









RESEARCH ARTICLE

Predicting the spatio-temporal dynamics of biological invasions: Have rapid responses in Europe limited the spread of the yellow-legged hornet (*Vespa velutina nigrithorax*)?

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Abstract

1. Invasive alien species can have severe impacts on biodiversity, economies, and well-being and their long-term management can involve massive costs. There is an increasing policy imperative to determine whether the management of biological invasions is effective, particularly at biological invasion fronts, but this can often be difficult to determine without extensive data collection. Furthermore, risk assessment frameworks are often used to guide decision-making and management, but these can be hampered by a lack of information about the extent and dynamics of a biological invasion following an introduction within a new region. Incorporating information on the dynamics of biological invasions into these frameworks could provide useful information for decision-makers including a baseline for evaluating ongoing management approaches.
2. Here, we outline a generalisable mechanistic species distribution modelling framework that is informed by patterns of spread observed in other invaded regions and can provide a relatively rapid assessment of the likely spatial and temporal dynamics of a biological invasion in the absence of interventions.
3. To demonstrate this approach, we consider the effectiveness of rapid eradications carried out in four European countries to prevent the spread of the yellow-legged hornet (*Vespa velutina nigrithorax*) following the implementation of Regulation (EU) 1143/2014 on invasive alien species.
4. *Synthesis and applications.* By predicting the extent of a biological invasion in the absence of timely interventions and comparing this to the current distribution of the yellow-legged hornet, we found that management measures implemented in these countries appear to have been effective in limiting the spread of the species in Europe. Additionally, the model framework may be useful to inform the identification of high-risk areas for surveillance measures to be prioritised in view of rapid detection and early eradication activities.

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KEYWORDS

interventions, invasive alien species, risk assessment, species distribution model, *Vespa velutina*, yellow-legged hornet

1 | INTRODUCTION

The introduction of species into new regions via human intervention, so-called alien (non-native) species, has the potential to severely affect biodiversity, economies, and human well-being (IPBES, 2019, 2023; Paine et al., 2016; Stoett et al., 2019; Vanbergen et al., 2018). This has prompted policy responses at multiple scales including national, regional, and globally coordinated efforts with international agreements in place to prevent and manage invasive alien species (CBD, 2019; Defra et al., 2023; European Commission, 2020a, 2020b; IPBES, 2023). In many cases these policies have set specific and measurable targets for slowing the spread, reducing negative impacts, and measuring the success of management of invasive alien species. For example, Target 6 of the Convention on Biological Diversity Kunming-Montreal Global Biodiversity Framework (GBF) commits parties to eliminate, minimise, reduce, and or mitigate the impacts of invasive alien species on biodiversity and ecosystem services (CBD, 2022). However, some of the key obstacles identified to meeting targets have been the quality and quantity of data on invasive alien species available and the suitability and policy-relevance of indicators for measuring progress (Essl et al., 2020; IPBES, 2023; McGeoch & Jetz, 2019; Vicente et al., 2022).

Risk analysis frameworks are important to underpin decision-making and inform management (Roy et al., 2018) but are often impeded by a lack of information and data on a focal species, such as the impact that an invasive species might have in an invaded region and the likely spatio-temporal dynamics of spread. Standardised approaches have been developed for classifying actual or potential environmental and socioeconomic impacts of invasive alien species, which leverage expert elicitation approaches (Bacher et al., 2017; European Food Safety Authority (EFSA) et al., 2019; IUCN, 2020). These frameworks could be complemented by spatio-temporal predictions of establishment and spread to inform environmental impact metrics within risk assessment frameworks (European Food Safety Authority (EFSA) et al., 2019) and could also be used as a baseline to evaluate the effectiveness of interventions.

In order for predictions to better inform interventions for invasive alien species, modelling frameworks must provide outputs for decision-makers that are useful and timely (Dunn & Laing, 2017; Jones & Kleczkowski, 2020). Researchers and decision-makers work on different timescales, with decision-makers often having to rapidly make decisions but research potentially yield results only some-time after action should have been taken (Dunn & Laing, 2017; Jones & Kleczkowski, 2020). Therefore, methods that can be readily implemented across multiple species may allow for pre-emptive planning or provide a rapid assessment in the absence of data and information at the early stages of biological invasions.

