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REVIEW
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A Scoping Review of Species Distribution Modeling Methods for Tick Vectors

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Background: Globally, tick-borne disease is a pervasive and worsening problem that impacts human and domestic animal health, livelihoods, and numerous economies. Species distribution models are useful tools to help address these issues, but many different modeling approaches and environmental data sources exist.

Objective: We conducted a scoping review that examined all available research employing species distribution models to predict occurrence and map tick species to understand the diversity of model strategies, environmental predictors, tick data sources, frequency of climate projects of tick ranges, and types of model validation methods.

Design: Following the PRISMA-ScR checklist, we searched scientific databases for eligible articles, their references, and explored related publications through a graphical tool (www.connectedpapers.com). Two independent reviewers performed article selection and characterization using *a priori* criteria.

Results: We describe data collected from 107 peer-reviewed articles that met our inclusion criteria. The literature reflects that tick species distributions have been modeled predominantly in North America and Europe and have mostly modeled the habitat suitability for *Ixodes ricinus* (n = 23; 21.5%). A wide range of bioclimatic databases and other environmental correlates were utilized among models, but the WorldClim database and its bioclimatic variables 1–19 appeared in 60 (56%) papers. The most frequently chosen modeling approach was MaxEnt, which also appeared in 60 (56%) of papers. Despite the importance of ensemble modeling to reduce bias, only 23 papers (21.5%) employed more than one algorithm, and just six (5.6%) used an ensemble approach that incorporated at least five different modeling methods for comparison. Area under the curve/receiver operating characteristic was the most frequently reported model validation method, utilized in nearly all (98.9%) included studies. Only 21% of papers used future climate scenarios to predict tick range expansion or contraction. Regardless of the representative concentration pathway, six of seven genera were expected to both expand and retract depending on location, while *Ornithodoros* was predicted to only expand beyond its current range.

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Conclusion: Species distribution modeling techniques are useful and widely employed tools for predicting tick habitat suitability and range movement. However, the vast array of methods, data sources, and validation strategies within the SDM literature support the need for standardized protocols for species distribution and ecological niche modeling for tick vectors.

Keywords: ticks, species distribution models, ecological niche models, habitat suitability models, climate change

INTRODUCTION

An urgency in understanding the geographic occurrence and epidemiology of emerging zoonotic pathogens has led to the continued interest in describing the climate and habitat suitability for ticks and tick-borne diseases (Tkadlec et al., 2018; MacDonald et al., 2019). Due to their impact on human and veterinary health, livelihoods, and numerous global economies (Jongejan and Uilenberg, 2004), identifying and prioritizing interventions for surveillance, prevention, and control of ticks is of the utmost importance (Signorini et al., 2019; Zanet et al., 2020). Globally, ticks and their associated pathogens cost billions of dollars annually in control measures, lost revenue due to livestock infestations and infection, and medical care (Jongejan and Uilenberg, 2004). Therefore, developing tools that identify suitable habitat for ticks can assist with creating strategies to slow the spread of both the ticks and tick-borne diseases, and further the understanding of environmental factors necessary for tick survival and reproduction (Wilson, 1996; Hahn et al., 2016). Knowledge of how climatic and habitat characteristics determine patterns of tick presence can be accomplished using species distribution models (SDM, Estrada-Peña et al., 2016).

Species distribution models, also referred to as ecological niche models and habitat suitability models [despite differences in depth of focus on defining fundamental species niches among these approaches (Peterson and Soberón, 2012)], represent a suite of statistical and machine-learning tools for predicting suitable species habitat ranges and niches based on correlated environmental conditions (Guisan and Zimmermann, 2000; Franklin, 2010; Peterson et al., 2011). These strategies range from deterministic (e.g., logistic regression) to stochastic (e.g., Bayesian regression trees) approaches, and utilize numerous model validation techniques. With the introduction of the BIOCLIM bioclimatic dataset in the mid-1980s, SDMs were applied to an increasing number of organisms over vast geographies (Booth, 2018). Improvements in modeling power and complexity occurred over the next several decades, but noted limitations still exist in both inherent sampling bias (Phillips et al., 2009; Eisen and Eisen, 2021; Mader et al., 2021) and autocorrelation (Veloz, 2009) of data sources, model assumptions (Stockwell and Peterson, 2002; Lobo et al., 2008; Peterson et al., 2008), and a lack of standardized reporting approaches to modeling parameters to ensure reproducibility (Feng et al., 2019; Wunderlich et al., 2019). Additionally, performance comparisons demonstrate that not all models are equally robust or appropriate depending on the species and its ecology (Stockwell and Peterson, 2002; Qiao et al., 2015; Wunderlich et al., 2019), therefore documenting the variety of SDMs used to predict tick distributions is critical to more thoroughly understanding the extent of their abilities and their limitations.

Predicting the global distributions of tick species often involves the use of climate projections to account for forecasted changes in abiotic conditions which subsequently affect tick survival. To effectively incorporate abiotic variables, many models use bioclimatic variables that summarize raster data derived from mean monthly temperature and precipitation to estimate climate ranges meaningful for biological species ([1]Fick and Hijmans, 2017). Of the 19 bioclimatic variables available, only 15 are now considered to be suitable for habitat suitability modeling due to presence of spatial artifacts among estimates of mean temperature of wettest and driest quarter (BIO 8–9) and precipitation of warmest and driest quarter (BIO 18–19; Escobar et al., 2014). In concert with spatial data on vegetation composition and/or elevation data, SDMs can be incorporated into climate projections using either Intergovernmental Panel on Climate Change (IPCC) climate scenarios or Representative Concentration Pathways (R) with or without the use of Global Circulation Models (GCMs). Global Circulation Models are mathematical representations of the physical processes in the atmosphere, ocean, cryosphere and land surface, where with the many GCMs available, it is crucial to distinguish between the nuances in how climate values are estimated and how these results impact spatial variability in species distributions (Guevara et al., 2019). In contrast, climate and RCP emission scenarios (e.g., A2, A2A, B2A, RCP 4.5, RCP 6.0, RCP 8.5) represent predictions of climate outcomes based on greenhouse gas and aerosol concentrations and land use change (Jubb et al., 2013). For example, RCP 4.5 is the lowest-emission scenario where atmospheric carbon is 650 parts per million (ppm) and stabilizes after the year 2100, whereas RCP 8.5 is the highest-emission scenario with > 1,370 ppm atmospheric carbon (Arora et al., 2011; Jubb et al., 2013). Combining both GCMs and climate projection scenarios allow for a greater understanding of how tick species distributions can potentially shift because of suitable habitat availability.

Species distribution models are relatively new in their application to tick vectors, and a standardized approach for reproducibility does not exist for data inclusion, model ensembles, and validation methods (Feng et al., 2019). Additionally, the focus on projecting distributions based on future climate scenarios for different species presents multiple possibilities for tick control and mitigation. These reasons make a scoping review a practical and useful approach to systematically

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[1] http://www.worldclim.org

examine, evaluate, and identify any gaps within the literature on this topic. A previous scoping review demonstrated the gaps in SDM studies involving ticks within the *Amblyomma* genus in conjunction with rickettsial bacteria, a major global pathogen of human and veterinary concern (Lippi et al., 2021a). Similarly, a recent systematic review sought to examine the past 20 years of distribution modeling on ticks and tick-borne pathogens, with a focused meta-analysis on 20 SDM studies conducted in Africa (Zannou et al., 2021). Our study sought to understand the state of SDM research surrounding all tick vectors since the beginning of SDM algorithms because differences in habitat requirements across species may impact the types of algorithms, environmental correlates, and modeling approaches chosen.

We conducted a scoping review examining all available peer-reviewed literature that employed habitat suitability and species distribution models to predict occurrence of tick species for the purposes of documenting the diversity of model algorithms and strategies, abiotic and biotic environmental predictors, tick occurrence data sources, types of model validation methods, and frequency and source of climate projection data for forecasting of future tick occurrence.

MATERIALS AND METHODS

Following the Preferred Reporting Items for Systematic Reviews and Meta-analyses (PRISMA) guidelines for scoping reviews (Tricco et al., 2018), we conducted literature searches through August 2021, using the databases Web of Science[2] and PubMed[3] since evidence suggests their keyword search tools together offer the best article update frequency and longitudinal coverage (Falagas et al., 2008). Our search criteria for all databases included "ticks" [AND] "species distribution model," [OR] "habitat suitability model," [OR] "ecological niche model." We selected all resulting peer-reviewed articles published in English, or with English translations, with no publication date or study region exclusions. Secondary and tertiary literature searches for additional publications meeting these search criteria were conducted by reviewing references from the initial search results, and by entering the original search results into Connected Papers[4], a graphical literature search tool that uses the concepts of co-citation and bibliographic coupling to compile relevant paper lists and graphics from Semantic Scholar Paper Corpus (Ammar et al., 2018). Duplicate papers were removed, and the final list was examined for eligibility by two independent reviewers.

We excluded records that were not primary research articles (e.g., reviews or synthesis articles), and did not include a statistical or machine learning modeling algorithm for evaluating tick distribution (e.g., articles that included a simple description of habitat types that a tick was found occupying). The remaining articles were assessed for relevant information including year of publication, where the study was published or conducted, study aims/purpose, tick species, modeling methodology, type of surveillance data used (active/passive), environmental or other correlative variables, and climate projections. Data were extracted and charted from the full-text versions of the articles. Currently, scoping review protocols are not eligible for registration in PROSPERO, so we instead deposited this protocol and relevant files in Open Science Framework[5].

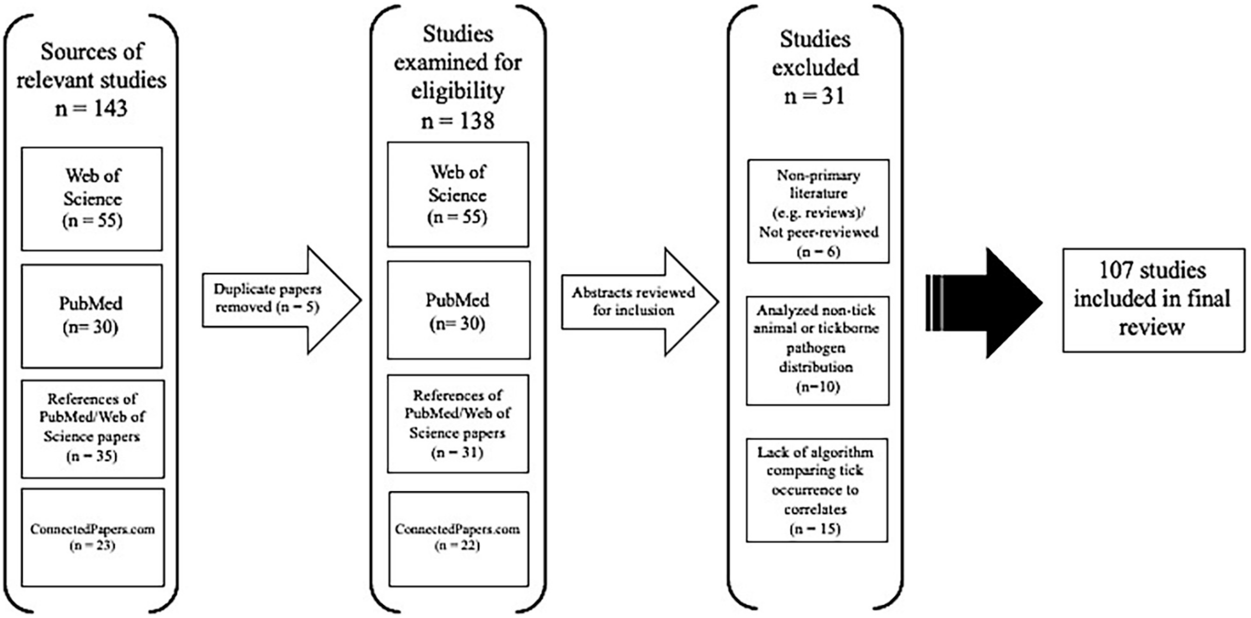

FIGURE 1 | Flow chart of tick species distribution model (SDM) article inclusion and exclusion based on PRISMA criteria.

