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Climate Analyses to Assess Risks from Invasive Forest Insects: Simple Matching to Advanced Models

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Abstract

Purpose of Review The number of invasive alien insects that adversely affect trees and forests continues to increase as do associated ecological, economic, and sociological impacts. Prevention strategies remain the most cost-effective approach to address the issue, but risk management decisions, particularly those affecting international trade, must be supported by scientifically credible pest risk assessments. Pest risk assessments typically include an evaluation of the suitability of the climate for pest establishment within an area of concern. A number of species distribution models have been developed to support those efforts, and these models vary in complexity from simple climate matching to mechanistic models. This review discusses the rationale for species distribution models and describes some common and influential approaches.
Recent Findings Species distribution models that use distributional records and environmental covariates are routinely applied when ecological information about a species of concern is limited, an all-too common situation for pest risk assessors. However, fundamental assumptions of the models may not always hold.
Summary A structured literature review suggests that many common species distribution models are not regularly applied to alien insects that may threaten trees and forests. For ten high-impact alien insect species that are invading North America, MaxEnt and CLIMEX were applied more often than other modeling approaches. Some impediments to model

development and publication exist. More applications of species distribution models to forest insects are needed in the peer-reviewed literature to ensure the credibility of pest risk maps for regulatory decision making, to deepen understanding of the factors that dictate species' distributions, and to better characterize uncertainties associated with these models.

Keywords Pest risk assessment · Species distribution model · MaxEnt · CLIMEX · Bioclim · Alien insect

Introduction

Biological invasions by alien species, particularly insects, remain the greatest ecological threat to many trees and forests [1]. Alien invasive forest insects often kill trees or impede normal physiological function with concomitant ecological, economic, or social impacts. Estimates of the annual economic impact from forest invasions vary from $4.2 billion in the USA [2] to between $7.7 and $20 billion in Canada [3], though both estimates have been criticized [4]. Aukema et al. [5•] suggest that annual economic impacts from alien forest insects already present in the USA are likely $2 billion in local government expenditures, $1.5 billion in lost residential property values, $1 billion in homeowner expenses, $216 million in federal government expenditures, and $150 million in lost timber value. These estimates do not fully account for impacts to other ecosystem services or additional impacts from future invasions.

Over the past 150 years, an average of 2–3 new forest insect species has successfully established in the USA each year, with one "high impact" species establishing every 2–3 years [1]. Similar trends have been noted in other countries. This recurrent phenomenon of forest pest invasion likely has been associated with trade [6], especially the importation of

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live plants or wood packaging materials [1]. Although the continually increasing number of alien insects concerns forest health managers and others, this rate does not follow the exponential growth in global imports, providing indirect evidence that efforts to improve biosecurity are working [7] but could be further refined [1].

Prevention of biological invasions is widely recognized as the most cost-efficient approach to invasive species management [6, 8–10]. Such prevention measures include pre-border inspections, exterior quarantines, and quarantine treatments, each intended to keep a threatening species from arriving in an area of concern. Under terms of the Agreement on the Application of Sanitary and Phytosanitary Measures from the World Trade Organization, member nations agree to take actions that are only commensurate with the level of risk posed by a threatening pest species and are "not more trade restrictive than required to achieve their appropriate level of phytosanitary security" (Article 5, available at www.wto.org/english/tratop_e/sps_e/spsagr_e.htm). As a result, scientifically based pest risk assessments must underpin risk management decisions.

Pest risk assessment is a specialized application of ecological risk assessment [11]. The process begins with the identification of a hazard, often an alien species with a history of causing harm elsewhere but not occurring within an area of concern, or a commodity or conveyance that might bring such species, and consideration of relevant assessment endpoints (e.g., agricultural productivity or ecological diversity). The process then moves to exposure and effects assessments. In general, exposure assessments attempt to describe the spatial and temporal concentration (i.e., density) of the hazard, while effects assessments may evaluate the economic, ecological, or social (including harms to human health) impacts caused by the level(s) of the hazard. Risk characterization integrates the exposure and effects assessments to provide a measure of the probability of the adverse event weighted by the magnitude of the consequence of the event (i.e., risk). The general impact assessment framework for invasive alien species proposed by Parker et al. [12], where impact, I = Range × Abundance × Effect per individual has several analogous components.

In general, pest risk assessments attempt to characterize the probability (i.e., exposure) and consequence (i.e., effects) of an alien pest's arrival, establishment, and spread within an area of concern, and a number of frameworks exist to guide the assessment process. Orr et al. [13] developed one of the first frameworks for invasive alien species based on general principles from ecological risk assessment. In several pest-risk-assessment frameworks, one or more questions relate to the suitability of the climate within the area of concern for the invader in question [14]. For example, the Exotic Forest Pest Information System for North America (ExFOR) provides semi-quantitative assessments for 100 forest insect pests that threaten North America [15]. In ExFor, climate suitability

factors heavily into the assessment of establishment potential and overall risk. So, for example, the "very high" overall risk rating assigned to *Lymantria mathura* reflects the "high" likelihood of establishment based, in part, on suitable climate and host material in areas where the species might first arrive. This particular framework does not explicitly account for the extent or degree of climatic suitability.