Ecological niche models (ENMs) provide a useful tool for understanding the suitability of invasive alien species and the potential spatial extent of spread (Chapman et al., 2019; Elith & Leathwick, 2009). ENMs can be implemented relatively quickly using available occurrence data and a growing number of climatic and land use databases. However, these methods often do not consider dispersal constraints or life history traits of a species and using these outputs to infer occurrence requires an assumption that the distribution of a species is in equilibrium (all suitable habitat is occupied) (Chapman et al., 2019; Wiens et al., 2009). These limitations can hinder the ability to provide information on the likely spatial and temporal dynamics of biological invasions. There are mechanistic modelling approaches that have been developed to predict the spatial and temporal dynamics of biological invasions or explore different management approaches to informing decision-makers (Baker, 2017; Kovacs et al., 2014; Lustig et al., 2019; Prasad et al., 2010; Thompson et al., 2021) but these require extensive life history data and have rarely been used to evaluate the progress or success of management strategies.

Here, we propose a modelling framework to help support risk analysis and national reporting obligations on effectiveness of invasive alien species management in Europe (see Regulation (EU) No 1143/2014 (Council of the European Union, 2014)). To do this, we build on existing mechanistic species distribution modelling (SDM) approaches that couple ENMs with mechanistic spread models to simulate spread in the introduced range in the absence of any management (Engler et al., 2012; Lustig et al., 2017; Srivastava et al., 2021; Zhu et al., 2020) and use these predictions as a baseline to evaluate the success of ongoing management approaches.

We demonstrate the application of this framework by predicting the likely patterns of spread of the yellow-legged hornet (*Vespa velutina nigrithorax*), a species of Union Concern. We then evaluate the impact of the eradication programmes in Europe reported through the EASIN Notification System, NOTSYS the official tool developed by the Joint Research Centre (JRC) for the implementation of Regulation (EU) No 1143/2014 (European Commission, 2014). The datasets from ongoing monitoring schemes across Europe have been utilised in previous studies to model the environmental suitability for *V. v. nigrithorax* (Table S1.1). (Barbet-Massin et al., 2013, 2018, 2020; Fournier et al., 2017; Ibáñez-Justicia & Loomans, 2011; Keeling et al., 2017; Liroy et al., 2019; Villemant et al., 2011). Here, we build on these previous approaches by explicitly incorporating dispersal constraints using a mechanistic spread model to provide spatio-temporal predictions of spread based on suitability. These predictions are informed by observed patterns of spread where this species is now established allowing us to explore a number of different spread scenarios and use these as a baseline to assess the effectiveness of interventions by comparing scenarios of spread to the area currently occupied by *V. v. nigrithorax* in these countries.

2 | MATERIALS AND METHODS

2.1 | Distribution data

Species occurrence data for *V. v. nigrithorax*, on a global scale spanning from 1993 to 2020, were used within an Ecological Niche Model (ENM) to assess the environmental suitability for *V. v. nigrithorax* across Europe. Data were obtained from multiple data sources, including existing recording schemes in Europe (Aktion-Wespenschutz, 2020; BRC, 2020a, 2020b; GBIF, 2020; iNaturalist Community, 2020; MAGRAMA, 2016; Observation International and local partners, 2020; Rome, 2020; StopVelutina, 2016) (Table S1.2). Problematic records, such as records located in biodiversity institutions, records with identical longitude and latitude, records from centroids of countries or provinces and records in the sea were removed using the 'CoordinateCleaner' package (Zizka et al., 2019). Records with a geographic uncertainty greater than 10km were also excluded. The remaining 23,147 records (Figure S1.1) were gridded at five arcminute resolution (0.083×0.083 degrees of longitude/latitude) yielding 3803 grid cells with occurrences. As a proxy for recording intensity, the number of *Insecta* records held by GBIF was also compiled on the same grid (Figure S1.2).

2.2 | Abiotic variables used for environmental niche model

Climatic variables were obtained from WorldClim version 2.1. Variables used to represent current climatic conditions were taken from historical data (1970–2000) (Fick & Hijmans, 2017). The climate variables used in this study were the same as those used in a previous ENM used to project suitability for *V. v. nigrithorax* in France (Fournier et al., 2017). This study and another study also found that *V. v. nigrithorax* tended to favour nesting in anthropogenically disturbed areas in France (Fournier et al., 2017; Rome et al., 2015) and Italy (Lioy et al., 2019). Therefore, the Global Human influence index (HII) was included as another abiotic variable (WCS & CIESIN, 2005). This index was developed from nine global data layers incorporating population density, land use, infrastructure, and human access. To assess potential issues with collinearity between environmental predictors, we assessed the correlation between each of these variables and included only one variable where two variables were highly correlated (Pearson correlation coefficient >0.7). On a global scale, three pairs of variables were highly correlated (Figure S2). Therefore, we selected a single variable from each pair of highly correlated variables. Given the duration of the lifecycle of *V. v. nigrithorax* (April–November) (Monceau et al., 2014), we selected those variables that are more likely to represent temperature or precipitation across the year as opposed to those variables that represent climatic conditions in a single quarter. Therefore, annual mean temperature (BIO 1) was included instead of the mean temperature of the warmest quarter (BIO 10), and annual precipitation (BIO 12) was included instead of

precipitation in the driest quarter (BIO 17). We also selected temperature seasonality (BIO 4) instead of isothermality (BIO 3) to represent temperature fluctuation across the year.

