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Short review

Modelling for risk and biosecurity related to forest health

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23 Abstract

24 Modelling the invasion and emergence of forest pests and pathogens (PnPs) is necessary to quantify
25 the risk levels for forest health and provide key information for policy makers. Here, we make a short
26 review of the models used to quantify the invasion risk of exotic species and the emergence risk of
27 native species. Regarding the invasion process, models tackle each invasion phase, e.g., pathway
28 models to describe the risk of entry, species distribution models to describe potential establishment,
29 and dispersal models to describe (human-assisted) spread. Concerning the emergence process,
30 models tackle each process: spread or outbreak. Only a few spread models describe jointly dispersal,
31 growth and establishment capabilities of native species while some mechanistic models describe the
32 population temporal dynamics and inference models describe the probability of outbreak. We also
33 discuss the ways to quantify uncertainty and the role of machine learning. Overall, promising
34 directions are to increase the models' genericity by parameterization based on meta-analysis
35 techniques to combine the effect of species traits and various environmental drivers. Further
36 perspectives consist in considering the models' interconnection, including the assessment of the
37 economic impact and risk mitigation options, as well as the possibility of having multi-risks and the
38 reduction of uncertainty by collecting larger fit-for-purpose datasets.

39 **Introduction**

40 Forests provide ecological, economic, social, and aesthetic services. In addition, they largely
41 contribute to carbon sequestration and they could thus represent an important means of climate
42 change mitigation [1]. However, forest health is threatened by various pests and pathogens (PnPs).
43 Global change, including climate change but also other changes at global scale such as the
44 intensification of international trade, has triggered the emergence of an increasing number of tree
45 PnPs. The number of biological invasions of exotic species in new areas has been dramatically
46 increasing [2,3], and climate change has been promoting the range expansion or population
47 outbreaks of many native species (so called emergent species; [4-7]). Both invasive exotic species and
48 emerging native species thus represent important risks for forest health.

49 To quantify the current and projected risk levels, and to provide key information for decision-support
50 experts and policy makers, modelling the invasion and emergence dynamics of these forest PnPs is
51 necessary. Pest risk mapping is particularly useful to support strategic and tactical decisions [8].
52 Improving methods contributing to risk mapping has thus become an important challenge during the
53 last few years [9]. Quantitative pest risk assessment allows for a higher transparency, the assessment
54 of uncertainty, and the exploration of various risk reduction options [10]. To assess the invasion or
55 emergence risk of a species, one may develop and parameterize a model for that species (so called
56 “species-specific models”). Such an approach requires a lot of information on the not-yet-
57 introduced/emerged species. On the contrary, “generic models” utilise what is known about the
58 invasion or emergence process of other species by describing species by their traits and feeding
59 those traits into the model. This is an important advantage because the estimation of various
60 parameters has been proven difficult for not-yet-introduced species, and for those that previously
61 did not cause any damage. Generic models can thus be applied more easily and more rapidly to a
62 newly arriving or emerging species, but their predictive value should be proven across a range of
63 forest PnPs.

64 In this short review, we make a synthesis of models developed to assess the invasion risk of exotic
65 forest PnPs, and the emergence risk of native forest PnPs. We also discuss the ways to quantify
66 uncertainty and the role of machine learning. For each part, we also identify promising directions.

67

68 **Modelling the invasion risk of exotic forest pests and pathogens**

69 The invasion process can be described as a sequence of four phases: entry (transport from country of
70 origin and arrival in the new area), establishment, spread and impact [11]. The factors determining
71 the outcome of each phase can be grouped into three broad categories related to: (i) the vectors
72 carrying the PnPs (understood widely to include animal vectors, abiotic factors such as wind and
73 weather, and human actors), (ii) the environment the pest or pathogen interacts with during the first
74 three phases, and (iii) the characteristics of the pest or pathogen [12]. Modelling entails capturing
75 only the relevant processes and factors to produce tractable and valuable insights for risk assessors
76 and managers. To assess the risk posed to biosecurity, models are needed that tackle each invasion
77 phase [9] (Fig. 1).