Climate suitability plays a central role in the degree of risk posed by invasive alien insects that might affect trees or forests. Climate shapes geographic range limits and, with knowledge of the distribution of hosts and other biotic or abiotic constraints, where establishment is possible [16]. The confluence of suitable areas for establishment with areas of economically valued resources dictates the endangered area [17], while the area at highest risk is where the ecological, economic, or social effects of an alien species are likely to be greatest [16]. Climatic suitability also affects population dynamics, the rate and course of future spread, the extent of damage, and the effectiveness of management responses. The relationships between climate and spread or impact can be difficult to forecast reliably or precisely, and this remains an active area of research [18, 19]. Of necessity, many pest risk assessments make simplifying assumptions. For example, in areas judged to be climatically unsuitable, establishment and associated impacts often are considered unlikely or ephemeral [19]. In climatically suitable areas, the presence of suitable hosts may be assumed, a reasonable assumption for polyphagous species. Similarly, dispersal to climatically suitable areas, either by natural or human-mediated means, might be given. These assumptions allow one to estimate the maximum geographic extent of an invading species and help to provide an upper bound on impact. However, great care needs to be taken when attempting to infer abiotic requirements for, or limits to, population growth from distributional records, particularly for species that are undergoing range expansions. The areas presently occupied by a species are a reflection of abiotic requirements for growth, biotic requirements, and dispersal limits [20, 21] and, as such, may under-represent the range of abiotic conditions that a species might find to be suitable. Conversely, for highly mobile species, distributional records may reflect ephemeral populations and misrepresent temporarily suitable locations as permanently fitting. Nevertheless, assessments of climatically suitable areas provide a critical backdrop to determine where alien insects might invade and harm trees and forests.

Several tools have been developed to assess climate suitability for invasive alien species [19]. Numerous other reviews and texts have been written about these tools or about the challenges of developing species distribution models for invasive species [22–24, 25•, 26, 27]. Applications of these tools to invasive alien species, in general, continue to increase, yet seem relatively rare for alien insects that may affect trees and forests. This review discusses several common approaches to

climate analysis that are applicable to forest insects. It includes a structured review of the literature to determine if certain approaches are applied to forest insects more commonly than others. Commentary is offered about why climate suitability analysis may not yet be widely applied and encourages more applications, not only to support complex management decisions but also to develop a more rigorous ability to infer climatic constraints/requirements from distribution records.

Climate Matching

Climate matching for invasive alien species, in general, involves comparisons of the climate, especially with respect to temperature and moisture, in areas where a species of concern occurs (by definition classified as suitable or optimal) with areas of interest where the species does not yet occur. The rationale is simple: the more similar the two climates are, the more likely that a species will encounter climatic conditions that are suitable for establishment should it arrive in these new areas. This approach has appeal because it requires little detailed information about the effects of temperature or moisture on the autecology of a threatening species.

All methods of climate matching begin with the collection of presence records in as precise geographic detail as possible, preferably individual points specified by longitude and latitude [22]. These points are associated with one or more environmental covariates and analyzed in "climatic space" to determine relationships between presence and climate. More advanced analyses also consider climatic conditions where the species has not been reported. Those relationships are then applied to conditions at points within the area of concern to characterize the likelihood of being present. Methods to establish those relationships vary in complexity.

The simplest qualitative climate matching techniques rely on existing descriptions of biomes or other pre-existing climate zones. For example, the Köppen-Geiger classification system [28] or "Olson biomes" [29], with predefined areas of the world with similar temperature, moisture, geology, and dominant vegetation, have been used to forecast the distribution of invasive alien species [30, 31]. In fact, a variation of this approach was used in 1896 to forecast within the USA and Canada the potential distribution of San Jose scale, now recognized as *Quadraspidiotus perniciosus*, with ecological zones proposed by C. Hart Merriam (reviewed in [32]). Likewise, USDA Plant Hardiness Zones, based on the mean annual extreme low temperature [33], have been used to forecast northern limits to the distributions of several alien species [23], including forest insects, such as winter moth, *Operophtera brumata* [34].

Application of a zone-based method is quick and relatively simple. Each presence point falls in a single zone, so the zones in which those points occur are considered suitable. The list of suitable zones is compared with zones in the area of concern to determine whether climatically suitable habitat occurs there. Venette and Ragsdale [35] describe a variation of this approach that relies on an analysis of parsimony to identify which of Olson's biomes might be suitable when presence points are included with national or subnational descriptions of presence. This method was applied to quickly identify regions of the USA that might have suitable habitat for some alien forest insect pests, such as the oak splendor beetle, *Agrilus biguttatus* [36], and the oak ambrosia beetle, *Platypus quercivorus* [37], that are not known to be established in the USA.

Other methods of climate matching focus on an analysis of climate records to distinguish areas that might be suitable for establishment. The "match climates" feature within CLIMEX has an algorithm to measure the similarity in climates between two or more locations based on 30-year monthly averaged temperatures and precipitation [38••, 39]. The user can control which climatic variables are of interest or assign different weightings to each climatic variable in an aggregate index. CLIMEX scales similarity between 0 and 100, with 100 indicating a perfect match between a reference location (home) and an area of concern (away). Sutherst [40] suggested a similarity index <60 was unlikely to be suitable, while Kriticos [41] considered values >70 to be likely suitable and Fowler and Takeuchi [42] judged values >80 to be a good match. "Match climates" was used to identify areas within North America that might be climatically suitable for two parasitoids of the emerald ash borer [43]. Peacock and Worner [44] took the reciprocal approach and used CLIMEX to compare Auckland, New Zealand, the area of concern, with the rest of the world to identify regions that might be a source for future invasive alien species.