2.3 | Projecting environmental suitability

To project the environmental suitability in each cell for *V. v. nigrithorax* based on the abiotic variables outlined above, we fitted a selection of ENMs both globally and only for Europe. For both sets of models, we used six different pseudo-absence selection procedures to determine which performs best for this species. These approaches each have different consideration of abiotic factors and movement in pseudo-absence selection. They ranged from random selection to selecting pseudo-absences in areas only deemed to have suitable climate and that species are likely to have sampled based on dispersal constraints. We also used these approaches with and without weighting selection by recording effort (number of *Insecta* records) (see Supporting Information S3). To evaluate how well our ENM predicted species occurrences, we used the Boyce Index (Boyce et al., 2002; Hirzel et al., 2006) and reserved 1000 randomly sampled occurrence records from Europe for model evaluation prior to fitting models. The data used for modelling were randomly split, using 70% of the data for model training and 30% for model evaluation. To account for potential influence of spatial sorting bias on evaluation metrics, we calculated a calibrated AUC (cAUC) using a geographic null model as described in Hijmans (Hijmans, 2012) and calculated the true skill statistic (TSS) using the maximum sum of sensitivity and specificity, as this metric is not affected by pseudo-absences in the data (Comte & Grenouillet, 2013; Liu et al., 2013). For each model, an ensemble model was fitted using BIOMOD ('Biomod2' R package V3.3-7) (Thuiller et al., 2009) with six statistical algorithms: generalised linear models (GLM) with both linear and quadratic terms for each predictor, generalised additive models (GAM) with a maximum of four degrees of freedom per variable, multivariate adaptive regression splines (MARS), generalised boosting models (GBM), random forests (RF), and artificial neural networks (ANN). The selection of best-performing algorithms for the final ensemble model was based on modified Z-scores (Chapman et al., 2019; Iglewicz & Hoaglin, 1993). Normalised variable importance was assessed, and variable response functions were produced using BIOMOD2's default procedure. The best-performing ensemble model across all evaluation metrics was chosen to project environmental suitability.

Depending on the focal invasive alien species, it may be necessary to include biotic factors (such as competition and prey availability) that may influence suitability for establishment. In the case of *V. v. nigrithorax*, there is still limited evidence to confidently include biotic interactions. Current evidence suggests no significant competitive interactions with native *Vespidae* species (Carisio et al., 2022). A recent study has also highlighted prey availability may not be an important factor given that *V. v. nigrithorax* is a generalist opportunistic predator that preys on locally abundant prey (Rome et al., 2021).

2.4 | Predicting spatio-temporal patterns of spread

To predict the future distribution of *V. v. nigrithorax* in the countries for which NOTSYS notifications are available, we utilised the MIGCLIM model ('MigClim' package in R) (Engler et al., 2012; Engler & Guisan, 2009). This approach allows suitability projections from ENMs to be used to predict a species' current and future distribution by simulating dispersal across landscapes. It also incorporates important life history traits and time to propagule production. We used suitability estimates from the best-performing ensemble ENM as the landscape and used patterns of spread in other European countries where *V. v. nigrithorax* is established to inform the selection of appropriate dispersal kernels.

To develop different spread scenarios, we used the combination of dispersal kernel and threshold value that best predicted the pattern of spread observed in France, Spain, and Italy. To do this, we generated a range of dispersal kernels using Gaussian, negative exponential, and power law equations (Supporting Information S4) and used three different thresholds to classify cells as suitable and unsuitable using the 'minROCDist', 'Default' and 'Max Sens +Spec' methods in the PresenceAbsence package in R (Freeman & Moisen, 2008). We ran the MigClim model for 50 simulations from the first year of records in each country. Using existing distribution data in Spain (2010–2016), Italy (2013–2019), and France (2004–2014), we then selected the combination of dispersal kernel and threshold that best predicted the current distribution in each country using AUC and the Boyce index. To reduce the inclusion of human-mediated dispersal events when determining dispersal kernels, we identified those clusters that are segregated from the cluster including the earliest records. To do this, we first calculated the distance between all records in each country, after which we used hierarchical clustering ('hclust' function in R) (R Core Team, 2017) to establish which clusters were segregated by a distance greater than 100 km. This resulted in multiple clusters of records in each country (Figure S5). The cluster containing the earliest records in each country was used to establish the best-suited dispersal kernel.