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[2] https://clarivate.com/webofsciencegroup/solutions/web-of-science/

[3] www.ncbi.nlm.nih.gov/pubmed

[4] www.connectedpapers.com

[5] http://www.osf.io/bd6qn

TABLE 1 | Summary of tick species (n = 95) modeled across all included literature (n = 107), and frequency of each species' appearance.

Tick species modeled	Frequency	References
Amblyomma americanum	10	Brown et al., 2011; Springer et al., 2015; Raghavan et al., 2016a, 2019b, 2020; Kessler et al., 2019a,b; Mangan et al., 2018; Pascoe et al., 2019; Glass et al., 2021
Amblyomma cajennense	4	Illoldi-Rangel et al., 2012; de Oliveira et al., 2017; Acevedo-Gutiérrez et al., 2018; Pascoe et al., 2019
Amblyomma dissimile	1	Polo et al., 2021
Amblyomma dubitatum	1	Donalisio et al., 2020
Amblyomma hebraeum	4	Estrada-Peña, 2003a; Estrada-Peña et al., 2007b; Estrada-Peña and Thuiller, 2008; Yawa et al., 2018
Amblyomma maculatum	1	Pascoe et al., 2019
Amblyomma mixtum	1	Pascoe et al., 2019
Amblyomma rotundatum	1	Polo et al., 2021
Amblyomma sculptum	2	de Oliveira et al., 2017; Donalisio et al., 2020
Amblyomma spp.	3	Cumming, 2000, 2002; Clarke-Crespo et al., 2020
Amblyomma testudinarium	1	Namgyal et al., 2021
Amblyomma variegatum	2	Estrada-Peña et al., 2007a,b; Estrada-Peña and Thuiller, 2008
Aponoma spp.	1	Cumming, 2000
Argas spp.	3	Cumming, 2000, 2002; Zhao et al., 2021
Boophilus spp.	2	Cumming, 2000, 2002
Dermacentor marginatus	9	Estrada-Peña et al., 2004, 2013a,b; Estrada-Peña and Venzal, 2007; Torina et al., 2008; Ceballos et al., 2014; Williams et al., 2015; Walter et al., 2016; Wang et al., 2019; Huercha et al., 2020
Dermacentor nuttalli	1	Wang et al., 2019
Dermacentor occidentalis	1	Eisen L. et al., 2006
Dermacentor reticulatus	2	Estrada-Peña et al., 2013a; Tkadlec et al., 2018
Dermacentor silvarum	2	Sun et al., 2017; Wang et al., 2019
Dermacentor spp.	4	Cumming, 2000, 2002; Clarke-Crespo et al., 2020; Zhao et al., 2021
Dermacentor variabilis	9	Eisen L. et al., 2006; Atkinson et al., 2012; James et al., 2015; St. John et al., 2016; Minigan et al., 2018; Kessler et al., 2019b; Boorgula et al., 2020; Glass et al., 2021; Lippi et al., 2021b
Haemaphysalis bispinosa	1	Namgyal et al., 2021
Haemaphysalis concinna	1	Sun et al., 2017
Haemaphysalis elliptica	1	Yawa et al., 2018
Haemaphysalis japonica	1	Sun et al., 2017
Haemaphysalis leporispalustris	2	Eisen L. et al., 2006; Gabriele-Rivet et al., 2015
Haemaphysalis longicornis	7	Du et al., 2014; Lawrence et al., 2017; Raghavan et al., 2019a; Rochlin, 2019; Miao et al., 2020; Namgyal et al., 2020; Zhao et al., 2021
Haemaphysalis punctata	3	Estrada-Peña et al., 2004, 2013a; Ceballos et al., 2014
Haemaphysalis silacea	2	Yawa et al., 2018
Haemaphysalis spinigera	2	Namgyal et al., 2021
Haemaphysalis spp.	3	Cumming, 2000, 2002; Zhao et al., 2021
Haemaphysalis sulcata	2	Estrada-Peña et al., 2013a; Williams et al., 2015
Hyalomma anatolicum	1	Estrada-Peña et al., 2013a,b
Hyalomma excavatum	2	Estrada-Peña and Venzal, 2007; Estrada-Peña et al., 2013a
Hyalomma impeltatum	1	Estrada-Peña et al., 2013a
Hyalomma lusitanicum	2	Estrada-Peña et al., 2013a; Williams et al., 2015
Hyalomma marginatum	7	Estrada-Peña et al., 2007c, 2013a, 2015b; Estrada-Peña and Venzal, 2007; Torina et al., 2008; Williams et al., 2015
Hyalomma rufipes	1	Yawa et al., 2018
Hyalomma scupense	1	Estrada-Peña et al., 2013a
Hyalomma spp.	4	Cumming, 2000, 2002; Messina et al., 2015; Zhao et al., 2021
Hyalomma truncatum	1	Estrada-Peña, 2003a
Ixodes angustus	1	Eisen L. et al., 2006
Ixodes auritulus	1	Eisen L. et al., 2006
Ixodes boliviensis	1	Illoldi-Rangel et al., 2012
Ixodes canisuga	1	Estrada-Peña et al., 2013a
Ixodes conepati	1	Illoldi-Rangel et al., 2012
Ixodes cookei	1	Illoldi-Rangel et al., 2012
Ixodes eadsi	1	Illoldi-Rangel et al., 2012
Ixodes frontalis	1	Ceballos et al., 2014
Ixodes hexagonus	1	Estrada-Peña et al., 2013a
Ixodes kingi	1	Illoldi-Rangel et al., 2012
Ixodes marxi	1	Illoldi-Rangel et al., 2012
Ixodes muris	1	Gabriele-Rivet et al., 2015
Ixodes ovatus	1	Sun et al., 2017
Ixodes pacificus	4	Eisen R. J. et al., 2006; Hahn et al., 2016; MacDonald et al., 2019, 2020

(Continued)

TABLE 1 | (Continued)

Tick species modeled	Frequency	References
Ixodes persulcatus	3	Tokarevich et al., 2011; Sun et al., 2017; Ala-Hulkko et al., 2019
Ixodes pilosus	1	Yawa et al., 2018
Ixodes ricinus	23	Estrada-Peña, 1999b; Estrada-Peña et al., 2005, 2006b, 2013a,b, 2015a; Torina et al., 2008; Jaenson and Lindgren, 2010; Porretta et al., 2013a,b; Boeckmann and Joyner, 2014; Ceballos et al., 2014; Jore et al., 2014; Boehnke et al., 2015; Williams et al., 2015; Tkadlec et al., 2018; Aivelo et al., 2019; Ala-Hulkko et al., 2019; Li et al., 2019; Signorini et al., 2019; Fernández-Ruiz and Estrada-Peña, 2020; Walter et al., 2020; Zanet et al., 2020; Rochat et al., 2021
Ixodes scapularis	16	Estrada-Peña, 2002b; Guerra et al., 2002; Brownstein et al., 2003, 2005; Diuk-Wasser et al., 2010; Illoldi-Rangel et al., 2012; Feria-Arroyo et al., 2014; Gabriele-Rivet et al., 2015; Hahn et al., 2016; Johnson et al., 2016; Peterson and Raghavan, 2017; Lieske and Lloyd, 2018; Soucy et al., 2018; Kessler et al., 2019b; Slatculescu et al., 2020; Glass et al., 2021
Ixodes sculptus	1	Illoldi-Rangel et al., 2012
Ixodes spinipalpis	1	Eisen R. J. et al., 2006
Ixodes spp.	4	Cumming, 2000; Clarke-Crespo et al., 2020; Namgyal et al., 2021; Zhao et al., 2021
Ornithodoros alactagalis	1	Vial et al., 2018
Ornithodoros asperus	1	Vial et al., 2018
Ornithodoros erraticus	1	Vial et al., 2018
Ornithodoros hermsi	1	Sage et al., 2017
Ornithodoros lahorensis	1	Moradi-Asl and Jafari, 2020
Ornithodoros nereensis	1	Vial et al., 2018
Ornithodoros papillipes	1	Vial et al., 2018
Ornithodoros sonrai	1	Vial et al., 2018
Ornithodoros tartakovskyi	1	Vial et al., 2018
Ornithodoros tholozani	2	Vial et al., 2018; Moradi-Asl and Jafari, 2020
Ornithodoros turicata	1	Donaldson et al., 2016
Ornithodoros verrucosus	1	Vial et al., 2018
Ornithodoros spp.	1	Cumming, 2000
Otobius megnini	1	Estrada-Peña et al., 2010
Otobius spp.	1	Cumming, 2000
Rhipicentor spp.	1	Cumming, 2000
Rhipicephalus annulatus	5	Estrada-Peña and Venzal, 2007; Torina et al., 2008; Estrada-Peña et al., 2013a; Giles et al., 2014; Williams et al., 2015
Rhipicephalus appendiculatus	5	Estrada-Peña, 2003a; Olwoch et al., 2003; Leta et al., 2013; Vajana et al., 2018; Yawa et al., 2018
Rhipicephalus bursa	5	Estrada-Peña et al., 2004, 2013a; Estrada-Peña and Venzal, 2007; Torina et al., 2008; Williams et al., 2015
Rhipicephalus capensis	1	Olwoch et al., 2003
Rhipicephalus decoloratus	4	Estrada-Peña, 2002a, 2003a; Sungirai et al., 2018; Yawa et al., 2018
Rhipicephalus evertsi evertsi	1	Yawa et al., 2018
Rhipicephalus follis	1	Yawa et al., 2018
Rhipicephalus haemaphysaloides	1	Namgyal et al., 2021
Rhipicephalus longus	1	Olwoch et al., 2003
Rhipicephalus microplus	11	Estrada-Peña, 1999a, 2006; Estrada-Peña et al., 2005, 2006a,d; Sutherst and Bourne, 2009; De Clercq et al., 2013, 2015; Giles et al., 2014; Sungirai et al., 2018; Marques et al., 2020; Namgyal et al., 2021
Rhipicephalus sanguineus sensu lato	2	Estrada-Peña et al., 2013a; Alkishe et al., 2020
Rhipicephalus simus	1	Yawa et al., 2018
Rhipicephalus spp.	7	Cumming, 2000; Ceballos et al., 2014; Estrada-Peña et al., 2014; Alcala-Canto et al., 2018; Hadgu et al., 2019; Clarke-Crespo et al., 2020; Zhao et al., 2021
Rhipicephalus turanicus	3	Estrada-Peña et al., 2004; Estrada-Peña and Venzal, 2007; Torina et al., 2008
Rhipicephalus zambeziensis	1	Olwoch et al., 2003
Total number of tick species modeled		Total number of tick distribution modeling studies
95		107

RESULTS

Our literature search, after duplicate article removal and examination of references and related papers, revealed 138 peer-reviewed articles on species distribution models and tick vectors that were assessed for eligibility (**Figure 1**). Fifteen studies were removed from consideration because they lacked a statistical algorithm that evaluated tick occurrence based on abiotic or biotic environmental correlates. Six papers were excluded from analysis because they were reviews, not a primary literature article, or were gray literature (i.e., not peer-reviewed), and 10 papers were removed from analysis because they focused the ecological niche analysis primarily on a tick-borne pathogen or a non-tick animal. A total of 107 full-text articles were included in the final analysis (**Figure 1**).