78 *Modelling species entry.* Different types of pathway models including epidemic networks and gravity
79 models have been developed so far [13]. They track the PnP from their source area to their
80 destination area where transfer to a suitable host may take place [13- 15]. Such models help to
81 identify locations where high propagule pressure (i.e., a set of PnP individuals) is expected (e.g.,
82 ports, trucks, ships, or factories) and to explore the effects of phytosanitary measures to prevent
83 entry. The drawback of pathway models is the parameterization. They request many parameters and
84 data for both the species and their vectors on for instance interception and transportation. This
85 information is often scarce, inconsistent and variable in time. Sampling methodology, frequency and
86 reporting of intercepted PnPs may actually differ per commodity, per country and per year. In risk
87 assessment this issue is often solved by simplifying the pathway models [10], and/or using Expert
88 Knowledge Elicitation (EKE) to derive sensible parameter values [16].

89 *Modelling species establishment.* The risk of PnP establishment is often modelled using Species
90 Distribution Models (SDMs). These models are generally based on a correlation between presence
91 points (and if available absence points) of the species and climate in the native or already invaded
92 areas [17]. Models are generally purely correlative (e.g., MaxEnt [8]) but more process-based niche
93 models can also be used (e.g., CLIMEX [19]). Caution is needed with such methods, as the resulting
94 potential distribution is a 'worst case' estimate, assuming that the PnP actually arrived in that area.
95 These methods require sufficient spatial data on the target species' presence and eventually absence
96 at large scale. Note that even when a PnP may establish in an area, sufficient propagule pressure is
97 needed to overcome Allee and demographic stochasticity effects occurring at low densities [20].

98 *Modelling species spread.* Once arrived and established, PnPs can disperse in the new area. Spread
99 involves population growth, individual dispersal and population establishment further in the new
100 area. Spread models can be used separately or as part of a combined model with entry and
101 establishment [21,22]. Generally, they focus on the dispersal component only, and describe dispersal

102 through kernels in case of natural (unassisted and assisted by natural vectors) dispersal or with
103 network/correlative models in case of human assisted spread, or combinations of the above [23].
104 Most spread models are pest-specific, requiring detailed information on population and dispersal
105 characteristics [24-26]. Even simpler models with few parameters may still be difficult to
106 parameterize for new biosecurity risks [27].

107 **Promising approaches.** Using models for assessing invasion risk is challenging because of
108 information scarcity on not-yet-introduced species. As a result, one has to rely on existing data of
109 related species – if available, or Expert Knowledge Elicitations, introducing unquantifiable uncertainty
110 in predictions. Because scientific studies in the field of invasion science often focus on a single well
111 characterized pest species, invasion phase, area or vector, it is unclear whether generalisation to
112 species with similar traits, propagule pressure and habitat characteristics is possible [12, 25]. Some
113 studies have been performed on finding generalities in establishment and spread characteristics of
114 species [28-30, 31]. These studies do not focus on pest-specific drivers, but try to unveil general
115 patterns by going beyond species. For example, Fahrner & Aukema [31] reported in a meta-analysis
116 across 147 studies a four-fold difference in spread rates of univoltine and multivoltine species. Meta-
117 analyses, such as the one mentioned are often static analyses, but they could be combined with
118 dynamic models. A recent example is the generic spread model by Hudgins et al. [28]. Hudgins et al.
119 used a spread model with a negative exponential dispersal kernel with its parameters being a
120 function of covariates such as species traits and environmental traits. Optimal parameters for these
121 covariates were obtained by running the model inversely (“inverse modelling” (Table 1, Fig. 1). For
122 each species, spread was simulated by running the model from the moment of establishment to the
123 final time of the observed distribution. They compared this final predicted distribution to the
124 observed one of all species to get best fits for the model parameters and structure. Mech et al. [32]
125 also used this kind of approach to compare impact of currently established pest insects with insect
126 and host traits and evolutionary relationships between native and novel hosts and insects to show
127 that the evolutionary history of a pest’s host species may be a good predictor for impact. Using meta-
128 analysis approaches to generalise results across species invasions, by identifying the factors that
129 drive invasions and exploring how these factors interact with species traits, could be the way forward
130 to build models that are fit for purpose. When combined with model selection techniques [33], it is
131 ensured that models do not become more complex than warranted by available data.