To predict spread in Belgium, Germany, the Netherlands, and the UK, we adapted the MIGCLIM approach to incorporate records of introductions and nest removals each year. To do this, the MIGCLIM model was run for each year individually and the initial distribution for each year was updated to include any additional NOTSYS notifications in later years. The MIGCLIM model for each country with NOTSYS notifications was run for 100 simulations from the first NOTSYS notification for 10 years using each of the different spread scenarios. To produce a spatial map of the probability of occupancy in each country with NOTSYS notifications, we calculated the mean probability of occupancy across the three different spread scenarios. We also summarise the proportion of sites predicted to be occupied over time in each country. The modelling framework is summarised in Figure 1.

In Belgium, *V. v. nigrithorax* is no longer considered a notifiable species under Article 16 but is now considered a widespread species under Article 19. Therefore, we used additional records from

Belgium to determine whether the mean probability of occupancy estimated from three different spread scenarios was able to predict the spread of *V. v. nigrithorax* in the country.

3 | RESULTS

3.1 | Environmental suitability in Europe

Of all fitted models, the model using the accessible regions, pseudo-absence selection method had the best performance across all evaluation metrics (calibrated AUC=0.56, TSS=0.88, Boyce Index=0.96) (Table S2; Figure S6). Using this pseudo-absence selection procedure, our ensemble model suggests that suitability for *V. v. nigrithorax* is most strongly influenced by precipitation seasonality and temperature seasonality, which together accounted for 82% (64% and 18%) of the variation explained in occurrence. This is followed by mean annual temperature seasonality, which explains 14% of the variation. Annual precipitation explained 2% of variation, and anthropogenic influence explained 2% of the variation (Table S3).

Environmental suitability varied across Europe, with areas of high suitability in France, Spain, Portugal, Italy, Belgium, the Netherlands, Denmark, Germany, the United Kingdom, Northern Ireland, and the Republic of Ireland (Figure 2). Regions with an annual mean temperature of ~10–15°C have the highest suitability for *V. v. nigrithorax*, with decreased suitability in areas below and above this temperature. Regions with high-temperature seasonality are also least suitable for *V. v. nigrithorax*. Results for precipitation variables show a lower suitability of areas with low and high annual precipitation and that suitability is highest in those areas with low seasonality in precipitation. Our results also show an increase in suitability for *V. v. nigrithorax* in areas with higher anthropogenic disturbance (Figure S7).

3.2 | Spread scenarios and validation of spread model

Our projected distribution of *V. v. nigrithorax* in Belgium used the three different scenarios of spread parametrised using data from France, Italy, and Spain (that differed in estimated dispersal rates and suitability thresholds). These three scenarios all performed well in explaining the observed pattern of spread in each country when parameterised with the suspected initial introduction in each country (AUC=0.86 (France), 0.93 (Italy), 0.97 (Spain) & Boyce Index=0.91 (France), 0.89 (Italy), 0.95 (Spain)) (also see Table S4; Figures S8, S9 and S10). Overall, estimates of distances of dispersal were highest in Spain and lowest in France and Italy. However, suitability thresholds associated with the best-performing dispersal estimates were higher in Spain (Threshold=0.59) and Italy (Threshold=0.72) and lower in France (Threshold=0.5). This resulted in generally faster spread using the Spain scenario when compared with France and Italy. Projections from these three scenarios resulted in a projection that 73–96% of suitable