Species Geographic Representation Over Time

Within this collection of 107 papers, 95 tick species representing 12 genera (**Table 1**) were modeled across six continents between the years of 1998 to 2021 (**Figure 2**). Seventy-three percent of these studies were published within the past decade (**Figure 2**). The most frequently modeled species was

Ixodes ricinus (23 papers), followed by *Ixodes scapularis* (16 papers), *Amblyomma americanum* (10 papers), *Rhipicephalus microplus* (10 papers), *Dermacentor marginatus* (nine papers), and *Dermacentor variabilis* (nine papers) (**Table 1**). Most tick distribution modeling studies represented species that are endemic to or invading the North American continent (51%; 55/107), followed by those species present in Europe (30%; 32/107), Africa (26%; 28/107), Asia (15%; 16/107), Australia (2.8%; 3/107), and lastly, two studies modeled *Rhipicephalus* species that have distributions spanning several continents (**Figure 3**).

Tick Occurrence and Environmental Data Sources

Tick occurrence records were sourced from a variety of collections worldwide that included both active (*n* = 21) and passive (*n* = 16) surveillance methods, often both within a single paper (*n* = 106). The most frequently used source of tick location data was published literature records (*n* = 62), followed by field collections (*n* = 30) conducted by the authors (**Figure 4**). Four publicly accessible, internet-based databases of tick occurrence records were also observed in the literature, namely the Global Biodiversity Information Facility (GBIF) (*n* = 8), Walter Reed Biosystematics Unit (WBRU) (*n* = 7), VectorMap (*n* = 6), and Biodiversity Information Serving our Nation (BISON) (*n* = 1) (**Figure 4**).

There were 60 different databases and sources of environmental and other correlates used across the included literature (**Supplementary Table 1**). The most frequently used database for abiotic variables was WorldClim, included in just over half (56%) of papers. Variables representing tick host presence were rarely included and appeared in the form of host availability in only two papers (Li et al., 2019; Miao et al., 2020).

The finest scale resolution observed for environmental correlates was 15 m^2 for elevation and land cover data extracted from the Southern Ontario Land Resource Information System (SOLRISv3.0) (Soucy et al., 2018; Slatculescu et al., 2020),

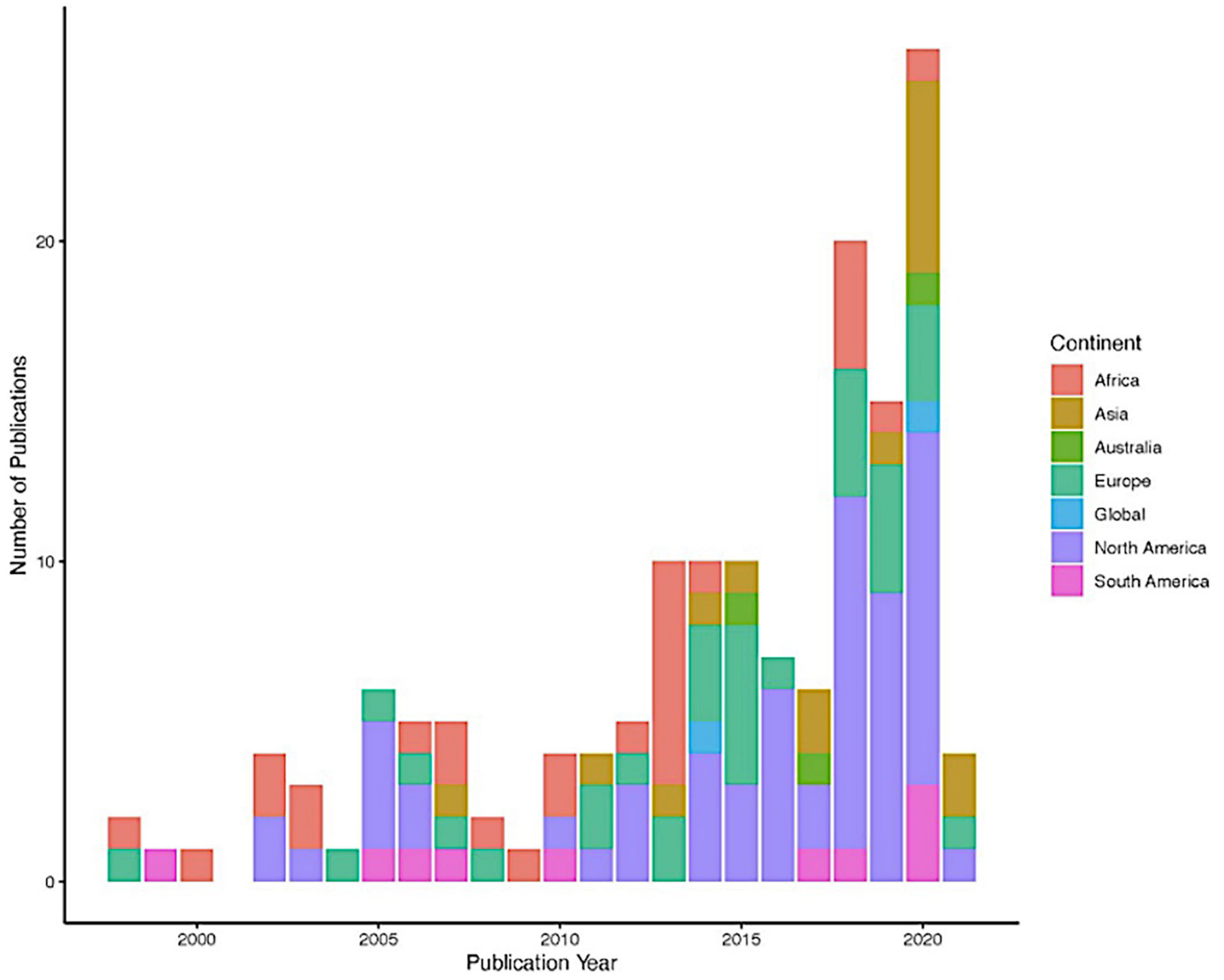

FIGURE 2 | Timeline of included published tick species distribution literature.

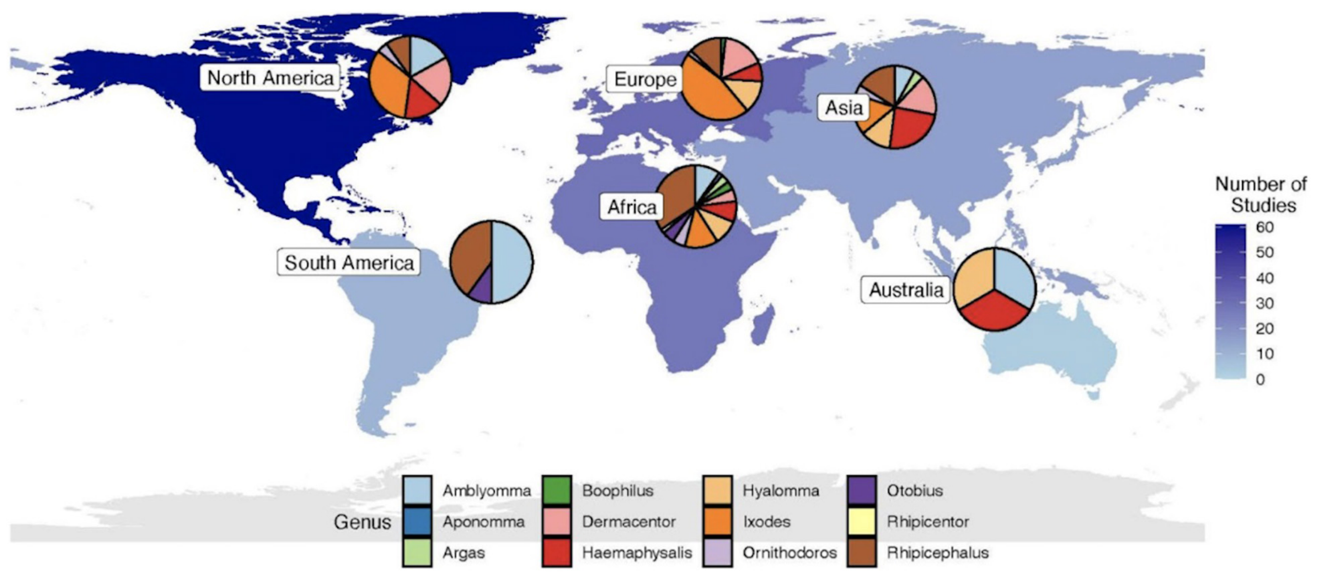

FIGURE 3 | Global distribution of included tick habitat suitability studies by tick genus.

while the coarsest scale observed was 600 km^2 for rainfall, temperature, vegetation type, NDVI, and elevation from the Center for Resource and Environmental Studies (Cumming, 2002; **Supplementary Table 1**). Most papers examined tick distribution probabilities at a spatial resolution between 1 and 10 km^2 (n = 65) (**Supplementary Table 1**). Analyses in 12 papers were conducted at a spatial resolution less than 1 km^2, and tick species distribution modeling was performed in 18 papers at spatial resolutions greater than 10 km^2 (**Supplementary Table 1**). Finally, 12 papers did not report the spatial resolution at which the analysis was performed.

Modeling and Validation Methods

Thirty-two different habitat distribution modeling methods were represented in this sample of publications. The most frequently chosen modeling approaches were maximum entropy, otherwise known as MaxEnt, which appeared in 56% of papers (n = 60), followed by generalized linear models (n = 24; 22.4%) (**Figure 5** and **Table 2**). The remaining methods were used nine times or fewer, each accounting for less than 10% of the remaining papers (**Figure 5** and **Table 2**). Only 23 papers (21.5%) employed more than one algorithm, and just six (5.6%) used an ensemble approach that incorporated at least five different modeling methods for comparison and weighted averaging across the interpolated surface (**Table 2**).

There were 22 different model validation methods reported across 99 articles (**Figure 6** and **Table 3**). The most frequently employed evaluation strategies were receiver operating characteristic/area under the curve (ROC/AUC) (98 occurrences; 98.9% of articles), Akaike's information criterion (41; 41.8%), k-fold cross validation (30; 30.6%), measures of sensitivity and specificity (30; 30.6%), one of several correlation coefficients (18; 18.2%), and kappa index of agreement (11; 11.1%) (**Figure 6**). The remaining validation methods were reported once or twice across all included literature. More than half of papers with validation methods reported (49; 60.6%) used two or more evaluation techniques for each model. Ten papers (roughly 9% of the total papers included in this review) either did not include a description of validation methods, or supplemental files with this information were not available.

