. Beyond response variable considerations, predictor variables must also be appropriately selected to robustly inform models.

We found that most studies used spatiotemporally coarse predictor variables rather than localized climatic and water characteristic variables that have been shown to causally influence snail intermediate host distributions in some taxa ([Liu et al., 2021](#)). Acquiring fine-scale predictor data that mirrors the response variable's accuracy may be difficult, due to the understudied nature of many neglected tropical diseases and the lack of existing high-resolution water quality datasets in some endemic regions. While some studies achieved this through their own sampling of water quality measures (e.g. [Kagabo et al., 2024](#); [Nwoko et al., 2022](#)), freshwater characteristics were seldom used to estimate intermediate host distributions. This can result in reduced predictive accuracy, as water characteristics can be key drivers of snail occurrence and constitute the conditions directly experienced by snail populations; in contrast, widely used bioclimatic temperature predictors, for example, typically represent terrestrial conditions at 2 m above ground ([Domisch et al., 2019](#)). The expansion of freshwater characteristics as predictor variables is encouraged whenever possible to more accurately capture causative drivers of aquatic snail intermediate host distributions. This will improve model extrapolation into novel conditions which, in light of anthropogenic change, may prove crucial in mitigating disease expansion ([Austin and Van Niel, 2011](#)). Further, the presence of aquatic vegetation should also be considered and included in models whenever possible, as aquatic plants have been shown to be key drivers of snail persistence and trematodiasis transmission in some contexts ([Rabone et al., 2019](#); [Wood et al., 2019](#)). Beyond predictor variable type, the majority of studies did not justify their choice of predictor variable resolution based on the resolution at which the taxon is known to respond (77% of studies). Using an improper resolution, either spatially or temporally, results in lowered predictive accuracy ([Batalden et al., 2007](#); [Randin et al., 2009](#)). Per the best practice framework, achieving minimally acceptable practices regarding predictor variable resolution only requires justification for the specific taxon modeled. Accordingly, meeting this threshold is achievable in all studies screened here.

Beyond the selection and processing of response and predictor variables, decisions regarding the characterization of bias and uncertainty in the input data and model algorithms often reflected unacceptable practices. The impacts of sampling bias ([Syfert et al., 2013](#)), predictor selection and source ([Braunisch et al., 2013](#); [Synes and Osborne, 2011](#)), and algorithm choice ([Araújo and New, 2007](#)) on distribution estimates are well documented, and all constitute major sources of uncertainty in model outputs. Failing to present where uncertainties lie in model outcomes may result in overconfident interpretations of model outputs, potentially misleading snail control efforts. Characterizing and presenting uncertainty can be accomplished through the use of ensemble modeling across different sets of response and predictor data, and across multiple algorithms. Achieving acceptable practices regarding predictor uncertainty and model/parameter uncertainty was possible in all studies that reflected unacceptable practices by acknowledging and discussing the potential impact of predictor uncertainty on outcomes (79% of studies) and utilizing multiple SDM algorithms and discussing the potential impact of model/parameter choice on outputs (73% of studies). While adhering to acceptable practices regarding model and parameter uncertainty introduces greater computational load, this is readily achievable as the input data will already be formatted for use in SDM frameworks. Promisingly, we found that eight of the twelve studies which employ acceptable practices regarding the use of ensembles have been published since 2020, with one study ([van der Deure et al., 2024](#))

reflecting current best practices. The importance of characterizing model uncertainty in snail-borne disease modeling is particularly well demonstrated by [Zhang et al., 2020](#), who used a framework to compare modeling approaches for snail vectors at the local scale. In a similar vein, current acceptable practices regarding response variable bias were achievable in all studies that reflected unacceptable practices (75% of studies), by merely acknowledging and discussing the impact of response variable bias on model outcomes. The continued and expanded use of ensemble modeling, in conjunction with considerations of the impact of response, predictor, and parameter uncertainty on model projections, is encouraged to present more robust and transparent model outcomes.