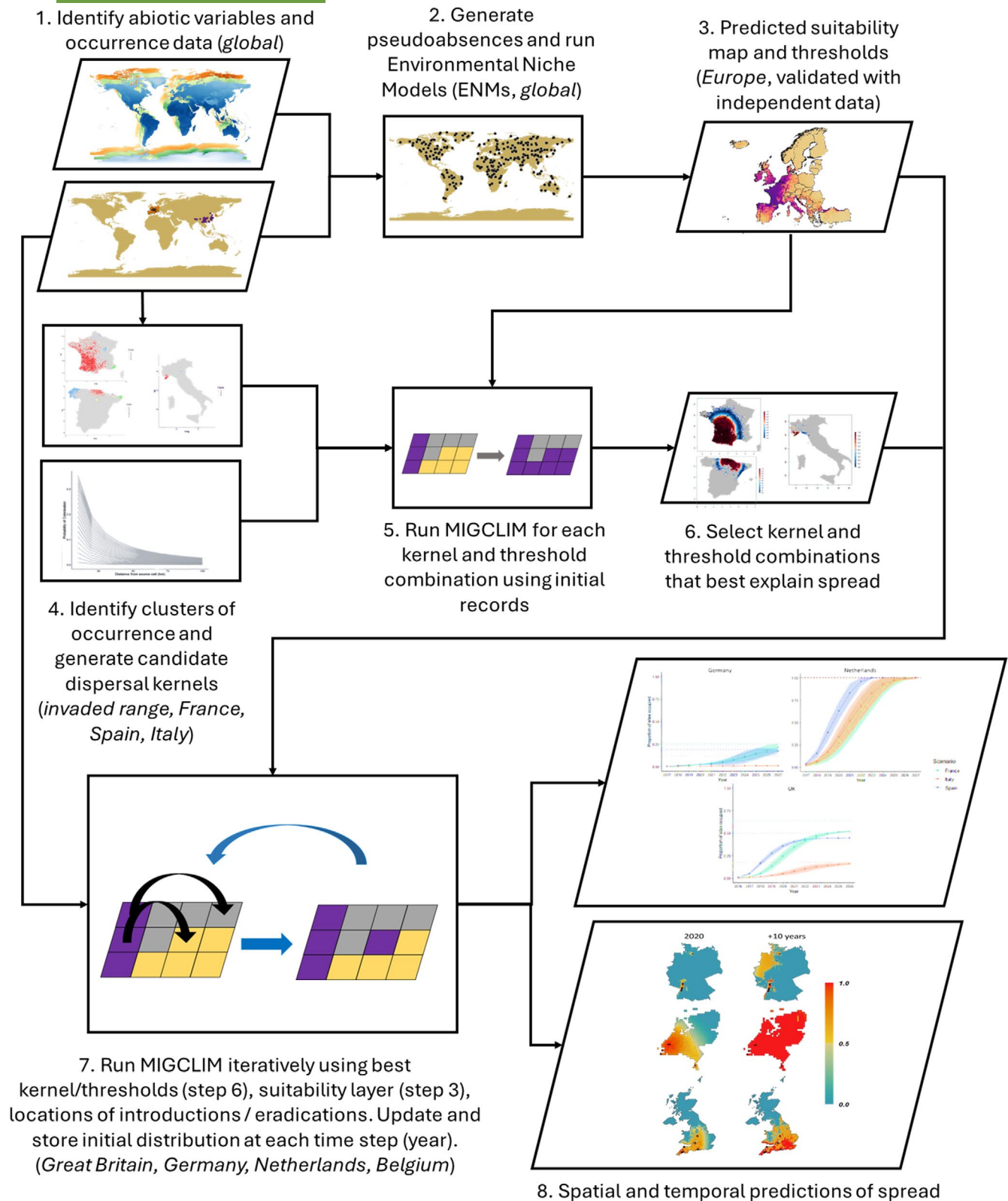


FIGURE 1 Overview of modelling framework used to predict the spatio-temporal dynamics of spread for *V. v. nigrithorax*. Parallelograms indicate data inputs and outputs and rectangles represent data processing or modelling steps.

sites in Belgium could be colonised by 2020 (Lowest CI=57%; highest CI=98%). Our projection also shows that 94%–98% of suitable sites could be occupied by 2026 (Lowest CI=96%; highest

CI=99%) (Figure 3). The current distribution of *V. v. nigrithorax* records in Belgium shows that 22% (suitability threshold=0.72) to 27% (suitability threshold=0.5) of suitable sites are currently