Inductive Models

Inductive species distribution models (synonymous with ecological-niche, climate-envelope, or habitat-distribution models) attempt to infer bioclimatic requirements for a species from presence points. Some prefer to call these statistical or correlative models because they attempt to establish relationships between the presence, absence, or abundance of a species and environmental covariates [45]. The models vary in complexity. Here, I focus on some common, foundational modeling approaches that have been influential in the development of inductive species distribution models in general.

BioCLIM

BioCLIM was one of the first standardized approaches to inductive species distribution modeling [46]. BioCLIM and its successor, AnuCLIM, rely on a bounding box (or

hypercube) analysis to determine the climate envelope, i.e., the range of environmental conditions under which an alien species might survive [46]. BioCLIM analyses typically depend on ecologically relevant summaries of the climate. Nineteen such summaries pre-exist (www.worldclim.org), including such factors as average annual temperature, minimum temperature of the coldest month, and precipitation of the driest month [47]. The limits of the bounding box are determined by the range of conditions under which a species has been reported to occur, though subsets of occurrence data may be examined to avoid potential outliers. Any location with conditions that fall within the bounding box are considered suitable. BioCLIM has appeal because the model is conceptually easy to understand, provides a binary classification of new sites as having suitable habitat or not, and the classifications have a good degree of accuracy [46]. Mendoza et al. [48] applied BioCLIM to *Dendroctonus rhizophagus*, a pest of *Pinus* spp. and native to Mexico, and found most of the Sierra Madre Occidental could provide a suitable climate, while no climatically suitable habitat was projected in the USA under current conditions. BioCLIM also was applied, with eight other species distribution models in OpenModeller, to forecast climatic suitability for the highly invasive red gum lerp psyllid, *Glycaspis brimblecombei*, a pest of *Eucalyptus* spp. and native to Australia [49]. In this application, BioCLIM did not accurately forecast any of the known occurrences of *G. brimblecombei* outside Australia.

The rectilinear approach used by BioCLIM has some potentially significant limitations [50••]. Firstly, bounding with straight lines gives the climatically "outermost" observations considerable weight and may overestimate the range of climatic conditions under which a species may survive [50••]. Analysis with a defined subset of the observations (e.g., 90, 80, or 50%) is possible to eliminate potential outliers. However, focusing on a subset of the data may exacerbate the negative consequences of sampling biases among the presence points on model accuracy [51]. Secondly, BioCLIM assumes that each climatic factor acts independently to determine suitability such that all conditions within the bounding box are treated as equally suitable. Suitability is likely to be a matter of degree, not a binary response, and some experiments are confirming that temperature and moisture can interact to affect population growth rates (e.g., [52]) and presumably distributional limits.

Climatic Distance Methods, Especially Mahalanobis Distance

A number of distance-based approaches have been developed for species distribution modeling. Particularly popular approaches are Mahalanobis [50••], Euclidean [24], and Gower

Distance [53], but all are meant to measure the distance in multivariate climate space of a site from optimal climatic conditions. The optimum follows the means of the climatic conditions among presence points. Mahalanobis distance has been particularly instrumental and follows the equation,

$$D^2 = (x{-}m)^T C^{-1} (x{-}m),$$

where D^2 represents the distance between a vector x and a set of vectors that specify environmental conditions at all known presence points, termed matrix S. The rows of S reflect different locations, and each column a different environmental measure. The vector x represents environmental conditions at a particular site, with or without the species of interest. In the distance equation, m is a vector of the mean of each environmental measure, T transposes the matrix, and C is covariance matrix among environmental measures, all within matrix S [50••]. The distances follow a chi-square distribution with n-1 degrees of freedom, where n is the number of environmental measures, so that the distances can be converted to a probability or simply rescaled from 0 to 1 [50••]. With a defined threshold for suitability, Mahalanobis distance describes an ellipse or ellipsoid in two or three dimensions, respectively, within which conditions can be considered suitable. Shatz et al. [54] used the Mahalanobis distance approach to evaluate the environmental conditions in central Massachusetts for the Asian longhorn beetle relative to conditions in an outbreak in Worchester County, MA, USA and found a significant fraction of the landscape to be suitable for continued spread of the insect.