Future Climate Projections

There were 23 studies that included future climate projections, representing seven tick genera and 27 species (**Table 4**). Of these, only 65% of studies (15/23) used climate projections with the most used climate projection being MIROC (8; 53%), followed by CCSM (6; 40%) and NCAR (4; 26%). Note that multiple climate projection scenarios were used in a study, often as a comparison, with an average of approximately four climate projections used per study. In contrast, 86% of studies (20/23) used AB (5; 25%) or Representative Concentration Pathways (RCP, 15; 75%) emission scenarios. For RCP emissions scenarios, the most used scenario was 8.5 (14; 93%), followed closely by RCP 4.5 (13; 86%), while the most used Special Report on Emissions Scenarios (SRES) scenario was A2 (4; 80%). Eleven studies used environmental data such as NDVI, vegetation cover and elevation to parameterize their models and 14/23 used BIOCLIM data.

For the seven tick genera, twenty studies used climate models to predict both global expansion and retraction of suitable habitat (**Table 5**). All genera (6/7) were expected to both expand and retract, except for *Ornithodoros* where only expansion was predicted. Of these studies, *Rhipicephalus* habitat suitability was predicted by seven studies (35%), with the range of *Ixodes* predicted by six studies (30%), followed by *Amblyomma* which was found in five studies (25%). In contrast, the habitat

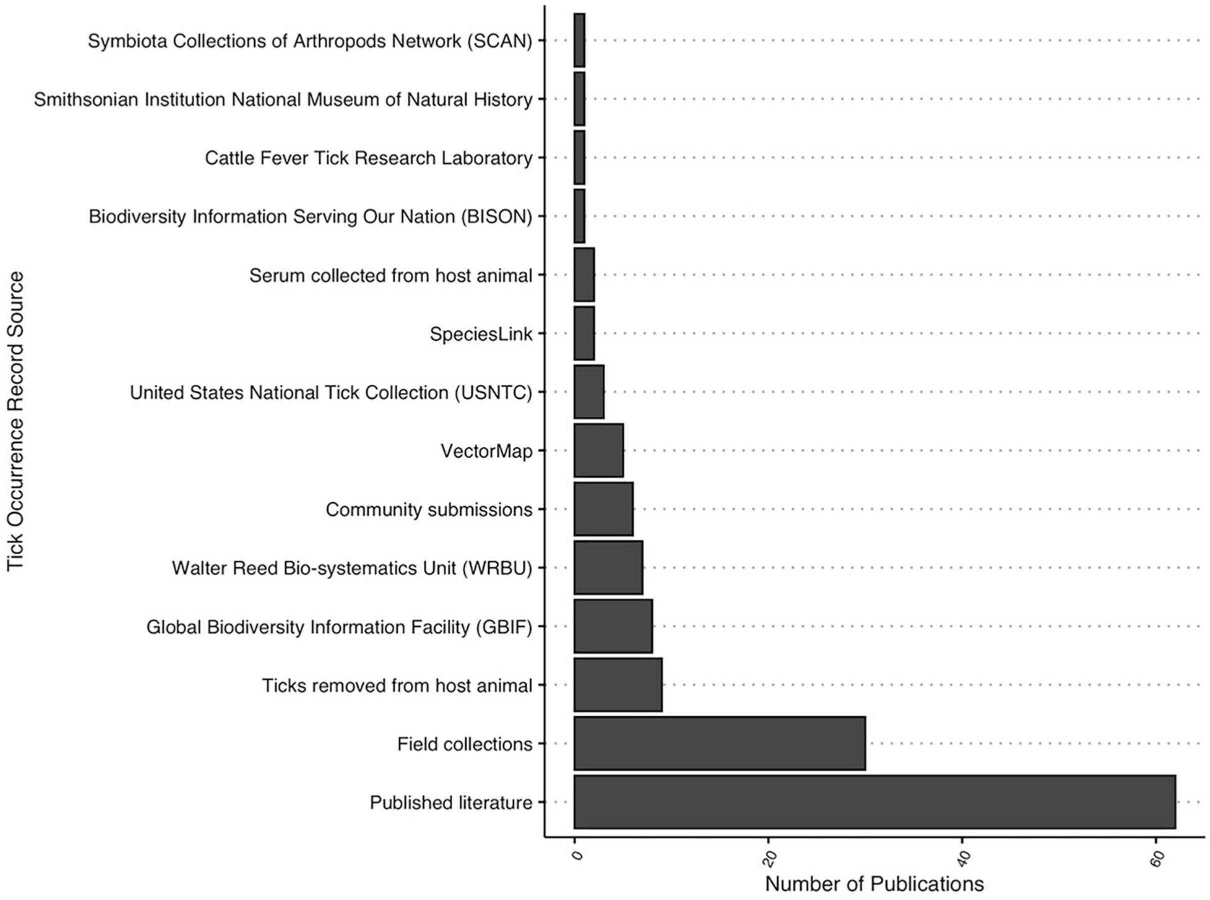

FIGURE 4 | Sources (*n* = 14) of tick occurrence data reported within included distribution modeling papers.

suitability, and future species distributions of *Dermancentor* and *Ornithodoros* were only forecasted by one study each.

DISCUSSION

Our scoping review of tick vector species distribution modeling literature identified 107 papers that represent a wide array of tick occurrence record sources, environmental correlates, model validation strategies, and future climate-related scenarios for tick habitat suitability and distributions. However, we found that certain modeling strategies and data sources are more frequently used than others. MaxEnt, a machine-learning application, was the most used algorithm, appearing in 56% of papers, for predicting tick habitat suitability and distributions. This modeling approach is often favored because it only requires knowledge of species presence locations and generates pseudo-absences to complete the background locations to predict the distribution of a species (Phillips et al., 2006). It is reported to routinely perform better than other presence-only models (Elith et al., 2006; Merow et al., 2013) and is also highly accessible in both open-source R programming packages as well as its own software and is highly user-friendly (Phillips et al., 2006). A recent comparison of presence-absence model performance found little difference in the general performance (accuracy, discrimination, calibration, and precision) of most of these other model strategies, however, the authors caution that because poorly performing models can generate overfit predictions and overconfident estimations, it is important to work within sets of models first that are complementary within their assumptions before creating multi-model ensembles (Norberg et al., 2019). Overall, machine-learning approaches appear to be a popular choice for predicting tick distributions and habitat associations, though relatively few studies incorporated model ensembles despite the importance of controlling for individual model biases and ecological circumstances to reduce uncertainty (Marmion et al., 2009; Roura-Pascual et al., 2009; Qiao et al., 2015), or to simply highlighting model agreement and disagreement (Stohlgren et al., 2010).

Within this body of tick distribution modeling literature were dozens of different tick occurrence data sources that include both active and passive surveillance methods. Given the absence of standardized collection efforts and data recording and data availability across large spatial areas, many types and sources of occurrence records were combined without controlling for sampling biases. Tick occurrence data is inherently biased due

TABLE 2 | Summary of species distribution modeling methods and associated tick species represented among studies that met scoping review inclusion criteria.