4.3. Comparison to other taxa

When comparing adherence to best practices across taxa, we found that studies focused on snail distributions lagged behind those of mosquitoes ([Barker and MacIsaac, 2022](#)) and those focused on biodiversity assessments irrespective of taxa ([Araújo et al., 2019](#)). With the exception of model evaluation, we found that snail SDMs exhibited comparable or lower adherence to best practices at the 50% and 90% quantile across modeling aspects. This difference in adherence may be attributed to a disparity in the number of publications across these systems: there are roughly three times as many studies published on mosquitoes and nine times as many studies published using SDMs to assess biodiversity compared to those focused on snail intermediate hosts. Despite this difference in publication numbers, both mosquito and snail SDMs were found to largely rely on a few readily available macroclimate datasets for predictor variables, namely WorldClim ([Barker and MacIsaac, 2022](#); [Lippi et al., 2023](#)).

Relative to mosquito SDMs, which generally used conglomerate datasets such as GBIF for sourcing the response variable, we found that snail SDMs more often utilize self-collected and governmental systematic surveys. As the use of non-systematic, heterogeneous surveys are known to introduce bias to the response variable due to uneven sampling effort and differences in species identification protocols, the continued use of systematic surveys in snail SDMs is encouraged, particularly as morphological identification can prove unreliable for mollusks ([Alharbi et al., 2022](#); [Allan et al., 2020](#)).

4.4. Expansion of modeling approaches and replicability

As SDMs of snail intermediate hosts are being increasingly made at scales relevant to local public health policy, it is vital that snail SDMs reflect robust modeling practices. Achieving adequate modeling practices, notably those highlighted in section 4.2, will improve the impact of snail SDM studies. However, beyond ensuring input data and modeling decisions reflect rigorous practices, we also recommend that practitioners expand their modeling toolbox beyond the few predominantly used approaches (e.g. single-species MaxEnt modeling). These current methods are only one of a variety of modeling approaches to make inference regarding the species-environment relationship and, here, may limit inference due to their strict and correlative nature ([Kearney and Porter, 2009](#)). As such, strictly adhering to these approaches could hinder model utility, even if that allows studies to achieve “gold” standards of practice. Cutting-edge approaches such as the modeling of species clusters and communities via multivariate modeling ([Ovaskainen et al., 2010](#)), process-based mechanistic modeling ([Kearney and Porter, 2009](#)), ensemble modeling based on the concept of using many “weak learner” models to inform one “strong learner” model ([Trevor Hastie et al., 2009](#)), and modeling which harnesses “Big Data” and cloud computing, such as Super SDMs ([Huettmann et al., 2024](#); [Steiner et al., 2024](#)), have been shown to outperform “traditional” SDM approaches in many cases, yet are not present in this field currently. The use of these cutting-edge modeling approaches in studying snail distributions could provide strong and novel inference in this field, ultimately

resulting in more realistic and transferable models.

Regardless of the modeling approach employed, we recommend that future snail SDMs use open access data and code sharing principles. The current lack of open access sharing ultimately means that many of the studies reviewed here are not repeatable, transparent, or sharable, in turn limiting inference and methodological improvement ([Huettmann and Arhonditsis, 2023](#)). In a similar vein, we recommend that future studies use accepted, verifiable, global taxonomic registries when presenting species names (e.g. WoRMS). The absence of such registries in snail SDM studies results in ambiguity regarding the true species modeled and can hinder research utility ([Garnett and Christidis, 2017](#)). Failure to use global taxonomic identifiers is particularly problematic for modeling snail hosts, as what were previously thought to be reliable taxonomic characteristics for freshwater mollusks, such as shell morphology, have recently been challenged by molecular analyses ([Vinarski et al., 2020](#)). The use of novel modeling approaches alongside open access data sharing principles and global taxonomic registries is achievable and could constitute a “diamond standard” of practice relative to those used today, and would result in snail SDM studies that are more repeatable, transparent, and applicable to policy.

5. Conclusion

The practice of modeling snail distributions in disease contexts through the use of SDMs is becoming more prevalent over time, a pattern found across many systems ([Barker and MacIsaac, 2022](#); [Pasanisi et al., 2024](#); [Vasconcelos et al., 2024](#)). Collectively, the studies screened in this review have helped further our understanding of a group of neglected, chronic diseases that disproportionately impact developing nations and reinforce cycles of poverty ([King, 2010](#)). It is therefore crucial that care is taken at every step of the modeling process to more accurately inform control measures, as these efforts involve costly interventions ([Ross et al., 2013](#)). One way to assess the adequacy of SDM studies and their outputs is to quantify adherence to current best practices, which, while derived from expert consensus, are subject to change as methodologies improve and philosophies evolve. While best practice recommendations are devised to maximize model adequacy, we acknowledge that achieving what are currently understood to be best or aspirational practices may be limited by the quantity and quality of available data and funding. This review highlights promising areas of future research regarding study system and model adequacy, namely expansion into understudied regions and trematode systems, the incorporation of uncertainty in model outcomes via ensemble modeling approaches, and the characterization of the effect that modeling decisions and data quality may have on model outcomes. Critically, this review highlights that in nearly all cases adherence to currently acceptable modeling and transparency practices is achievable; the same will be true for future snail SDM studies. Addressing the gaps identified in this review, summarized in [Table 3](#), will deepen our understanding of snail intermediate host distributions, make studies more rigorous and transparent, and will aid in achieving the WHO's goal of eliminating trematodiasis as public health issues in endemic regions.