132

133 **Modelling the emergence risk of native forest pests and pathogens**

134 Native species or species introduced a long time ago can also cause high damage. As these species
135 are present in the environment for a long time, they have reached an equilibrium (in population size
136 and spatial distribution) and they are generally not subject to specific regulation or official control.
137 Therefore, pest risk assessment and generic approaches are not as well developed as for newly
138 invasive species. However, a change in environmental conditions can break this equilibrium and lead
139 to an increase of the damage incurred by this species. Recently some species, such as *Thaumetopoea*
140 *pityocampa* [34] and *Lymantria monacha* [35] have expanded their distribution, while others, such as
141 *Operophtera brumata* [36], *Biscogniauxia mediterranea* [37], or *Dendrolimus pini* [38] have made
142 outbreaks. In the first case, spreading species invade territories that were previously not colonized
143 (mainly involving dispersal and growth processes), while in the second case, outbreaking species
144 suddenly increase in population density in territories (either newly colonized or not) where they have
145 been previously present but at a lower density (mainly involving growth processes). Hereafter, we
146 review models that describe such spread and outbreak dynamics (Fig. 2).

147 *Modelling species spread.* Many spread models have been developed [24] but very few of them
148 jointly describe population growth, individual dispersal and population establishment beyond the
149 previous species distribution. Although dispersal is the key process in the spread of invasive species,
150 population growth and establishment in new areas are also very important processes in the spread of
151 native species. We can distinguish three main approaches: 1) species distribution models (SDMs) or
152 ecological niche models, 2) dispersal models, and 3) spread models in changing environment (Fig.
153 2A). SDMs are widely used to project the potential establishment area under climate change [39].
154 Although they do not simulate spread explicitly, they predict the future potential distribution based
155 on climate change scenarios [19, 40]. A drawback of these models is that they ignore dispersal
156 capability and the population dynamics, elements that could limit the extent to which they can track
157 the shift of the climate envelope. In turn, dispersal models, such as reaction-diffusion models or
158 dispersal kernels generally ignore changes in habitat and climate conditions. Only a few spread
159 models describing both population growth and dispersal in a changing environment have been
160 developed [41]. These models could be seen as a mix of SDMs (or other models considering a change
161 in climate conditions on species establishment or survival) and dispersal models (Fig. 2A). However,
162 these models are generally tailor-made for a given species and require many parameters to estimate
163 [42]. They are thus not easily applicable to other species.

164 *Modelling species outbreaks.* The presence of forest PnPs does not necessarily imply damage on
165 forest trees. Their population size should exceed a given threshold to be considered as an outbreak
166 [43]. Various categories of outbreaks can be distinguished [44]. Populations can suddenly increase in
167 size due to a change in the environment. If the population size is correlated with an environmental

168 factor, the outbreak is called “gradient”, while if the population size depends on a threshold of an
169 environmental factor, the outbreak is called “eruptive”. Besides, some pests show periodic
170 outbreaks, which are then called “cyclic”. Whatever the outbreak category, two kinds of models can
171 be used to describe these outbreaks: models focusing on the PnPs’ dynamics (mechanistic models)
172 and models describing the probability that an outbreak occurs (inference models) (Fig. 2B).