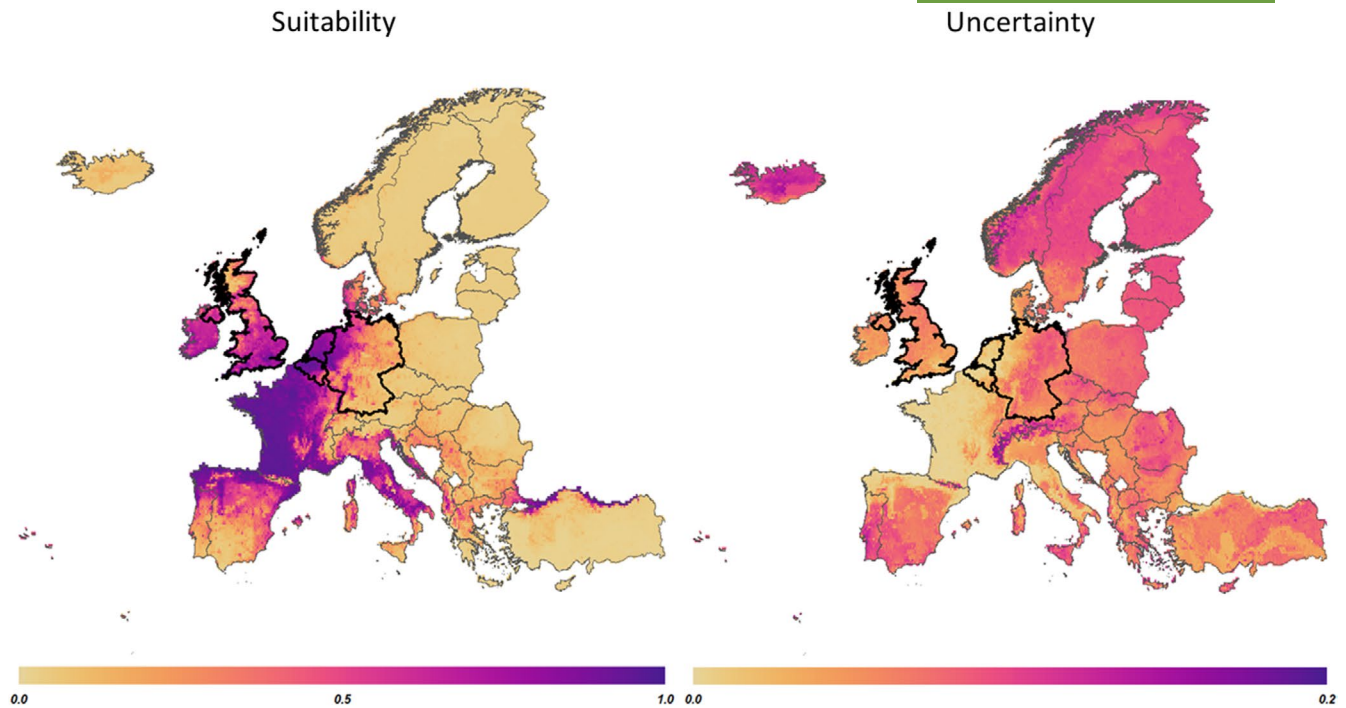


FIGURE 2 Left panel shows projected suitability for *V. v. nigrithorax* in Europe. The right panel shows uncertainty in the suitability projections for current climatic conditions, expressed as the among-algorithm standard deviation in predicted suitability, averaged across ten datasets. Countries that have submitted NOTSYS notifications and undertaken rapid eradication are highlighted in black (UK, Belgium, the Netherlands, and Germany).

occupied. When assessing the ability to predict spread based on the mean probability of occupancy across all three spread scenarios, we also found that our predictions of the probability of occupancy performed well in explaining the current distribution of *V. v. nigrithorax* in Belgium (AUC=0.88; Boyce Index=0.86 (Figure S11)).

3.3 | Predictions of spread in Germany, the Netherlands, and the UK

Using the same three spread scenarios, we then predicted the spatio-temporal dynamics of spread for *V. v. nigrithorax* in Germany, the Netherlands, and the UK if rapid eradication had not taken place (Figures 4 and 5). In Germany, 6%–16% of suitable sites were predicted to be colonised by 2020 (Lowest CI=4%; highest CI=18%) and 11%–100% of suitable sites were predicted to be colonised by 2027 (Lowest CI=6%; highest CI=100%). In the Netherlands, 27%–63% of suitable sites were predicted to be colonised by 2020 (Lowest CI=15%; highest CI=73%) and 99%–100% of suitable sites were projected to be colonised by 2027 (Lowest CI=97%; highest CI=100%). Finally, in the UK, 14%–52% of suitable sites were predicted to be colonised by 2020 (Lowest CI=8%; highest CI=56%), and 44%–66% of suitable sites were predicted to be colonised by 2026 (Lowest CI=41%; highest CI=66%). There have been further reports from these countries but still, there is no indication of notable spread after eradication efforts.