CRedit authorship contribution statement

Nicholas A. Galle: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Formal analysis, Data curation, Conceptualization. **Gracie Hedgpeth:** Writing – original draft, Visualization, Investigation. **Kevin Buck:** Writing – original draft, Investigation. **Matthew Woo:** Writing – original draft, Investigation. **Jason R. Rohr:** Writing – review & editing, Writing – original draft, Supervision. **Tyler C. Coverdale:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Conceptualization.

Table 3

Synthesis of gaps and future research opportunities identified through our literature search and quality assessment. Entries in the study aspect column are abbreviated such that 'R.V.' refers to 'Response Variable', 'P.V.' refers to 'Predictor Variables', 'M.B.' refers to 'Model Building', 'M.E.' refers to 'Model Evaluation', and 'Repl.' refers to 'Replicability.'

Study Aspect	Gaps	Opportunities
Focus	<ul style="list-style-type: none">● Current studies predominantly focus on hosts of <i>Schistosoma</i> spp.;● A majority of studies focus on South America, Africa, and east Asia.	<ul style="list-style-type: none">● Model snail intermediate hosts for under-studied systems (Ex: <i>Parafossarulus</i> spp., <i>Bithynia</i> spp., <i>Lymnaea</i> spp., <i>Galba</i> spp., <i>Pseudosuccinea</i> spp., <i>Melanoides</i> spp.);● Model snail hosts in under-represented regions with high prevalence (Ex: There is high prevalence of human and livestock Fascioliasis in the Middle East and Latin America, but few snail SDM studies in those regions (Lan et al., 2024)).
R.V.	<ul style="list-style-type: none">● Justifications as to whether response variable sampling covered the environmental or geographic range available to the taxon is not prevalent in the field.	<ul style="list-style-type: none">● Take steps to ensure that samples are representative of the conditions and areas accessible to the taxa, and screen for implausible records.
P.V.	<ul style="list-style-type: none">● Few studies employed freshwater characteristics as predictor variables;● Predictor variable uncertainty was often not accounted for.	<ul style="list-style-type: none">● Generate consensus projections using various sets of predictors (over different predictors or sources), integrating freshwater characteristics and biotic variables whenever possible.
M.B.	<ul style="list-style-type: none">● Model complexity and response variable bias are not often addressed;● Half of all studies do not account for predictor variable collinearity;● A majority of studies utilize only one SDM algorithm;● All studies here only use correlative, single-species SDM approaches.	<ul style="list-style-type: none">● Use cross-validation or independent datasets to inform model complexity and deal with response variable bias;● Conduct approximate methods to deal with collinearity between predictor variables;● Generate ensemble predictions across modeling algorithms and input data schemes to characterize uncertainty and confidence;● Expand modeling approaches to include Super SDMs, joint SDMs, and mechanistic models.
M.E.	<ul style="list-style-type: none">● Most studies do not test for or address model assumptions;● Current studies generally only evaluate model discrimination.	<ul style="list-style-type: none">● Test for assumption conformation, if assumptions are not met then discuss the impact that violations could have on model outputs;● Use goodness-of-fit metrics and characterize patterns of uncertainty.
Repl.	<ul style="list-style-type: none">● Most studies do not use open access data and code sharing principles;● No study explicitly references globally accepted taxonomies.	<ul style="list-style-type: none">● Share all input data (response and predictor datasets) and code used in analyses;● Include identifiers from global taxonomies (e.g. WoRMS) when listing species modeled.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecoinf.2026.103851>.

Data availability

Files for data and R code used in this manuscript can be found at the GitHub here <https://github.com/ngalle99/SnailHost-SDMreview.git>.

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