173 The first type of models focuses on the species traits. Using data on the biology and the phenology of
174 the species, these mechanistic models can predict population dynamics in a large set of conditions,
175 even if these conditions have not been observed yet. These models can describe the dynamics of the
176 species alone for instance with a logistic growth function [45], the effects of environmental factors
177 such as predators or parasites in prey-predator systems [46,47], or the effects of host with an alike
178 epidemiological Susceptible-Infected-Recovering-Susceptible model [48]. Natural enemies or host
179 plants are indeed often used to explain cyclic outbreaks [49]. The complexity of these models can
180 increase until it encompasses a precise description of the species traits and microhabitat [50].
181 However, these models require data about the population size and good knowledge on the species’
182 life cycle. The more complex a model is, the more realistic it could be, but it will also require more
183 data to infer the parameters and generate high uncertainties in the model output. These models also
184 require knowledge of the life-history traits, which are difficult to estimate, even for well-studied
185 species. Therefore, such models can fail to identify a less-known species that could outbreak.

186 The second type of models consist in inferring the probability of an outbreak based on previous
187 outbreaks in the same conditions. In these models, the description of the species is not required as
188 they only use environmental data (e.g., temperature, precipitations, density of host or dead wood)
189 related to the previous outbreak to identify the drivers of the outbreak. These data are analysed
190 using inference methods such as a regression [51] or random forest [52] to identify correlation
191 between past outbreaks and environmental factors and then to determine the probability of a next
192 outbreak. However, the probability model is calibrated on a set of observed conditions. Extrapolating
193 the probability beyond these conditions can lead to errors since the relationship between the
194 outbreak likelihood and the environmental conditions could be different outside the observed range.

195 **Promising approaches.** Most of spread and outbreak models for native species are not generic so
196 far. The challenge for spread models is to combine both dispersal capabilities and the effects of
197 changing climate conditions in time and in space on population survival and growth, as a function of
198 the species traits. The challenge for outbreak models is to determine the drivers in a way that the
199 model could be easily applied to other conditions, as a function of the species traits. Such outbreak
200 models do not necessarily describe the temporal dynamics of the population density (which would

201 be data demanding) but rather a probability of outbreaking as a function of environmental
202 conditions. The development of generic spread and outbreak models needs to account for the
203 process drivers, the species traits and eventually the effect of their interaction on the simulated
204 process.

205

206 **Parameterizing the models and quantifying uncertainty**

207 *Parameterisation.* To generate predictions, invasion and emergence models need to be
208 parameterized. Typically, three ways of parameterization are used or combined thereof: 1) collecting
209 information on a parameter by setting up experiments or doing field measurements (e.g., by rearing
210 the pest in the lab and running flight-mill experiments to determine the average flight distance [53-
211 54]; 2) using existing information from literature, sometimes on related species or vectors (e.g., [15,
212 28, 32, 55]); and 3) the use of Expert Knowledge Elicitation on plausible parameter values. Different
213 EKE methods can be used to estimate the most likely value for the parameters, such as fixed and
214 variable interval, and the roulette method [16]. For example, in the variable interval method the
215 expert can be asked to determine the parameter value at which the cumulative probability (quantile)
216 is 0.05, 0.5 and 0.95.

217 *Uncertainty.* Each model output is associated with a given level of uncertainty or confidence level,
218 which could rise from various sources, and notably from: 1) model choice, 2) parametrization, and 3)
219 stochastic processes.. It is thus crucial to communicate the uncertainty related to the model outputs,
220 all the more when these results are used for decision making. In particular, in the frame of pest risk
221 analyses, a large range of questions should be answered regarding entry, establishment, spread and
222 impact. For each question, risk assessors have to provide both a rating regarding the related
223 likelihood and a score of uncertainty [56].

224 To cope with uncertainty about the model to choose, it is possible: (i) to run various models
225 describing the same mechanism (ensemble prediction; for instance various climate models are
226 available to describe a single climate change scenario), (ii) to consider various scenarios describing
227 possible mechanisms (for instance, various climate change scenarios are considered based on
228 different greenhouse gas concentration trajectories hypotheses), or (iii) to build a consensus model
229 to combine all the tested models (e.g., [57-59]).