Species distribution modeling method	Tick species modeled	References
Agent-based modeling (*n* = 2)	*Ixodes ricinus; Rhipicephalus decoloratus*	Estrada-Peña, 2002a; Li et al., 2019
ANCOVA (*n* = 1)	*Dermacentor reticulatus; Ixodes ricinus*	Tkadlec et al., 2018
Bioclimatic envelope model (*n* = 7)	*Amblyomma* spp.; *Ixodes* spp.; *Dermacentor* spp.; *Rhipicephalus* spp.; *Dermacentor marginatus*; *Haemaphysalis longicornis*; *Ixodes ricinus*; *Rhipicephalus appendiculatus; Rhipicephalus capensis; Rhipicephalus longus; Rhipicephalus microplus; Rhipicephalus zambeziensis*	Olwoch et al., 2003; Estrada-Peña et al., 2005, 2006b; Walter et al., 2016; Lawrence et al., 2017; Li et al., 2019; Clarke-Crespo et al., 2020
Boosted regression trees (BRT) (*n* = 9)	*Amblyomma americanum; Argas* spp.; *Dermacentor silvarum; Dermacentor variabilis; Haemaphysalis concinna; Haemaphysalis japonica; Haemaphysalis longicornis; Hyalomma* spp.; *Ixodes ovatus; Ixodes pacificus; Ixodes persulcatus; Ixodes scapularis; Rhipicephalus* spp.	Messina et al., 2015; Springer et al., 2015; Hahn et al., 2016; Sun et al., 2017; Kessler et al., 2019b; Miao et al., 2020; Glass et al., 2021; Lippi et al., 2021b; Zhao et al., 2021
Classification and regression trees (CART) (*n* = 1)	*Amblyomma* spp.;, *Ixodes*, spp.; *Dermacentor* spp.; *Rhipicephalus* spp.	Clarke-Crespo et al., 2020
Climate response model (CLIMEX) (*n* = 1)	*Rhipicephalus microplus*	Sutherst and Bourne, 2009
Cokriging (*n* = 2)	*Ixodes ricinus; Rhipicephalus microplus*	Estrada-Peña, 1999a,b
Correspondence analysis (*n* = 1)	*Ixodes ricinus*	Jaenson and Lindgren, 2010
DOMAIN procedure (*n* = 1)	*Ixodes scapularis*	Estrada-Peña, 2002b
Ecological niche factor analysis (*n* = 1)	*Dermacentor marginatus; Hyalomma excavatum; Hyalomma marginatum; Rhipicephalus annulatus; Rhipicephalus bursa; Rhipicephalus turanicus*	Estrada-Peña and Venzal, 2007
Fourier analysis (*n* = 3)	*Amblyomma hebraeum*; *Dermacentor marginatus*; *Dermacentor reticulatus*; *Haemaphysalis punctata*; *Haemaphysalis sulcata; Hyalomma anatolicum*; *Hyalomma excavatum*, *Hyalomma impeltatum; Hyalomma lusitanicum; Hyalomma marginatum; Hyalomma scupense Hyalomma truncatum; Ixodes canisuga; Ixodes hexagonus; Ixodes ricinus; Rhipicephalus annulatus; Rhipicephalus appendiculatus*; *Rhipicephalus bursa; Rhipicephalus decoloratus*; *Rhipicephalus sanguineus* sensu lato	Estrada-Peña, 2003a; Estrada-Peña et al., 2013a, 2014
Generalized additive models (GAM) (*n* = 4)	*Ixodes persulcatus; Ixodes ricinus; Dermacentor variabilis*	Estrada-Peña et al., 2005; Tokarevich et al., 2011; Jore et al., 2014; Lippi et al., 2021b
Generalized linear models (GLM) (*n* = 24)	*Amblyomma americanum; Amblyomma hebraeum; Amblyomma* spp.; *Amblyomma testudinarium; Argas* sp.; *Boophilus* spp.; *Dermacentor marginatus; Dermacentor occidentalis; Dermacentor* spp.; *Dermacentor variabilis; Haemaphysalis bispinosa; Haemaphysalis elliptica; Haemaphysalis leporispalustris; Haemaphysalis punctata; Haemaphysalis silacea; Haemaphysalis spinigera; Haemaphysalis* spp., *Hyalomma rufipes; Hyalomma* spp.; *Ixodes angustus; Ixodes auritulus; Ixodes muris; Ixodes pacificus; Ixodes pilosus; Ixodes ricinus; Ixodes scapularis; Ixodes spinipalpis; Ixodes* spp.; *Ornithodoros* spp.; *Rhipicephalus bursa; Rhipicephalus decoloratus; Rhipicephalus evertsi evertsi; Rhipicephalus follis; Rhipicephalus haemaphysaloides; Rhipicephalus microplus; Rhipicephalus simus; Rhipicephalus turanicus*	Cumming, 2000, 2002; Guerra et al., 2002; Brownstein et al., 2003; Estrada-Peña et al., 2004; Brownstein et al., 2005; Eisen R. J. et al., 2006; Estrada-Peña et al., 2006d; Sutherst and Bourne, 2009; Brown et al., 2011; Jore et al., 2014; De Clercq et al., 2015; Gabriele-Rivet et al., 2015; Springer et al., 2015; Hahn et al., 2016; Sungirai et al., 2018 Vajana et al., 2018; Yawa et al., 2018; Kessler et al., 2019a,b; Clarke-Crespo et al., 2020; Glass et al., 2021; Lippi et al., 2021b; Namgyal et al., 2021
Genetic algorithm for rule-set prediction (GARP) (*n* = 3)	*Amblyomma cajennense; Ixodes ricinus; Rhipicephalus annulatus; Rhipicephalus microplus*	Boeckmann and Joyner, 2014; Giles et al., 2014; Acevedo-Gutiérrez et al., 2018
Gower metric (*n* = 1)	*Rhipicephalus microplus*	Estrada-Peña et al., 2006a
Joint distribution modeling (*n* = 1)	*Ixodes ricinus*	Aivelo et al., 2019
Linear discriminant analysis (LDA) (*n* = 1)	*Rhipicephalus microplus*	De Clercq et al., 2015
MaxEnt: (*n* = 62)	*Amblyomma americanum; Amblyomma cajennense; Amblyomma dissimile; Amblyomma dubitatum; Amblyomma hebraeum; Amblyomma rotundatum; Amblyomma sculptum; Amblyomma testudinarium; Amblyomma variegatum; Dermacentor marginatus; Dermacentor nuttalli; Dermacentor occidentalis; Dermacentor silvarum; Dermacentor variabilis; Haemaphysalis bispinosa; Haemaphysalis leporispalustris; Haemaphysalis longicornis; Haemaphysalis marginatum; Haemaphysalis punctata; Haemaphysalis spinigera; Haemaphysalis sulcata; Hyalomma lusitanicum; Hyalomma marginatum; Ixodes angustus; Ixodes auritulus; Ixodes boliviensis; Ixodes cookei; Ixodes conepati; Ixodes eadsi; Ixodes kingi; Ixodes marxi; Ixodes pacificus; Ixodes persulcatus; Ixodes ricinus; Ixodes scapularis; Ixodes sculptus; Ixodes spinipalpis; Ixodes texanus; Ornithodoros hermsi; Ornithodoros turicata; Otobius megnini; Rhipicephalus annulatus; Rhipicephalus appendiculatus; Rhipicephalus bursa; Rhipicephalus haemaphysaloides; Rhipicephalus microplus; Rhipicephalus turanicus*	Estrada-Peña et al., 2007a,b,c, 2006b, 2013b, 2014; Estrada-Peña and Thuiller, 2008; Torina et al., 2008; Atkinson et al., 2012; Illoldi-Rangel et al., 2012; De Clercq et al., 2013; Leta et al., 2013; Porretta et al., 2013a,b; Du et al., 2014; Feria-Arroyo et al., 2014; Giles et al., 2014; James et al., 2015; Springer et al., 2015; Williams et al., 2015; Donaldson et al., 2016; Hahn et al., 2016; Johnson et al., 2016; Raghavan et al., 2020, 2016a, 2019a,b, 2020; St. John et al., 2016; de Oliveira et al., 2017; Lawrence et al., 2017; Peterson and Raghavan, 2017; Sage et al., 2017; Acevedo-Gutiérrez et al., 2018; Alcala-Canto et al., 2018; Minigan et al., 2018; Soucy et al., 2018; Ala-Hulkko et al., 2019; Hadgu et al., 2019; Kessler et al., 2019b; MacDonald et al., 2019, 2020; Pascoe et al., 2019; Rochlin, 2019; Signorini et al., 2019; Wang et al., 2019; Alkishe et al., 2020; Boorgula et al., 2020; Clarke-Crespo et al., 2020; Donalisio et al., 2020; Fernández-Ruiz and Estrada-Peña, 2020; Huercha et al., 2020; Marques et al., 2020; Miao et al., 2020; Moradi-Asl and Jafari, 2020; Namgyal et al., 2020, 2021; Slatculescu et al., 2020; Zanet et al., 2020; Glass et al., 2021; Lippi et al., 2021b; Polo et al., 2021; Rochat et al., 2021
Minimum convex polygon (*n* = 1)	*Haemaphysalis longicornis*	Rochlin, 2019
Mixed effect logistic regression (*n* = 1)	*Ixodes persulcatus*	Tokarevich et al., 2011
Mixture discriminant analysis (MDA) (*n* = 1)	*Amblyomma* spp.; *Ixodes* spp.; *Dermacentor* spp.; *Rhipicephalus* spp.	Clarke-Crespo et al., 2020
Multi-criteria decision analysis (*n* = 1)	*Ornithodoros alactagalis; Ornithodoros asperus; Ornithodoros erraticus; Ornithodoros nereensis; Ornithodoros papillipes; Ornithodoros sonrai; Ornithodoros tartakovskyi; Ornithodoros tholozani; Ornithodoros verrucosus*	Vial et al., 2018
Multivariate adaptive regression splines (MARS) (*n* = 5)	*Amblyomma americanum*; *Amblyomma* spp.; *Ixodes pacificus*; *Ixodes scapularis*; *Ixodes* spp.; *Dermacentor* spp.; *Dermacentor variabilis*; *Rhipicephalus* spp.	Springer et al., 2015; Hahn et al., 2016; Kessler et al., 2019b; Clarke-Crespo et al., 2020; Glass et al., 2021
Negative binomial regression (*n* = 1)	*Dermacentor marginatus; Ixodes frontalis; Ixodes ricinus; Haemaphysalis punctata; Rhipicephalus* spp.	Ceballos et al., 2014

(Continued)

TABLE 2 | (Continued)

Species distribution modeling method	Tick species modeled	References
Occupancy models (*n* = 1)	*Ixodes scapularis*	Lieske and Lloyd, 2018
Point-to-point similarity metric (*n* = 2)	*Amblyomma hebraeum; Hyalomma truncatum; Rhipicephalus appendiculatus; Rhipicephalus decoloratus; Rhipicephalus microplus*	Estrada-Peña, 2003a; Estrada-Peña et al., 2006d
Poisson regression (*n* = 3)	*Amblyomma americanum*; *Dermacentor marginatus*; *Haemaphysalis punctata; Ixodes ricinus; Rhipicephalus bursa; Rhipicephalus turanicus*	Estrada-Peña et al., 2004; Boehnke et al., 2015; Mangan et al., 2018
Principle component analysis (PCA) (*n* = 2)	*Dermacentor marginatus; Dermacentor reticulatus; Haemaphysalis punctata; Haemaphysalis sulcata; Hyalomma anatolicum; Hyalomma excavatum; Hyalomma impeltatum; Hyalomma lusitanicum; Hyalomma marginatum; Hyalomma scupense; Ixodes canisuga; Ixodes hexagonus; Ixodes ricinus; Rhipicephalus annulatus; Rhipicephalus bursa; Rhipicephalus sanguineus* sensu lato; *Rhipicephalus turanicus*	Estrada-Peña and Venzal, 2007; Estrada-Peña et al., 2013a,b
Random forest (RF) (*n* = 7)	*Amblyomma americanum*; *Dermacentor variabilis*; *Ixodes pacificus; Ixodes ricinus; Ixodes scapularis; Rhipicephalus microplus*	De Clercq et al., 2015; Springer et al., 2015; Hahn et al., 2016; Kessler et al., 2019b; Walter et al., 2020; Glass et al., 2021; Lippi et al., 2021b
Spatial clustering (*n* = 1)	*Haemaphysalis leporispalustris; Ixodes muris; Ixodes scapularis*	Gabriele-Rivet et al., 2015
Zero-inflated negative binomial (*n* = 2)	*Amblyomma americanum; Ixodes scapularis*	Diuk-Wasser et al., 2010; Mangan et al., 2018
Zero-inflated Poisson regression (*n* = 1)	*Amblyomma americanum*	Mangan et al., 2018

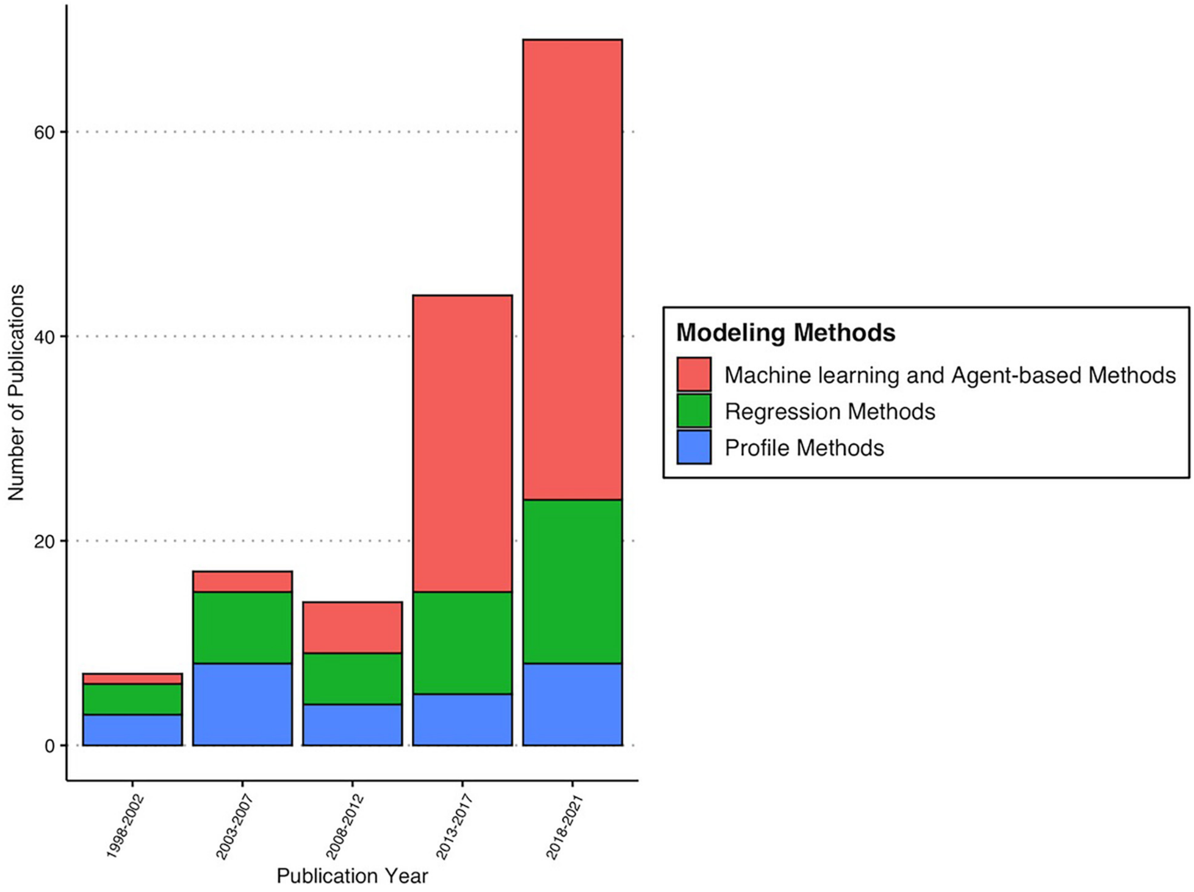

FIGURE 5 | Tick distribution modeling methods* used in included literature over time. *Machine learning/agent-based methods include MaxEnt, genetic algorithm for rule-set prediction, agent-based modeling, boosted regression trees, random forest, and classification and regression trees. Profile methods include DOMAIN procedure, ecological niche factor analysis, bioclimatic envelope model, Cokriging, principal component analysis, ANCOVA, climate response model (CLIMEX), correspondence analysis, Gower metric, joint distribution modeling, linear discriminant analysis, mixture discriminant analysis, multi-criteria decision analysis, minimum convex polygon, occupancy models, point-to-point similarity metric, spatial clustering, and Fourier analysis. Regression methods include generalized linear models, generalized additive models, multivariate adaptive regression splines, mixed effect logistic regression, negative binomial regression, Poisson regression, zero-inflated Poisson regression, and zero-inflated negative binomial regression.