4 | DISCUSSION

We have demonstrated a generalisable modelling framework for rapid assessment of the potential spatio-temporal dynamics of biological invasions, informed by patterns of spread in other invaded regions. The information from the model outputs is key for planning measures to prevent the introduction of alien species into new sites, that is, to identify priority areas for surveillance and monitoring. Additionally, information from these models can also be used to evaluate the effectiveness of interventions by projecting the extent of spread over time in the absence of interventions, that could be utilised as a baseline to assess the effectiveness of interventions, which is a fundamental to inform the efficacy of the legislation measures currently in place in the EU following the adoption of the Regulation (EU) No 1143/2014. Using this modelling framework, we identified areas of high environmental suitability for *V. v. nigrithorax* in Germany, the Netherlands, and the United Kingdom, all of which submitted NOTSYS notifications before the 21st of July 2020 and had undertaken early eradication attempts. Our predictive model suggests that a minimum of 6% (Germany), 27% (Netherlands), and 14% (UK) of suitable sites will be colonised in these countries by 2020 in the absence of eradication, respectively ~1740 km² (0.5%), 9000 km² (27%), and 1680 km² (5%) of land area (World Bank & Food and Agriculture Organization, 2021). However, as of April 2023, no significant spread has been reported through NOTSYS from Germany and the Netherlands. The UK no longer submits reports to NOTSYS following its withdrawal from the European Union and although there have been individual sightings of

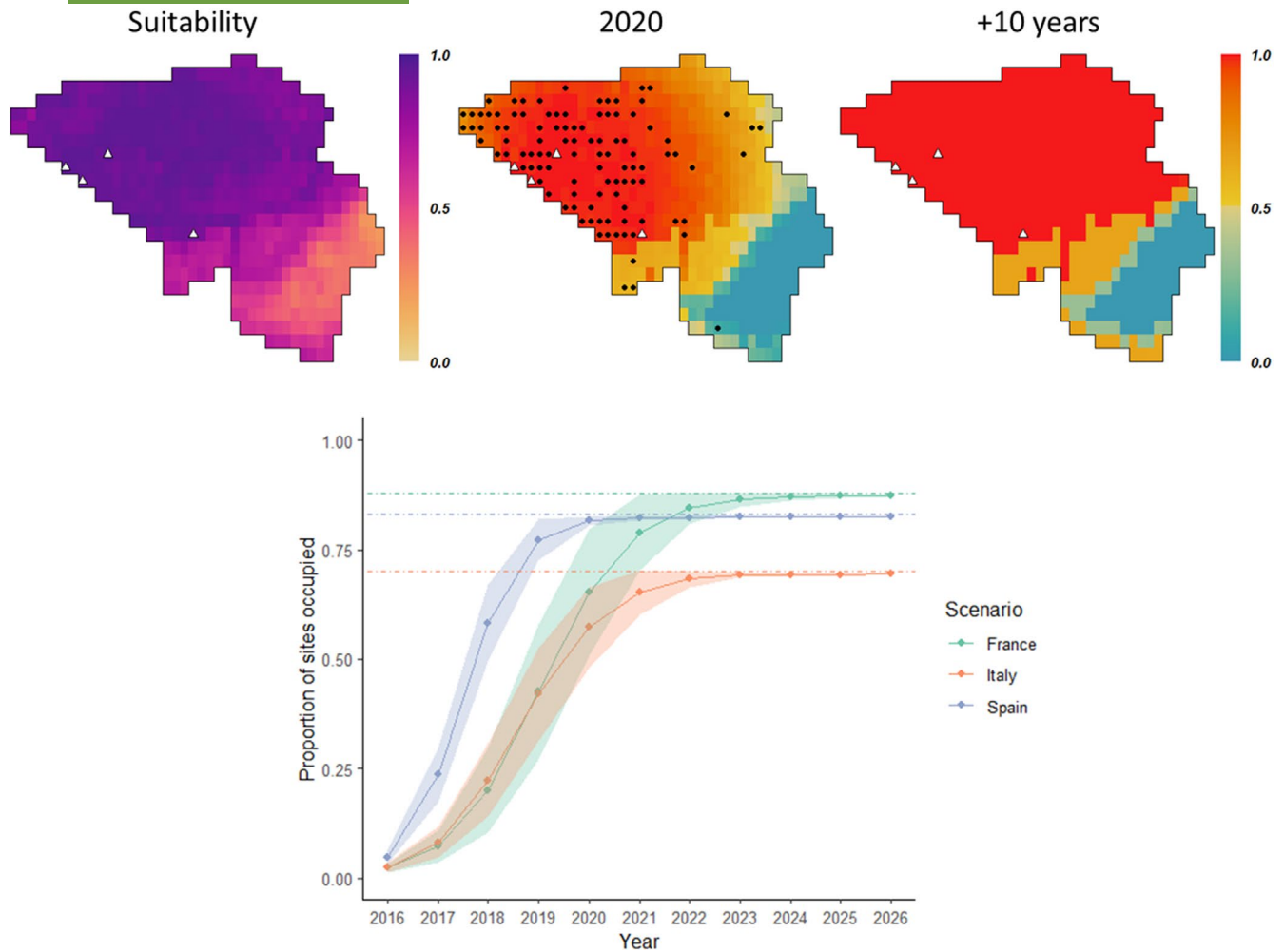


FIGURE 3 Top row shows suitability for *V. v. nigrithorax* in Belgium and predicted spread by 2020 and 10 years after initial introduction with the probability of a cell being occupied. White triangles show NOTSYS notifications in Belgium used to initialise spread models and black dots show records used to assess the predictive performance of the spread model in Belgium. The bottom panel shows the predicted temporal trend in the number of sites predicted to be occupied in Belgium using spread scenarios derived from patterns of spread observed in France, Italy, and Spain. Dashed lines indicate the proportion of sites predicted to be suitable using suitability thresholds from each spread scenario.