MaxEnt

One of the most popular approaches to species distribution modeling recently has been MaxEnt [55••, 56]. A discussion of the workings of MaxEnt is beyond the scope of this paper, but Elith et al. [57] and Merow et al. [58] provide particularly useful, cogent descriptions. In general, MaxEnt attempts to distinguish conditions at locations where a species of interest is known to occur from conditions at background points, sometimes called "pseudo-absences," where the presence of the species is not known. The approach has appeal because the software allows the user to generate forecasts of climate suitability relatively quickly from putatively simple datasets, specifically presence-only observations. The software can suggest complex relationships between the likelihood of species occurrence (often interpreted as an index of climate suitability) and one or more environmental predictors, and the resulting maps seem to capture considerable landscape heterogeneity. Much of the original development and testing of MaxEnt took place with species in their native ranges at equilibrium with their environments. The model was readily

applied to more complex questions, particularly involving species under non-equilibrium conditions. For example, Sobek-Swant et al. [59] applied MaxEnt to forecast that 1–47% of the range of ash in North America may be climatically suitable for the emerald ash borer, *Agrilus planipennis*; models developed with presence points from the native range in Asia differed somewhat from models developed with presence points from North America. Venette et al. [60] and López-Martinez et al. [61] also used MaxEnt to identify climatically suitable areas for the goldspotted oak borer, *Agrilus auroguttatus*, in the USA and Mexico, respectively.

More recent investigations have raised some cautionary notes about the application of MaxEnt and other presence-only species distribution models to invasive alien species. Four of these concerns are common and may be particularly relevant to applications in forest entomology: (1) selection of background locations, (2) correlation among predictor variables, (3) attention to sampling bias, and (4) extrapolation into novel climate space. Each concern is addressed in greater detail.

Selection of background locations

How background locations are selected can have a major impact on MaxEnt results. In general, MaxEnt is more likely to suggest smaller areas of climatic suitability (i.e., the model is more likely to be overfit to presence points) if the area from which background locations are selected is large (e.g., global) than if the background area is only slightly larger than the area currently occupied by the species of interest [45, 58, 62]. If default settings in MaxEnt are used, the background should come from the area that is within the dispersal distance of the species, i.e., locations that might be accessible to the species of interest [58, 63, 64]. Of course, this advice assumes that the dispersal characteristics of the species of interest are known and predictable, which are often not the case for invading forest insects. Jarnevich and Young [62] used minimum convex polygons constructed in a geographic information system from the set of presence points and added 2.5 arc-minutes to define the background. As an alternative, Webber et al. [27] defined the background by using all Köppen-Geiger zones in which presence points fell.

More significantly, the selection of background locations should follow any bias present among the presence points to limit the impact of the bias on the resulting model [65]. Three approaches have been proposed. If the bias is clear (e.g., all presence points occur within 100 m of a road), a bias file can be created for MaxEnt so that background points are equally restricted. An effective alternative, a target-group background, relies on locations of multiple species that might have been detected with the same sampling method as was applied to the species of interest [56]. Lastly, statistical models can be created to describe how landscape features affect the probability of

sampling types of sites, but care must be taken to avoid predictors that are used in MaxEnt [66••].

Correlation among predictor variables

Correlation among predictor variables (aka multicollinearity) is problematic in many statistical models because the relationships between predictor variables obscures the relationship(s) to the dependent variable [67•]. MaxEnt calculates a number of feature classes (i.e., multiple transformations of the original predictor variables) as a prelude to the development of potentially complex, non-linear models, and these feature classes may already be highly correlated [58]. So, the common recommendation is to avoid correlated predictors (e.g., climate variables) by excluding members of correlated pairs (i.e., with a Pearson correlation coefficient, $|r| > \sim 0.85$ [68] or $|r| > 0.7$ [69]) or using indices of climate predictors calculated through principal components analysis (PCA) [69]. Phillips [65] noted an interesting case, though, where the use of PCA-derived variables led to substantial overprediction of a species' distribution, but this problem was resolved when the raw predictors were used.

Attention to sampling bias

MaxEnt assumes that presence points come from a random sampling of the species distribution within the study area [55••]. In practice, though, presence points may come from near roads, towns, or other easily accessible areas and so may be a biased sample [65]. Museum records have proven vulnerable to sampling bias [70•, 71, 72]. Lahoz-Monfort et al. [73] demonstrate that detectability of invasive alien species also can create bias, particularly if detectability varies as a function of landscape features. This possibility seems highly likely for a number of invasive forest pests that often are not detected until populations begin to cause obvious tree symptoms [74]. Bias is likely to be introduced if variation in population growth or symptom expression is associated with a landscape feature, but bias can be addressed, in part, by selecting background points that follow similar patterns [75]. Fourcade et al. [72] suggest that selecting a subset of presence points that are regularly distributed in space may be a robust way to address sampling bias. If bias is strong and unknown, Phillips [65] recommends simpler models (i.e., fewer predictors and feature classes) to avoid unfounded assumptions about the background.

Extrapolation into climate space

MaxEnt assumes that a species is at equilibrium with its environment, and that presence locations are representative of other locations to which the model will be applied [25•]. However, for invasive alien species, the first assumption is

unlikely to be true, especially for species that are still spreading, and the validity of the second assumption is questionable at best. "Novel climates" occur when a model is applied to conditions outside the range of values of individual predictors or when unique combinations of environmental conditions occur [76]. Elith et al. [25•] developed the Multivariate Environmental Similarity Surface (MESS) to measure the similarity of any location to a set of reference points, typically presence and background points, by following an approach similar to that used by BioClim. Dissimilar points have negative values, and the greater the dissimilarity the more negative the value. MESS does not account for the covariance structure among predictors, so Mesgaran et al. [76] used Mahalanobis distances to measure (dis-)similarity of a site to presence and background points. These measures are a critical component of model interrogation, but how best to use them is still being explored. The nature of the challenge posed by invasive species may require some degree of extrapolation, so maps of climatic extrapolation may serve to highlight areas of uncertainty caused by a lack of knowledge.