230 To cope with uncertainty in the parameters' estimate for a given model, several approaches could be
231 considered. First, to assess the role of each parameter on the model output, sensitivity analyses are
232 generally conducted. Although it is possible to calculate sensitivity analytically (see [60] for local, and

233 [61] for global analyses) especially for not-too-complex models, the sensitivity is preferentially
234 estimated numerically. These estimations are made by using latin hypercube sampling on an
235 arbitrary range of values (e.g., estimated value or bounds of uniform distributions +/- 10%) for each
236 parameter and then identifying the parameters that have the greatest impact on the model output
237 using partial correlation (e.g. [62-63]). These parameters require a more precise estimate to reduce
238 uncertainty of the model outputs. Second, uncertainty analyses could be done. These consist in
239 assessing the range of possible outputs when varying the parameter values within their confidence
240 intervals. It could result in a confidence interval for the model output (e.g., for a probability of
241 outbreak or probability of introduction), or a series of maps to highlight the best case, the likely case
242 and the worst case (e.g., for potential spread; [27]).

243 To account for uncertainty arising from highly stochastic processes such as human-mediated
244 dispersal in species potential spread, it is possible to include this uncertainty into the final risk
245 estimates using second-degree stochastic dominance criteria [64].

246 ***Promising approaches.*** Since there is no common rule in the way to handle uncertainty in risk
247 models, it is most important to at least report the known uncertainty in one way or another [8].
248 Transparency about the main source of uncertainty and the level of confidence of the model outputs
249 is necessary for decision-making and for improving forest managers' trust in modelling approaches.
250 In addition, the combined effects of all uncertainties should be assessed [65].

251

252 **Role of machine learning**

253 In classical models in ecology, relationships between variables and parameters should be
254 determined, and a statistical algorithm only infers the values of the parameters. As the number of
255 available data and the number of measured variables increase, the number of possible relationships
256 to test increases as well, and it becomes more and more challenging to choose the most appropriate
257 one(s). Machine learning, defined as "a set of methods that computers use to make and improve
258 predictions or behaviours based on data" [66], allows overcoming this problem. Algorithms can
259 indeed infer the relevant relationships (e.g. the number of variables, the number of parameters, or
260 the shape of the functions), and thus improve or facilitate the development of models describing
261 invasion and emergence risks. The diversity of machine learning algorithms is too large to be
262 described here. However, the next paragraph provides a brief overview of these methods with a
263 focus on Species' Distribution Models (SDMs). More details on machine learning in SDMs can be
264 found in [39, 67-71].

265 Machine learning generally has two main components: (i) defining the structure of the model, and (ii)
266 obtaining realistic predictions with this structure. Many types of structures can be chosen, among the
267 most common, there are decision trees (as random forest, e.g. [52]), maps (SVM, e.g. [72]), or
268 functions (as in neural networks, e.g. [73] or GLM [51]). The algorithm will then build a huge amount
269 of the chosen structures by testing many different combinations of relationships. The second step is
270 to obtain predictions from these structures. To do so, the algorithm can either optimize, i.e. find the
271 structure with the predictions which are the closest to the observed data, or make a consensus of
272 every available prediction (bagging). MaxEnt [18] is commonly used for SDMs. In this method, the
273 structure is a distribution and MaxEnt optimizes this by maximizing the entropy. By doing so, MaxEnt
274 imposes a minimal number of constraints to fit the observed data. Another optimization method is
275 the evolutionary algorithm. Each structure has a score, based on the accuracy of the prediction
276 compared to the data. Different scores can be used for SDMs [74], but the most frequent are the
277 “number of correctly classified instances” and the AUC (Area Under the ROC Curve), which take into
278 account false positives and false negatives. The algorithm then mimics reproduction and natural
279 selection in order to select the prediction with the highest score [67]. On the contrary, random forest
280 [75] is a bagging method. Many different decision trees are built, and the prediction of the model is
281 either the average prediction of every tree (for quantitative predictions) or the result of a vote (for
282 qualitative predictions). More information can be found in [39, 67-71].