to sampling regime and location uncertainty, and the inclusion of data sources must reflect this (Zizka et al., 2021). In addition, data collection methods vary widely across and within datasets, affecting both the completeness and the accuracy of reported data. Active surveillance for ticks can vary by collection method (dragging/flagging, small mammal trapping, CO2 trapping), by

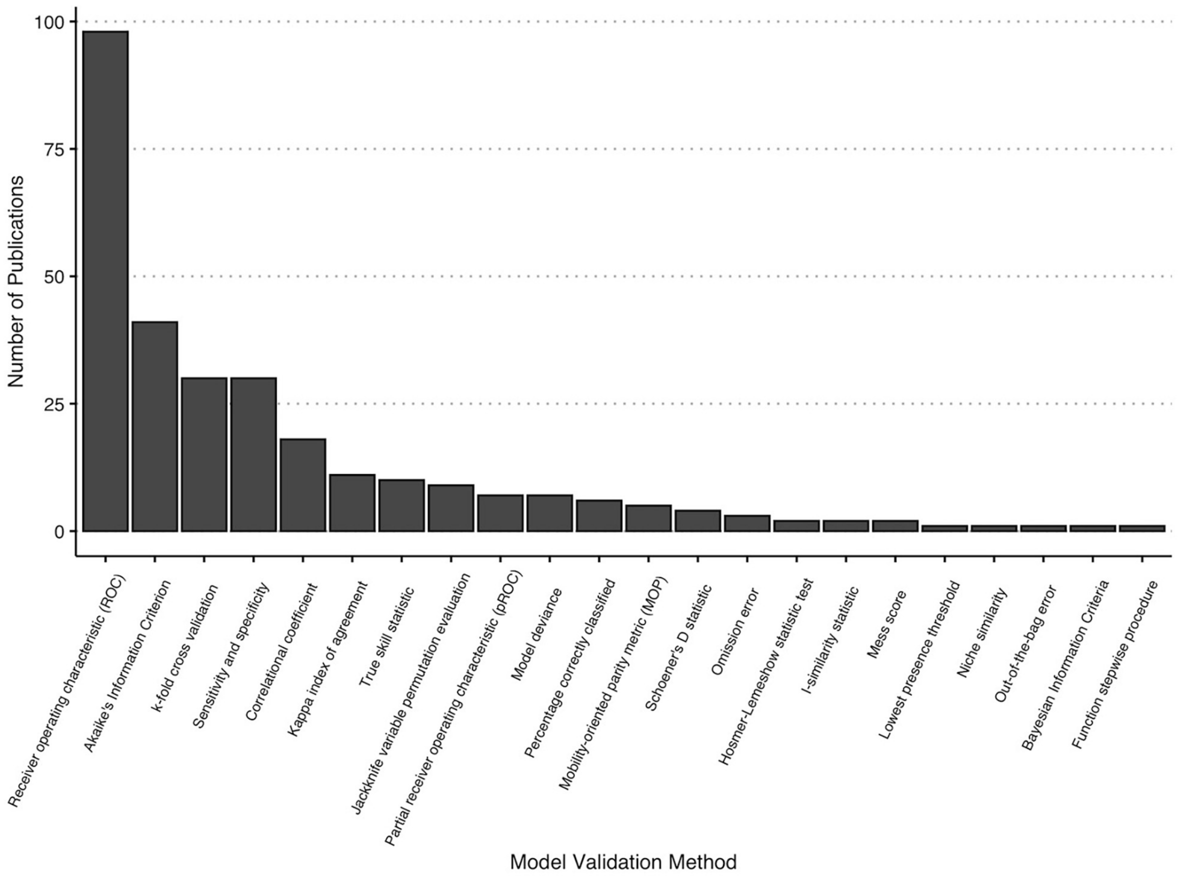

FIGURE 6 | Frequency of model validation methods (n = 22) reported across included literature.

sampling intensity (time, distance/trap density), and by sampling based on habitat, (Rydzewski et al., 2011, 2012) leading to variation in the certainty of absence data (Lyons et al., 2021). This can result in models fitted to sampling effort and not true species distribution (Hendrickx et al., 2021). Passive surveillance varies by participation type and by the accuracy of data collected, from GPS location to self-reported, from tick submission to photo identification to self-report (Eisen and Eisen, 2021). A recent review of passive methods in mosquito surveillance found little coherence among programs, resulting in non-comparable data; similar issues likely exist in passive tick surveillance data (Sousa et al., 2022). Inclusion of these data sources without consideration of the potentially conflicting biases could lead to underestimation of model uncertainty (Kramer-Schadt et al., 2013). Particularly of importance with the most common modeling methods is certainty of location data. Positional uncertainty in data points reduces the prediction accuracy of the model (Naimi et al., 2014), but models may be built using historical databases and natural history collections with widely varying certainty due to changes in location methods (Gilliam et al., 2020), as well as misidentifications, changing taxonomical classifications, and unknown origin of the specimens (Graham et al., 2004). It should be noted, however, that these historical and museum-based records may include a substantial level of detail in the data collected, suggesting that they should not be ignored due to the potential complications in data collection; larger data sets can counteract the effect of positional uncertainty (Mitchell et al., 2017). The importance of positional uncertainty may also be mitigated by spatial autocorrelation among bioclimatic variables (Naimi et al., 2014), particularly if the range of the spatial autocorrelation is no more than three times the standard deviation of the positional error (Naimi et al., 2011). Positional uncertainty is also more important among species with narrow ranges than among widespread species (Soultan and Safi, 2017). For example, tick species (3-host) and life stages that parasitize hosts with small dispersal ranges (e.g., small rodents) require stricter thresholds and consideration of positional uncertainty error than those tick species (1-host) and life stages that rely on larger mammals that are capable of much broader dispersal. While difficult, it would be prudent for future tick SDMs to include metrics of host biology within model covariates. In addition, explanatory variables, such as landscape and climate, are frequently time-dependent; temporal alignment of observations and these time-dependent variables is essential to ensure model fitting based on circumstances at the time of observation and the climate niche (Estrada-Peña et al., 2013b).

SDMs also differ in how they handle various sample sizes (Wisz et al., 2008) and proportions of true presence/absence data versus presence/pseudo-absences (Wisz and Guisan, 2009), therefore choosing the proper tools to handle these biases is crucial to reliable prediction outcomes. For example, MaxEnt (Phillips et al., 2017) is a prime option for handling data that contains known presence only, and would thus be a good choice for data structures that contain museum records. Sampling biases across a dataset can also be investigated prior to building models with software tools like "sampbias" which quantifies the biasing effect of human accessibility to data collection sites, and is available as a R package (Zizka et al., 2021). Similar to the variety of tick occurrence records were the numerous sources of bioclimatic data correlates. We reported 60 different databases for environmental parameters used across modeling papers, however, bioclimatic variables from WorldClim were the most frequently modeled. Since 1984, WorldClim has existed as a database of interpolated global climate data derived from weather stations using thin-plate splines, now including up to 35 different measures of temperature and precipitation/moisture (Hijmans et al., 2005). Variables 1–19, drawing from the years 1970–2000, are the most frequently used in modern SDM models (Booth, 2018), and a new high-resolution (1-km^2) set of WorldClim monthly climate surfaces was released in 2017 (Fick and Hijmans, 2017). Many of these sources of environmental variables appear to be chosen due to ease of use and access, as well as due to the wide scale spatial coverage. For example, the WorldClim bioclimatic parameters are widely available *via* numerous spatial and targeted species distribution modeling R packages (e.g., SDM, krigR, envirem, etc.), and allow a user to apply them without having to upload and merge separate raster files (Naimi and Araújo, 2016; Title and Bemmels, 2018; Kusch and Davy, 2022). These data are also available in several resolutions and at a global scale, providing applicable climate resources regardless of the distribution locations chosen for model projections. Despite the common use and user-friendliness of these interpolated environmental variables to fit SDMs, it is important for modelers to recognize their limitations. Global bioclimatic datasets have not been validated on a smaller, local scale and could produce erroneous predictions in ecological niche modeling (Bedia et al., 2013). For this reason, it is important to also consider the use of satellite-derived remote sensing data for environmental parameters because they can provide more up-to-date and more precise measures of local climate and landscape (Amiri et al., 2020). Many of the bioclimatic variables also exhibit multicollinearity and spatial autocorrelation problems, and tests to exclude these biases from the models are inconsistently performed across the SDM literature (Araújo and Guisan, 2006; Estrada-Peña et al., 2013b).

We also tracked the types of species distribution model validation methods employed across the literature, with the understanding that there can be differences in how well validation applications can evaluate spatial models. The vast majority (98.9%) of papers used the receiver operating curve/area under the curve (ROC/AUC) metric to determine model fitness, and more than half of papers (60.6%) included two or more evaluation techniques. Nearly 10% of the body of literature reviewed did not report the validation method used to evaluate models, presenting challenges to the reproducibility of those modeling approaches. Similarly, the predominant use of WorldClim variables within this body of literature, there appears to be over-reliance on ROC/AUC to determine sensitivity and specificity of the model results (Lobo et al., 2008). Some researchers have cautioned that while ROC/AUC is helpful in that it is a threshold-independent measure and thereby more objective, it is a poor measure of model accuracy specifically in species distribution modeling. Lobo et al. (2008) report five issues with using ROC/AUC alone, including that ROC/AUC does not provide a spatial distribution of the model errors, and most critically, that the extent of the model can erroneously inflate the AUC score. Alternatives to basic ROC/AUC can include partial receiver operating curves (pROC), which avoids these criticisms and allows for differential weighting of omission and commission errors, as well as True Skill Statistic (TSS) (Lobo et al., 2008; Peterson et al., 2008). However, since many of the evaluation metrics can be biased by the proportions of occurrence presences to absences, strategies from other disciplines have also been suggested. Wunderlich et al. (2019) proposed the Odds Ratio Skill Score and the Symmetric Extremal Dependence Index (SEDI) to replace TSS in the evaluation of presence-background SDM methods, arguing that TSS can be biased depending on the number of true absences within a dataset. Overall, care must be taken in choosing evaluation methods that fit the type of species data and modeling algorithm.