Deductive Models

These models, also known as mechanistic or process-based models, rely on controlled laboratory experiments or carefully designed field studies to determine how different biotic or abiotic conditions may affect birth, death, or developmental rates or other physiological functions. Such studies may focus on a single environmental covariate (e.g., temperature) and can be especially informative if ecologically relevant conditions are measured.

Most deductive models make simplifying assumptions about the species of interest. The models often treat the species as being genetically homogenous with invariant traits over time [77]. Genetic homogeneity, or extremely limited diversity, may be a reasonable assumption for invading populations which frequently experience genetic bottlenecks during the initial phases of establishment. This assumption allows one to apply results from a laboratory colony of insects, for example, to wild populations but obviously ignores genotypic or phenotypic changes that may occur through time (e.g., [78]). Nevertheless, deductive models have proven to be robust and transferable.

CLIMEX The "compare locations" feature within CLIMEX [38••, 39] is a step from purely inductive models towards deductive models but is not a purely deductive model in its own right [45]. The model integrates climate data (often 30-year monthly climate normals) with measures of the effects of temperature and moisture on population growth to generate indices of climatic suitability at multiple locations (i.e.,

weather stations or grid cells) or to describe changes in suitability through a year at a location [38••].

CLIMEX relies on a fundamental premise that all poikilothermic species share qualitatively similar responses to temperature and moisture. In essence, individual and population growth is possible if temperature (and moisture) falls within an upper and lower bound (i.e., cardinal requirements). Within that range of temperatures (or moistures), a narrower set of conditions occurs where population growth rate is maximized (i.e., optimal). Between the threshold and optimal condition, population growth rate changes linearly with each unit of change from the threshold. These temperature and moisture parameters provide the basis for calculation of a weekly Temperature Index and Moisture Index and their product, the Growth Index [38••]. The Growth Index can be considered an indicator of local population density [79]. Near the threshold conditions, populations begin to experience stress due to cold, heat, drought, excessive wetness, or their interactions. Each stress function is characterized by a threshold (i.e., the condition under which stress begins to accumulate) and a rate (i.e., how quickly stress accumulates over time for each unit of difference from the threshold). Options exist in CLIMEX to model diapause induction and termination to capture periods when a species may be more resilient to environmental stresses. Stress indices are calculated from 0 to 999, but any value ≥100 indicates a site that should be climatically unsuitable for the year-round persistence of a species.

Each of the component indices contributes to an overall measure of climatic suitability, the Ecoclimatic Index (EI). EI is formally calculated as:

$$EI = \left(100 \sum_{w=1}^{52} \frac{GI_w}{52}\right)\left(1 - \frac{CS}{100}\right)\left(1 - \frac{HS}{100}\right)\left(1 - \frac{DS}{100}\right)\left(1 - \frac{WS}{100}\right)(SX)$$

where GI_w is the weekly growth index, and CS, HS, DS, and WS are cold, heat, drought, and wet stress, respectively [38••]. SX is the potential interaction among cold and drought (CDX), cold and wet (CWX), heat and drought (HDX), and heat and wet (HWX) and is calculated as:

$$SX = \left(1 - \frac{CDX}{100}\right)\left(1 - \frac{CWX}{100}\right)\left(1 - \frac{HDX}{100}\right)\left(1 - \frac{HWX}{100}\right)$$

EI has values from 0 to 100, with 0 indicating an area that is unsuitable and 100 indicating perfect climatic suitability for a species. Sites rarely remain stable within optimal conditions to earn a score of 100 [80], so many interpretations of the EI exist, particularly for values >0. For example, Saavedra et al. [81] considered EI values of 0 to be unsuitable, 1–4 to be marginal, 5–12 to have low suitability, 13–24 to have moderate suitability, and ≥25 to be optimal. In comparison, Olfert et al. [82] judged EI values of 0–5 to be unfavorable, 6–20 to

be suitable, 20–30 to be favorable, and >30 to be very favorable. Other interpretations also exist.

Parameters for CLIMEX models are typically estimated in one of two ways. Firstly, controlled laboratory studies can be conducted to measure changes in population growth rates with changes in conditions, most often changes in temperature [40]. Secondly, and more commonly, CLIMEX parameters are adjusted iteratively until the forecast of climatically suitable habitat provides a qualitatively reasonable approximation of the known distribution (presence points) or of regional or seasonal differences in population density [40]. However, this approach has some of the same sensitivities to presence data as other inductive models have [45]. Typically, CLIMEX models assume that a species is absent if no record of presence exists. If presence points for a species have only been reported from a climatically homogenous area, it may not be possible to reliably estimate all of the stress functions [40, 83]. An appealing aspect of CLIMEX is that each parameter has a clear ecological interpretation, so expert biologists can comment on the reasonableness of a parameter estimate.