283 ***Promising approaches.*** A huge diversity of algorithms exists, with varying performance depending
284 on the issue they have to address. The differences between the different approaches are mainly
285 linked to the extrapolation to non-observed cases. Each model extrapolates differently and, as long
286 as there is no data, all assumptions are equally true. Therefore, maintaining a diversity of models can
287 be useful, as global changes can lead to situations not observed yet. Another issue is the
288 interpretability of the model, which is not limited to machine learning in ecology [66,76]. Some
289 models are based on assumptions and structure which are easier to interpret, as a decision tree,
290 while others are based on complicated functions which are harder to interpret even if their
291 predictions are accurate. A model easy to interpret is simpler to share with ‘non-modellers’ and can
292 easily be compared with expert knowledge.

293

294 **General perspectives**

295 This review points out the need of making a quantitative synthesis of literature and data to integrate
296 species traits and various drivers into models to allow application to other species. Further model

297 development, listed hereafter, could improve the risk assessment and the support to policy makers
298 regarding forest biosecurity.

299 Models tackling biological invasions and emergence of native species are generally considered
300 separately. The two processes rely on different mechanisms: the invasive species are in a transient
301 state, as they are arriving and establishing in a new territory, while the native species are initially
302 supposed to be in equilibrium with their environment. Changes in native species are therefore
303 generally triggered by a change in the environment, while changes in invasive species are mostly
304 associated with their own population traits (e.g. growth and dispersal capabilities) and human
305 activities (for their entry and spread). However, some processes such as population dispersal are
306 common to both types of species. In addition, the factors involved in the emergence (spread or
307 outbreak) of native species, such as climate change, also apply to exotic species newly arrived in the
308 territory. As a result, it could be interesting to explore the extent to which both modelling
309 approaches could eventually be merged into a unified framework.

310 As previously explained, various models have already been developed to describe each phase of
311 biological invasions. However, for pest risk analyses and decision-support, decision makers need to
312 have a global estimate of the risk for forest biosecurity. All these models need to be interconnected
313 at the end. Since these models are often very different, it is very challenging to combine them.
314 Therefore, it is of utmost importance to design these models so that they can be interconnected
315 since the beginning of their development. Since pathway models are data-demanding and should
316 cope with different types of uncertainties, considering both entry and establishment simultaneously
317 could be a solution to determine the locations where invasive species could be first established.
318 These locations could then be used as starting points for spread models. The outputs of spread
319 models should then be appropriate inputs for models describing the economic impact of PnPs (not
320 described here).

321 The assessment of the economic impact of forest PnPs is an extra layer that should be considered to
322 have a full risk analysis. It should include not only the direct impact of PnP on the yield reduction and
323 the quality loss, but the indirect impacts such as changes in prices, the demand and supply [77,78]. In
324 addition, this economic impact should also rely on the costs and effectiveness of the risk mitigation
325 options. These final cost-benefit analyses are useful for decision makers to choose the best
326 measure(s). However, this is the final step of a long and complex modelling work, and the uncertainty
327 accumulated along all these interconnected models should be clearly highlighted. Furthermore, the
328 economic impact is only one side of all possible impacts of these forest PnPs. Social and

329 environmental impacts are also of high importance but very difficult to estimate so far, and the total
330 cost is usually underestimated [79].