The importance of model evaluation and validation methodology should not be understated as species distribution models are increasingly being used in the context of future climate-related projections to inform public policy on ticks and TBDs and improve priorities associated with One Health (Semenza et al., 2012). Approximately twenty percent of the studies included in this review included climate projection, of which fifty-six percent were published within the last 5 years. This showcases not only the increased interest in using SDM as a tool to understand the current distribution of tick species but also future possibilities to better control and mitigate TBDs. However, it is crucial that before integrating climate projections within SDM, there needs to be improved understanding of climate models and the inherent uncertainty within (Harris et al., 2014). Estrada-Peña (2003a) was the first to predict habitat suitability 15 years into the future for four tick species in South Africa using Fourier series analysis using decadal abiotic data from 1983 to 2000. More recently, researchers are using newer tools such as climate and emissions scenarios as well as Global Circulation Models (GCMs). When developing a SDM for projecting future species distributions, there are several considerations, including not only spatial resolutions and type of baseline data but also which environmental or climate variables to use. In addition, to avoid irrelevant or correlated climate variables there is need to account for phylogenetic data as species traits determine their distribution (Soberón, 2007; Morales-Castilla et al., 2017). Using an integrated approach that combines climate and phylogeny can clarify whether the underlying mechanism for differences in species richness or distribution shifts across space is more closely related to time and diversification rates (Kozak and Wiens, 2012; Wang et al., 2019).

TABLE 3 | Species distribution model validation methods reported across included literature according to respective modeling algorithms.

Model type	Validation method reported in literature	References*
Agent-based model	Receiver operating characteristic (ROC) Percentage correctly classified	Estrada-Peña, 2002a; Li et al., 2019
ANCOVA	Function stepwise procedure	Tkadlec et al., 2018
Bioclimatic envelope model	Akaike's Information Criterion *k*-fold cross validation Kappa index of agreement Percentage correctly classified Receiver operating characteristic (ROC) Sensitivity and specificity	Olwoch et al., 2003; Estrada-Peña et al., 2005, 2006b; Walter et al., 2016; Li et al., 2019; Clarke-Crespo et al., 2020
Boosted Regression Trees	Akaike's Information Criterion Correlation coefficient Model deviance *k*-fold cross validation Kappa index of agreement Partial receiver operating characteristic (pROC) Receiver operating characteristic (ROC) Sensitivity and specificity True skill statistic	Messina et al., 2015; Springer et al., 2015; Hahn et al., 2016; Sun et al., 2017; Kessler et al., 2019b; Miao et al., 2020; Glass et al., 2021; Lippi et al., 2021b; Zhao et al., 2021
Classification and regression trees	Akaike's Information Criterion Receiver operating characteristic (ROC)	Clarke-Crespo et al., 2020
Climate envelope model	Correlation coefficient I-similarity statistic	Lawrence et al., 2017
Cokriging	Correlation coefficient Sensitivity and specificity	Estrada-Peña, 1999a
Ecological niche factor analysis	Receiver operating characteristic (ROC)	Estrada-Peña and Venzal, 2007
Fourier analysis time series	Receiver operating characteristic (ROC) Percentage correctly classified Sensitivity and specificity Schoener's D statistic	Estrada-Peña, 2003a; Estrada-Peña et al., 2013a,b, 2014
Generalized additive models	Akaike's Information Criterion Model deviance Receiver operating characteristic (ROC) Sensitivity and specificity Correlation coefficient True skill statistic	Estrada-Peña, 2005; Jore et al., 2014; Lippi et al., 2021b
Generalized linear models	Akaike's Information Criterion Bayesian Information Criterion Correlation coefficient *k*-fold cross validation Kappa index of agreement Hosmer-Lemeshow statistic test Model deviance Percentage correctly classified Receiver operating characteristic (ROC) Sensitivity and specificity True skill statistic	Cumming, 2000, 2002; Guerra et al., 2002; Brownstein et al., 2003; Estrada-Peña et al., 2004, 2006d; Eisen R. J. et al., 2006; Brown et al., 2011; Jore et al., 2014; De Clercq et al., 2015; Gabriele-Rivet et al., 2015; Springer et al., 2015; Hahn et al., 2016; Kessler et al., 2019a,b; Sungirai et al., 2018; Vajana et al., 2018; Clarke-Crespo et al., 2020; Glass et al., 2021; Lippi et al., 2021b; Namgyal et al., 2021
Genetic Algorithm for Rule Set Production	Receiver operating characteristic (ROC)	Boeckmann and Joyner, 2014; Acevedo-Gutiérrez et al., 2018
Gower metric	Kappa index of agreement Receiver operating characteristic (ROC)	Estrada-Peña et al., 2006a
Linear discriminant analysis	Kappa index of agreement Percentage correctly classified Receiver operating characteristic (ROC) Sensitivity and specificity	De Clercq et al., 2015
MaxEnt	Akaike's Information Criterion Correlation coefficient Model deviance I-similarity statistic Jackknife variable permutation evaluation *k*-fold cross validation Kappa index of agreement Lowest presence threshold Mess score Mobility-oriented parity metric (MOP) Niche similarity Omission error Partial receiver operating characteristic (pROC) Receiver operating characteristic (ROC) Schoener's D statistic Sensitivity and specificity True skill statistic	Estrada-Peña et al., 2007a,b,c, 2010, 2013a,b, 2015a; Estrada-Peña and Thuiller, 2008; Atkinson et al., 2012; Illoldi-Rangel et al., 2012; De Clercq et al., 2013; Leta et al., 2013; Du et al., 2014; Feria-Arroyo et al., 2014; Giles et al., 2014; James et al., 2015; Donaldson et al., 2016; Hahn et al., 2016; Johnson et al., 2016; Lawrence et al., 2017; Acevedo-Gutiérrez et al., 2018; Alcala-Canto et al., 2018; Ala-Hulkko et al., 2019; Hadgu et al., 2019; Kessler et al., 2019b; Alkishe et al., 2020; Boorgula et al., 2020; Clarke-Crespo et al., 2020; Donalisio et al., 2020; Fernández-Ruiz and Estrada-Peña, 2020; Huercha et al., 2020; Glass et al., 2021; Lippi et al., 2021b; Torina et al., 2008; Porretta et al., 2013a,b; Springer et al., 2015; Williams et al., 2015; Raghavan et al., 2016a, 2019a,b, 2020; St. John et al., 2016; de Oliveira et al., 2017; Peterson and Raghavan, 2017; Sage et al., 2017; Minigan et al., 2018; Soucy et al., 2018; Pascoe et al., 2019; Rochlin, 2019; Signorini et al., 2019; Wang et al., 2019; MacDonald et al., 2020; Marques et al., 2020; Miao et al., 2020; Moradi-Asl and Jafari, 2020; Namgyal et al., 2020, 2021; Slatculescu et al., 2020; Zanet et al., 2020; Polo et al., 2021; Rochat et al., 2021

(Continued)

TABLE 3 | (Continued)

Model type	Validation method reported in literature	References*
Minimum convex polygon	Akaike's Information Criterion *k*-fold cross validation Mess score Partial receiver operating characteristic (pROC)	Rochlin, 2019
Mixture discriminant analysis	Akaike's Information Criterion Receiver operating characteristic (ROC)	Clarke-Crespo et al., 2020
Multivariate adaptive regression splines	Akaike's Information Criterion Correlation coefficient *k*-fold cross validation Kappa index of agreement Receiver operating characteristic (ROC) Sensitivity and specificity	Springer et al., 2015; Hahn et al., 2016; Kessler et al., 2019b; Clarke-Crespo et al., 2020; Glass et al., 2021
Negative binomial regression	Correlation coefficient	Ceballos et al., 2014
Occupancy model	Akaike's Information Criterion Receiver operating characteristic (ROC)	Lieske and Lloyd, 2018
Point-to-Point similarity metric	Sensitivity and specificity	Estrada-Peña, 2003a
Poisson regression	Akaike's Information Criterion Correlation coefficient Model deviance *k*-fold cross validation Receiver operating characteristic (ROC)	Estrada-Peña et al., 2004; Boehnke et al., 2015; Mangan et al., 2018
Principle component analysis	Receiver operating characteristic (ROC) Schoener's D statistic	Estrada-Peña and Venzal, 2007; Estrada-Peña et al., 2013a,b
Random forest	Akaike's Information Criterion Correlation coefficient *k*-fold cross validation Kappa index of agreement Model deviance Out-of-the-bag error Percentage correctly classified Receiver operating characteristic (ROC) Sensitivity and specificity True skill statistic	De Clercq et al., 2015; Springer et al., 2015; Hahn et al., 2016; Kessler et al., 2019b; Walter et al., 2020; Glass et al., 2021; Lippi et al., 2021b
Spatial clustering	Hosmer-Lemeshow statistic test Receiver operating characteristic (ROC)	Gabriele-Rivet et al., 2015
Zero-inflated negative binomial	Akaike's Information Criterion	Diuk-Wasser et al., 2010; Mangan et al., 2018
Zero-inflated Poisson	Akaike's Information Criterion	Mangan et al., 2018

**References only listed once. Individual references may have used more than one validation methods for a model, and/or a method may have been used by multiple references.*

The potential options allow for multiple combinations and corresponding divergence in climate estimates as the patterns of temperature and precipitation differ between GCMs (Guevara et al., 2019). To compensate for these differences, those studies in our review that used GCMs tend to use multiple models when evaluating future distributions. For example, Minigan et al. (2018), used ten GCMs when projecting the future distribution of *Dermacentor variabilis* in North America to incorporate uncertainty of possible future distributions and be able to showcase potential minimum and maximum range shifts (Harris et al., 2014). For those studies that used only one or two GCMs, the spatial extent of the projected area was limited, such as Lieske and Lloyd (2018) predicting *I. scapularis* in the province of New Brunswick or de Oliveira et al. (2017) predicting *A. cajennense s.s.* and *A. sculptum* in Brazil. Regardless of the number of GCMs incorporated within SDMs, it is important when drawing conclusions to consider that climate projections do not predict future climate, but instead provide possible futures under a given scenario (Rosentrater, 2010).

Emission and climate scenarios were included in most articles that included climate projections with less variation in which scenarios are included and compared. Most included a version of the Representative Concentration Pathways (RCPs) or the Intergovernmental Panel on Climate Change (IPCC) climate scenarios upon which the GCMs act to derive possible future climates. These climate and emission scenarios acted as possible futures with many including the recommended high and low emissions scenario to compare potential shifts in tick distributions under a changing climate. For example, at a simple level, Estrada-Peña (2003) found that increasing temperature by 2°C would potentially result in reduction of tick habitat in South Africa for *A. hebraeum, B. decoloratus*, *H. truncatum*, and *R. appendiculatus.* For more complex models using IPCC climate such as A2 (equivalent of RCP 8.5), a high emissions scenario that describes rapidly rising temperatures, there tends to be a loss of habitat range for *I. ricinus* in the southern range of its present distribution range in Poland and Italy yet expansion in Norway and Sweden (Boeckmann and Joyner, 2014). In contrast, in the southern hemisphere, in Brazil, for the RCP 8.5 emissions scenario, there is retraction of *A. cajennense* and *A. sculptum* in northern Brazil and expansion of suitable habitat in southern Brazil (de Oliveira et al., 2017). Alternative scenarios show similar expansion and retraction, however, the extent varies. For example, for low emission scenarios such as B1 (equivalent RCP 4.5) where there is a leveling of temperatures, there is increased loss of suitable habitat for *Rhipicephalus*

TABLE 4 | Databases used for tick occurrence, climate projections, and environmental/host species variables.