CLIMEX has been applied to some notorious alien insects that can affect trees. An early application of CLIMEX was to the invasion of the USA by the European gypsy moth, *Lymantria dispar dispar*, to determine whether portions of the southeastern USA might be climatically suitable [14]. Though values for EI were not given, much of the southeast was judged to be "moderately" suitable with CLIMEX, but southern Florida was considered climatically unsuitable. Matsuki et al. [84] later developed a similar model for the Asian gypsy moth, *L. dispar asiatica*, and found similar results. EI values were between 25 and 50 for much of the eastern two thirds of North America (but still 0 for southern Florida), much of New Zealand, and southeastern Australia, suggesting that this insect could encounter suitable climate in many parts of the world. MacLeod et al. [85] applied CLIMEX to the Asian longhorned beetle, *Anoplophora glabripennis*, and found significant portions of Europe to have a highly suitable climate.

Process-Oriented Population Models Process-oriented population models provide a mechanistic description of the potential effects of climate, particularly temperature and/or moisture, on populations. The processes of interest are typically vital rates (i.e., birth, death, development, or dispersal, the fundamental determinants of population dynamics). Process-oriented population models may be divided conceptually into an ecophysiological component that describes how vital rates change under different environmental conditions and an environmental component that describes how conditions vary over space and time (typically, the "environment" refers to one or more abiotic components, particularly temperature or moisture, but could also include host distribution/abundance or natural enemies). The integration of these components

characterizes how populations might be expected to vary in response to spatial or temporal environmental variation. These models rely less on "canned" software than inductive models and frequently require the development of specialized applications.

Process-oriented models for gypsy moth illustrate the requisite integration of ecophysiological and environmental information. Numerous researchers contributed to the development of an understanding of environmental effects on the population ecology of this insect. Studies of the effects of temperature on egg hatch [86–90] and larval development [91, 92] were particularly important. Régnière and Sharov [93] and later Régnière and Nealis [94] relied on these studies and the software BioSIM, software to estimate finer-grain spatial variation in climate than is captured by weather-station arrays, to characterize regional variation in the developmental phenology of gypsy moth, particularly when eggs deposited in 1 year (e.g., late summer) might hatch the following spring, how long larval development might require, and when adult flight might begin. Alternatively, Gray [95•] developed a multi-generational, gypsy-moth-phenology model driven by climatological records for approximately 4500 locations in North America from which he was able to derive a measure of the likelihood that each location (and interpolated areas) would consistently meet climatic requirements for a local population to persist. Both models were motivated by the general question of where in North America gypsy moth might find suitable climates to become established.

Other process-oriented models may attempt to characterize the effects of specific environmental stresses on invading insect populations. For instance, Régnière and Bentz [96] modeled effects of cold on the mountain pine beetle, *Dendroctonus ponderosae*, before, during, and after a transition to a fully cold hardened condition. The development of this model depended on the careful study of the effects of cold on mountain pine beetle mortality, especially the work of Bentz and Mullins [97]. The advantage of process-based models is that if the underlying mechanisms are properly characterized the models should be readily transferable to other locations or future climate conditions and the model outputs can be evaluated readily against field observations [98]. The disadvantage is that the requisite data for an alien insect species may be unavailable when a projection is needed and may take years to collect.

Efforts are underway to develop simpler, standardized process-based models that might be useful for pest risk assessment (e.g., [99]). For example, degree-day models provide a relatively simple means to integrate time and temperature to forecast development in insect populations. Magarey et al. [100] were able to apply a relatively simple degree-day model for *L. dispar asiatica* to gridded climate surfaces to forecast flight periods. Results were consistent with forecasts from the more complex model of Gray [101] for Kobe, Japan, the only

city common to both studies. Other such modeling platforms are in development.

Applications of Species Distribution Models to Invading Forest Insects

Although species distribution models have certainly been developed for invading forest insects (see examples above), most of the literature is dominated by applications to plants and vertebrates. In an effort to determine if certain approaches are used more frequently in the study of invading forest insects, I conducted a structured literature analysis by using Thomson Reuters' Web of Science with queries to the Science Citation Index (1975-present), Conference Proceedings Citation Index (1990-present), Book Citation Index (2005-present), and the Emerging Sources Citation Index (2015-present). Matching literature was reviewed for relevance to forecasts of species distribution.

The analysis began with the compilation of search terms. Venette et al. [19] provided a list of 19 approaches to forecast invasive species' distributions. From the list, 22 search terms were identified: artificial neural networks, BIOCLIM, ANUCLIM, BioMOD, CART, classification regression trees, minimum bounding rectangle, climate envelope, CLIMEX, DOMAIN climate, ENFA, ecological niche factor analysis, geographic information system (GIS), FloraMap, GARP, genetic algorithm, GRASP, MaxEnt, Maximum Entropy, NAPPFAST, and STASH. Many of the terms refer to specific software that had been developed for species distribution modeling. Other logical or statistical procedures (e.g., expert driven rule sets or generalized additive models) were not included, nor were process-oriented population models. Process-oriented population models can be time consuming to produce and are unlikely to precede the development of other species distribution models (the European gypsy moth being a notable exception). Results of searches for each of these terms were cross referenced with the scientific names of ten alien insects classified as (potentially) high-impact in North America [1]: *Adelges piceae*, balsam wooly adelgid; *Adelges tsugae*, hemlock wooly adelgid; *Agrilus planipennis*, emerald ash borer; *Anoplophora glabripennis*, Asian longhorned beetle; *Cryptococcus fagisuga*, beech scale; *Euwallacea* sp., polyphagous shot hole borer; *Lymantria dispar*, gypsy moth (Asian and European subspecies); *Operophtera brumata*, winter moth; *Sirex noctilio*, European woodwasp; and *Xlyeborus glabratus*, redbay ambrosia beetle.