331 Lastly, decision-makers do not face a single threat. Modelling researches in forest biosecurity should
332 consider as far as possible multi-risks in forest stands, e.g. simultaneous attacks of several PnPs on
333 the same forest stand, or attack of a given PnP combined with an extreme climate event impacting
334 the tree health. Identifying the cause of a tree decline is all the more difficult when different factors
335 are impacting the tree. Modelling can help to analyse threats with multiple factors and to explore the
336 best risk reduction options. A huge amount of data is therefore needed to continuously monitor all
337 these risks and reduce uncertainty of the model. The use of large datasets coming from citizen
338 science (e.g., for species occurrence points) could complement available datasets and thus
339 contribute to refinement of model parameterization [80,81]. However, some specific data can only
340 be collected by specific specialists or official bodies (e.g., inspections at the country border), and
341 standardization is actually needed even for this type of data collection [82].

342

343

344 **Summary Points**

- 345 • Developing generic models to describe the invasion of exotic forest pests and pathogens
346 (PnPs) and the emergence of native ones is necessary to aid rapid assessment of risks and
347 provide support to policy makers.
- 348 • Each invasion phase can be described by a set of models but data is often missing and
349 uncertainty is often very high. Meta-analysis could be used to identify the main drivers and
350 species traits to be considered in parsimonious generic models.
- 351 • Most spread and outbreak models for native species are tailor-made for given species.
352 Identifying the drivers, species traits and their interaction is also needed to develop generic
353 models.
- 354 • Collecting appropriate data to parameterize risk models is a big issue. Models should be
355 designed to be easily applicable, even when poor information is available on the PnP.
- 356 • Models should be interconnected, linked to economic impact models, and ideally consider
357 multi-risks to fully answer the decision-maker's needs.

358

359 **Author contributions**

360 CR and JCD designed the structure of this short review, RvdD and JCD mainly focused on the invasion
361 part, CR and DC mainly focused on the emergence part, and CR lead the paper writing, all others
362 contributed to later versions of the manuscript.