Tick species	Global circulation models	Climate variables	Environmental variables	Climate/emissions scenarios	References
Boophilus decoloratus, Amblyomma hebraeum, Rhipicephalus appendiculatus, Hyalomma truncatum		Surface temperature, water vapor pressure deficit	NDVI		Estrada-Peña, 2003a
Dermacentor variabilis	CC-CSM1, CCSM4, HadGEM2-AO, HadGEM2-ES, GISSER-2, IPSL-CM5A-LR, MIROC5, MIROC-ESM, MRI-CGCM3, and NorESM1-M	BioClim 1–19	Elevation	RCP 2.6, RCP 4.5, RCP 6.0, and RCP 8.5	Minigan et al., 2018
Ixodes scapularis		Minimum, maximum and mean monthly temperature, and Monthly vapor pressure	Deciduous forest cover	RCP3.85, RCP4.91	Brownstein et al., 2005
Rhipicephalus microplus		BioClim 1–19, mean yearly evaporation, vapor pressure deficit			Estrada-Peña et al., 2005
Dermacentor marginatus, Rhipicephalus bursa, Rhipicephalus turanicus, Hyalomma marginatum, Hyalomma excavatum, and Rhipicephalus annulatus	Created new climate layers with monthly increases and decreases in temperature of 1 and 2C, and monthly variations in rain-fall of 60, 80, 120, and 140% of actual values		Normalized derived vegetation index (NDVI)		Estrada-Peña and Venzal, 2007
Ixodes ricinus	RCA3		Vegetation index, oak, alder, and hazel distribution	A2, B2	Jaenson and Lindgren, 2010
Rhipicephalus microplus, Rhipicephalus annulatus	BCCR-BCM 2.0, CSIRO-Mk 3.5, MIROC 3.2-HIRES, NCAR-CCSM 3.0	Present climate: BioClim 1–19, Past climate: monthly temperature and precipitation products from the PRISM climate database		A1B, A2, B1	Giles et al., 2014
Ixodes ricinus	CSIRO SRES	Monthly measures of solar radiation, precipitation, and temperature, annual mean solar radiation, iso-thermality, annual total precipitation, precipitation of wettest quarter, and precipitation of driest quarter at a resolution of 50	Soil type	A2	Boeckmann and Joyner, 2014
Ixodes scapularis	CCCMA, CSIRO, HADCM3	BioClim 1,3,5–7,9–19		A2A, B2A	Feria-Arroyo et al., 2014
Dermacentor marginatus, Haemaphysalis punctata, Haemaphysalis sulcata, Hyalomma marginatum, Hyalomma lusitanicum, Ixodes ricinus, Rhipicephalus annulatus, Rhipicephalus bursa	GCMs; IPSL-CM5A-LR, MIROC-ESM-CHEM, GFDL-ESM2M, and NorESM1-M	BioClim 1–19, saturated vapor pressure		RCP 2.6, RCP 4.5, RCP 6.0, RCP 8.5	Williams et al., 2015
Amblyomma americanum	CCSM4, MPI-ESM-LR, HadGEM2-ES, CNRM-CM5, ACCESS1-0.70	BioClim 2, 12 vapor pressure		RCP 4.5, RCP 8.5	Springer et al., 2015
Ornithodoros hermsi	ACCESS1-0, HadGEM2-ES, CCSM4	BioClim 5–8, 15, 18	Elevation	RCP 4.5, RCP 8.5	Sage et al., 2017
H. longicornis		Mean rain, mean temp, mean frosts, mean July max, mean July min	Elevation	RCP 4.5, RCP 8.5	Lawrence et al., 2017
Amblyomma cajennense, Amblyomma sculptum	C-CSM4, HadGEM2-AO	BioClim 1–2, 5–6, 12–14		RCP 8.5	de Oliveira et al., 2017
Ixodes scapularis	CMIP5	Mean annual temperature, mean animal precipitation, precipitation as snow, frost free period, degree days below 0°C	Elevation, tree land cover%, deciduous species cover%, coniferous species cover%, mean height of leading species, river density, area of water bodies	RCP 4.5, RCP 8.5	Lieske and Lloyd, 2018
Amblyomma americanum	CSIRO Mk3, MIROC, CCSM4, NCAR, CanESM2, CCCMA	BioClim 1–19		RCP 4.5, RCP 8.5	Raghavan et al., 2019b

(Continued)

TABLE 4 | (Continued)

Tick species	Global circulation models	Climate variables	Environmental variables	Climate/emissions scenarios	References
Rhipicephalus spp.	ACCESS1-0, CCSM4	BioClim 1–19		RCP 4.5, RCP 8.5	Hadgu et al., 2019
Ixodes ricinus		Monthly average daily mean temperature	Land-use/cover change: urban land use, irrigation availability, flood frequency, and food and timber Demand., Water availability	RCP2.6, RCP4.5, RCP8.5	Li et al., 2019
Rhipicephalus (Boophilus) microplus		BioClim 1–7, 10–17		RCP 4.5, RCP 8.5	Marques et al., 2020
Amblyomma rotundatum, Amblyomma dissimile	CCSM4, NCAR, MIROC5	BioClim 1–7, 10–17		RCP 4.5, RCP 8.5	Polo et al., 2021
Ixodes pacificus	CNRM 8.6, MIROC 8.5, MPI 4.5, MIROC 4.5	Monthly and annual averages of temperature and precipitation	Vegetative cover data, current and forecasted land cover layers were retrieved from the USGS FORE-SCE model LULC	A1B, A2, B1, B2	MacDonald et al., 2020
Rhipicephalus sanguineus		BioClim 1–7, 10–17		RCP 4.5, RCP 8.5	Alkishe et al., 2020
Amblyomma americanum	CSIRO MK3, MIROC 5, NCAR CCSM4, CCCMA CANESM2	BioClim 1–7, 10–17		RCP 4.5, RCP 8.5	Raghavan et al., 2020

ACCESS1-0/ACCESS1-0.70 (Australian Community Climate and Earth System Simulation Model), CSIRO MK3 (Climate System Model), MIROC5 (Model for Interdisciplinary Research on Climate, Center for Climate System Research, University of Tokyo), CanESM2 (Canadian Earth System Model-2), AOGCMs (Atmosphere Ocean General Circulation Models), CCSM4 (Community Climate System Model version 4), MPI-ESM-LR (Max Planck Institute Earth System Model low resolution version), HadGEM2-ES/HADCM3 (Full Earth-system version of the Met Office Hadley Center, Second generation family of coupled climate models), CNRM-CM5, Canadian the CSIRO/CSIRO MK3 (Commonwealth Scientific and Industrial Research Organization), NCAR CCSM4 (National Center for Atmospheric Research, Community Climate System Model-4), and CCCMA CANESM2 (Canadian Center for Climate Modeling and Analysis, Canadian Earth System Model-2).

TABLE 5 | Expected expansion and retraction of tick genera habitat based on future climate variables projections for various species.

Genus	Expansion	Retraction	References
Amblyomma	Expansion of suitable habitat north and east across Iowa, Illinois, Indiana, and Ohio, central portions of South Dakota, Minnesota, Wisconsin, and Michigan, Eastern Tennessee and Kentucky and Western West Virginia, Northwest coast of New Zealand's South island.	South Africa, Florida, Alabama, Mississippi, Louisiana, and Southeastern Texas, Northeastern Arkansas and Western Tennessee, Southern and Northwestern Brazil	Estrada-Peña, 2003a; Springer et al., 2015; de Oliveira et al., 2017; Raghavan et al., 2019b; Polo et al., 2021
Dermacentor	Southern Europe and Northern Africa	Mexico and Southeastern United States	Minigan et al., 2018
Haemaphysalis	Northern Italy, Central France, West Coast, Marlborough, Tasman, Canterbury, Otago and Southland, Nelson regions of New Zealand	North Iberia	Williams et al., 2015; Lawrence et al., 2017
Hyalomma	Southern Europe and Northern Africa, Croatia, France, Balkans	South Africa, Southern Iberia, Northern Africa	Estrada-Peña, 2003a; Estrada-Peña and Venzal, 2007; Williams et al., 2015
Ixodes	Canada, Norway, Sweden, Finland, Norwegian coastline, Northeastern Texas, Poland; South-central New Brunswick, Southeast Cape Tormentine	Alps, Pyrenees, interior Italy, and Northwestern Poland (A2), Portugal, and Greece	Brownstein et al., 2005; Jaenson and Lindgren, 2010; Boeckmann and Joyner, 2014; Feria-Arroyo et al., 2014; Williams et al., 2015; Li et al., 2019
Ornithodoros	Northern Baja California, México		Sage et al., 2017
Rhipicephalus	Southern Europe, Northern Africa, Southern United States, Mexico, the Caribbean islands, Colombia, Venezuela, Bolivia, Paraguay, Uruguay, Southern Brazil and Northern and Central Argentina, Bulgaria, Romania, Northern Ethiopia, Argentina, Brazil, Colombia, Venezuela, Northern and Eastern Europe, India, Bhutan, Nepal, Myanmar, China, Mexico, Southeastern United States, West Africa, Sudan, South Sudan, Chad	South America, South Africa, Turkey	Estrada-Peña, 2003a; Estrada-Peña et al., 2005; Estrada-Peña and Venzal, 2007; Giles et al., 2014; Hadgu et al., 2019; Alkishe et al., 2020; Marques et al., 2020

sanguineus in South America as compared to the RCP 8.5 scenario (Alkishe et al., 2020). This suggests that moderate increases in temperature decreases habitat suitability without resulting in habitat changes elsewhere where tick species could find refuge. Overall, understanding how climate change could potentially influence tick distributions and range shifts will depend not only on the tick species, but also the region and climate model (Minigan et al., 2018).

We acknowledge several limitations to this review that also present opportunities for further research and investigation. Since we did not include gray literature or unpublished manuscripts, there are likely numerous applicable and appropriate analyses that are not represented in these data. The date cutoff for inclusion was August 2021, so there also are likely several relevant papers that have been released since that time that would have been included but are not. Within the assessment of validation methods, we did not include a question about training/testing dataset splitting, or in other words, how much of a dataset was used in prediction and forecasting. This is particularly important for ensuring reproducible projections of future climate-based tick habitat suitability. We also did not document whether researchers included location uncertainty thresholds to tick occurrence data. Some researchers recommend setting the limit of tick species observation position uncertainty to match that of the WorldClim data (i.e., 4,000 m) (Polo et al., 2021), and others (Pascoe et al., 2019) have set the limit to at a finer resolution (e.g., 1,000 m). Regardless, it is important for reproducibility of these analyses as well as accuracy of the model prediction for these thresholds to be set as well as reported in the literature. Researchers employing these modeling strategies for ticks or any species should consult checklists and guides on how to generate and report SDM studies in a reproducible manner (Araújo and Guisan, 2006; Austin and Van Niel, 2011; Feng et al., 2019).

CONCLUSION

Since the 1980s, species distribution modeling methods and data sources have greatly improved the ability to predict suitable tick habitat and likely distribution ranges. However, given the wide range of options that are used to estimate current and future tick habitat, it is critical to establish standardized methodologies for conducting, validating, and reporting species distribution model predictions. These parameters are necessary to create reproducible, comparable, and reliable guides to monitor tick vectors and their global risk to humans, domestic animals, and wildlife.

AUTHOR CONTRIBUTIONS

RS and HK: conception. HK and SH: data collection and analysis. HK, SH, and RS: writing. RS: funding. SH: supervision. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

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