This targeted analysis revealed that certain species distribution models have been applied to the ten high-impact forest insects and published in peer-reviewed journals more often than others (Fig. 1). MaxEnt, CLIMEX, and GIS were applied to the greatest number of species. Most other tools that had been used were only used in one or two cases. Nine of the 18
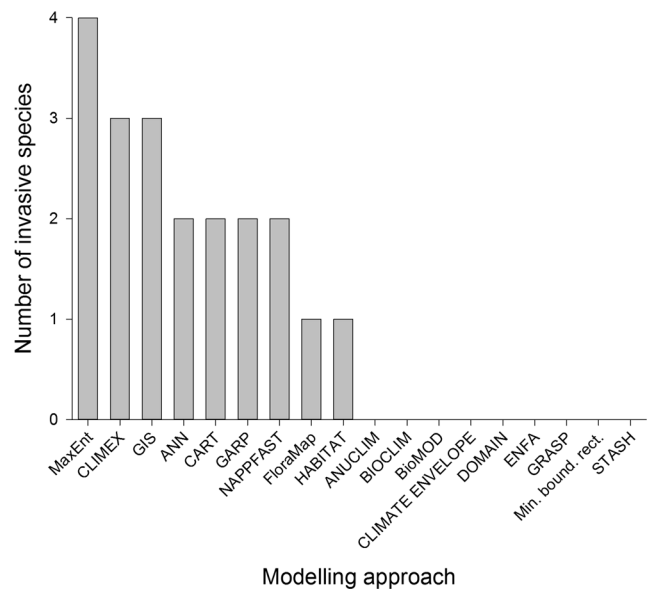
Fig. 1 Application of different modeling approaches to forecast the distribution of ten (potentially) significant invasive insect species in North America (searches for MaxEnt included maximum entropy, CART included classification and regression trees, and ENFA included ecological niche factor analysis. *ANN* artificial neural networks, *min. bound. rect.* minimum bounding rectangle)

modeling tools or approaches had either not yet been applied to, or published for, any of these important alien forest pests. Some species had been studied with multiple approaches. For instance, six approaches had been applied to *L. dispar*, some more than once [14, 84, 100, 102–107]. Four approaches had been published for *A. planipennis* [59, 108–111]. Three had been reported for *A. glabripennis* [54, 85, 112] and *S. noctilio* [113–115]. Two were applied to *A. tsugae* [116–118]. It was surprising to learn that none of the above referenced species distribution models had been published for *A. picea*, *C. fagisuga*, *Euwallacea* sp., or *O. brumata*. This targeted analysis suggests that species distribution models are not being applied routinely to alien insects that affect trees and forests.

A number of factors may explain this pattern of use. Firstly, not all models perform equally well. Elith et al. [68] provide one of the most comprehensive direct comparisons of the performance of 16 methods to generate species distribution models. Some modeling approaches, especially MaxEnt and Boosted Regression Trees among others, consistently outperform models such as BIOCLIM, DOMAIN, or desktop GARP, while many regression-based approaches and the OpenModeller version of GARP had intermediate performance [68]. Some of the "older" modeling platforms seem to have underperformed because they do not always include an analysis of background environmental conditions. However, the comparison of different species distribution models did not focus on invasive alien species, and the assessment metrics may not be entirely appropriate for species with expanding ranges [25•].

Secondly, model availability and educational opportunities can be limited for several approaches, so users may have difficulties learning the idiosyncrasies of a particular software package or analysis method [119]. The International Pest Risk Mapping Workgroup (now International Pest Risk Research Group) highlighted the need for additional training among its top ten recommendations to improve the development of pest risk maps [19]. It should be noted that on-site training opportunities are available for CLIMEX and several on-line training tools are available for MaxEnt. In addition, numerous examples of applications of both models exist in the peer-reviewed literature to guide future efforts.

Thirdly, models may be developed for operational purposes [120] and not reported in peer-reviewed literature. For example, the US Department of Agriculture Forest Service has utilized expert-driven rule sets in a geographic information system to produce risk maps for four alien *Agrilus* spp., *A. glabripennis*, *Ips typographus*, *L. dispar*, *Orthotomicus erosus*, and *S. noctilio* (www.fs.fed.us/foresthealth/technology/invasive_species.html as of 12 Sept 2016). The maps have undergone extensive internal reviews, but have not been published in the primary literature.

"Model fatigue" also may be an issue for reviewers of certain species distribution models. Editors typically solicit reviews of species distribution models from experts on the organism or the modeling approach. Organismal experts may question the added value of another species distribution model if one or more models already exist. Modeling experts can ensure that an approach was applied properly and output interpreted correctly, but may question the novelty of the work, especially if the model is an application of a well-established technique.