363

364 **Declaration of Interests**

365 None.

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370

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375

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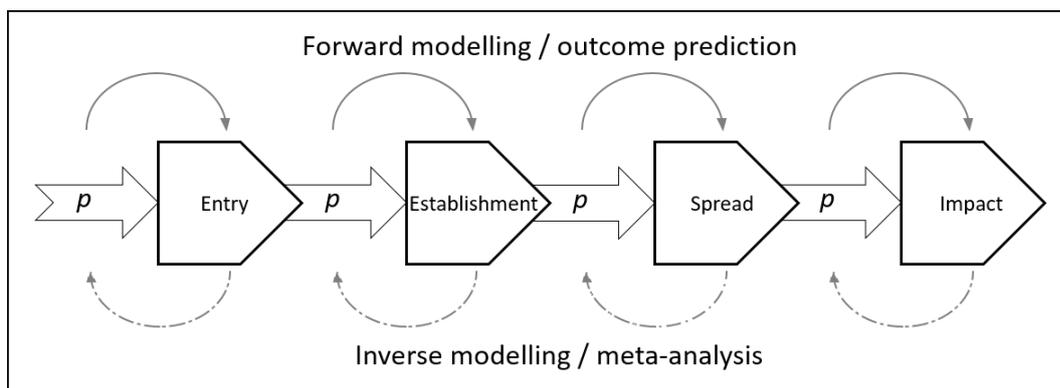
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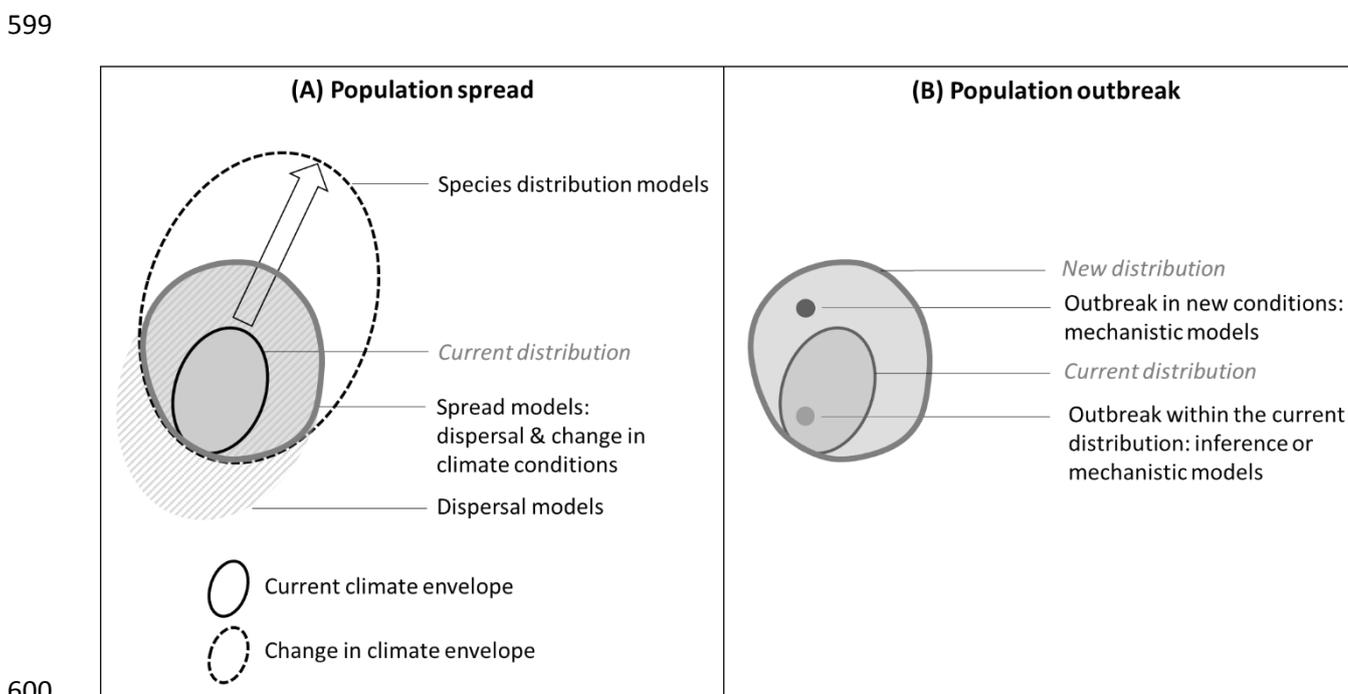
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595 **Figures and tables**



596
 597 **Figure 1: Two different approaches (forward modelling and inverse modelling) could be used to**
 598 **describe the risk of invasion from entry to impact.**



600
 601 **Figure 2: Models describing population spread (A) and outbreak (B) emerging species.** The dark
 602 grey area indicates the current species distribution and light grey area the change in the species
 603 distribution with climate change. (A) The climate envelope extends from the full black curve to the
 604 projected envelope (dotted black curve) due to climate change in the direction indicated by the
 605 arrow. Three types of models could describe spread: they take into account climate suitability,
 606 dispersal capability, and eventually both together. . (B) Two kind of models could describe outbreak:
 607 they are either based on statistical correlations (inference models – appropriate within the current
 608 range) or mechanistic processes (more robust in new conditions).

610

611 **Table 1:** Overview of model types for each invasion phase from entry to spread.

<i>Model type</i>	<i>Phase</i>	<i>Modelling approach</i>	<i>Limitations</i>
Pathway	Entry Establishment	Forward	Data on entry quite limited, this approach has high uncertainty
Species distribution	Establishment Spread	Inverse (mostly)	Result is worst-case scenario, no temporal dynamics, limited by occurrence data quality
Mechanistic spread	Spread	Forward	Often requires detailed PnPs information
Network model / stochastic spread	Spread	Inverse / Forward	Limited by occurrence data quality
Meta-analysis	Any	Inverse	Needs sufficient data on PnPs and predictor variables for a meaningful model

612