Lastly, limited availability of data may be a significant impediment. In fact, as Baker et al. [23] suggest, pest risk modelers may feel fortunate to have even reliable presence data. Frequently, for an alien species of concern, presence points are unavailable (i.e., no historical surveys or reported in un-indexed foreign literature), unreliable (i.e., misidentification of the species of interest), imprecise (i.e., reported as present within a nation or subnational boundary), or unrepresentative (i.e., likely only from a portions of a species' range). These situations occur frequently for forest insect pests that cause little economic damage within their native range, but cause significant damage when introduced to new areas. Equally problematic are cases where climatic data do not reflect microclimates or modified-landscapes that an alien species might occupy. For example, alien species may thrive where irrigation overcomes drought stresses or human dwellings shelter against cold winter temperatures. Thus, the challenge is to find reliable, representative presence points and meaningful environmental covariates for model development and testing.

Conclusions and Future Directions

The complexities of developing reliable species distribution models for species that are invading novel climates are becoming more apparent (e.g., [26]). Many of the fundamental assumptions that are central to the development of inductive species distribution models do not apply, particularly the species' distributional limits being at equilibrium with the environment. As a result, the output from the same analytical method may have a very different interpretation if it was developed with presence-background, presence-absence, or occupancy-detection data [26]. At one level, a model may only provide relative differences in habitat suitability. In other cases, the model may provide reliable estimates of relative occurrence rates [58]. Great care is needed in the development and interpretation of any species distribution model.

More applications of species distribution models to alien insects that may affect trees and forests are needed. Resulting forecasts are necessary to estimate the longer-term impacts that these species might have and to support appropriate management responses. These new applications should not be developed lightly. Some could seek to evaluate the robustness of the model result to different methods of background selection, to determine whether presence points reflect potential biases, or to explore the utility of simpler models to avoid issues with multicollinearity among predictors. These studies could provide a clearer sense of ways to resolve common issues that complicate the development of species distribution models. In addition, applications to bark and ambrosia beetles or other wood-boring insects may be particularly interesting because conditions measured at weather stations, on which many of these modeling approaches depend, are only partially indicative of the microclimate experienced within a tree. Thus, opportunities exist to explore how microscale phenomena may drive macroscale patterns such as range limits.

As species distribution models and our understanding of them become more sophisticated, paradoxically more uncertainties likely will become evident. In pest risk assessment as in ecology, uncertainty stems from limits to knowledge (i.e., epistemological uncertainty) and limits to language (i.e., linguistic uncertainty) [121]. For analyses of climate suitability for alien species, uncertainty manifests in different forecasts for the same species in the same space and time [19]. For example, Sobek-Swant et al. [59] assessed climate suitability for the emerald ash borer in Canada and the contiguous USA with MaxEnt and GARP models by using presence points from Asia, North America, or both continents. While the six models typically classified the northeastern USA as highly suitable, forecasts of climatic suitability diverged substantially within the range of green ash, *Fraxinus pennsylanica*, one of the insect's primary hosts. Suitability estimates from the different models ranged from 0 to >80% in the mid-continent (i.e., North Dakota, South Dakota, Minnesota,

Saskatchewan, and Manitoba) and 0 to 60% in the southeastern USA. The authors acknowledged this variability among models but offered few insights about how to reconcile differences. Some of these differences likely reflect complex interactions between limits to knowledge of the system being studied and differences in how each software package deals with the analytical problem to be solved.

All modeling demands an abstraction of the system under study, and modelers often trust that requisite simplifying assumptions have little impact on outputs and/or that the model has utility despite any error. The impact of choices made during model construction is evaluated during model verification and validation, the processes by which model forecasts are compared with cases that were used to develop the model and cases that are independent of model development, respectively. The area under the receiver-operator curve (AUC) and kappa remain the most common statistics to measure the performance of species distribution models [22]. A number of modeling approaches use subsets of data for model development (i.e., training data) and evaluation (i.e., testing data) of replicate models, but this approach is more accurately considered internal validation. Measures of internal validity approximate the true error rate, but do not provide reliable estimates of error associated with the application of the model to truly independent cases (i.e., the transferability of the model) [65]. Error rates should be expected to increase when applied to new locations or time periods [122••].

In the absence of external validation, it is difficult to determine which model is most likely to correctly forecast future presences and future absences. Model comparisons then often focus on apparent violations of first principles which reflect our current understanding of how systems ought to operate and which simplifying assumptions are appropriate or not [32]. Debates about first principles can linger for decades [19].

New approaches are needed to quantify, communicate, and explore the consequences of uncertainty for decision makers (e.g., [115, 123]). At the same time, empirical biological research also is needed to inform model components or rigorously evaluate model outputs. Each forecast of future distribution of an invasive alien species should be considered a hypothesis in need of testing. Models identify particular research needs, and research identifies opportunities for model improvement. Together, species distribution models and empirical research provide vital elements to effective biosecurity.

Compliance with Ethical Standards

Conflict of Interest   Dr. Venette declares no conflicts of interests.

Human and Animal Rights and Informed Consent   This article does not contain any studies with human or animal subjects performed by any of the authors.

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