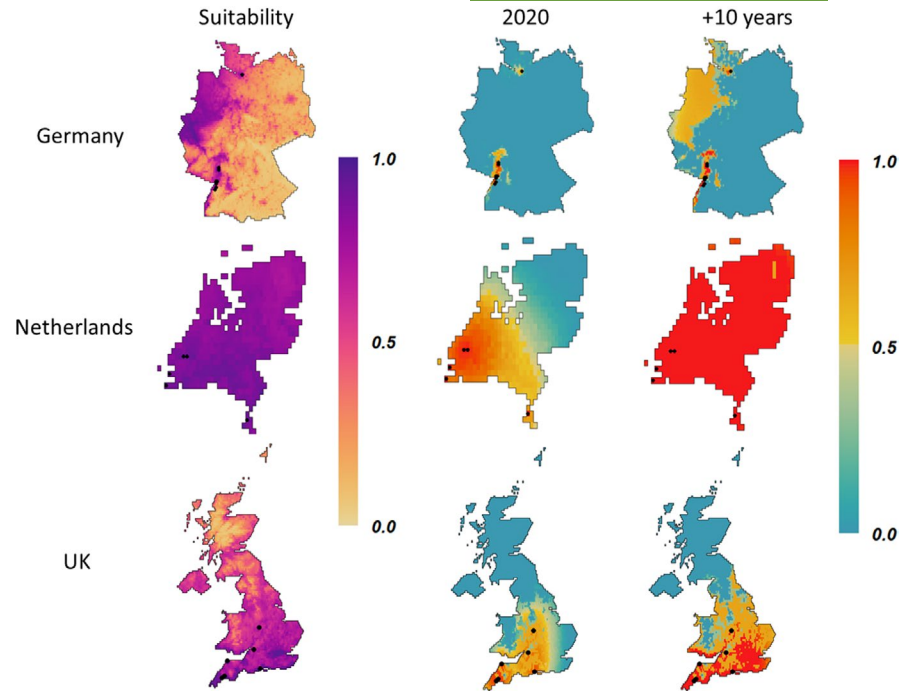
V. velutina nigrithorax since 2016, there has been no spread across the UK because all nests have been removed. These results suggest that surveillance and rapid eradication attempts outlined in NOTSYS notifications may have contributed to limiting the spread of *V. v. nigrithorax* in the UK, Germany and the Netherlands. These predictions are further supported by testing this model in Belgium, a country with initial rapid containment attempts followed by further spread and a reduction in eradication efforts.

In the case of Belgium, rapid containment attempts reported in NOTSYS notifications do not appear to have been successful in preventing the spread of *V. v. nigrithorax*, which occupied around 22%–27% of suitable sites but model predictions do suggest that this species could have been more widespread by 2020 (minimum of 57% of suitable sites occupied) if there had not been attempts to contain the spread through rapid eradication. This lack of successful containment may be because populations had gone undetected or containment attempts were not entirely successful, but most

notably it is also likely that the high propagule pressure in this area of Belgium due to widespread occupancy of *V. v. nigrithorax* in neighbouring France led to rapid incursion and spread.

This modelling framework has the benefit of being generalisable and flexible as it considers many common pseudo-absence selection procedures to establish which of these perform best when predicting habitat suitability for the focal species and allows dispersal parameters to be estimated from snapshots of previous spread. Therefore, the approach could be used to look at the effectiveness of rapid eradication for other invasive alien species of concern and the potential extent of biological invasion and future spread of new invasive alien species. This ultimately may inform decision-makers about the actual effectiveness of the legislation in place, namely, the GB Invasive Non-Native Species Strategy and Regulation (EU) No 1143/2014, and in particular, the provisions of Art. 17 and Art. 24 on the effectiveness of early eradication measures. Indeed, the model outputs from this approach have been included within the recently published GB Invasive

FIGURE 4 Predicted suitability for *V. v. nigrithorax* and predicted probability of occupancy for all sites across Germany, The Netherlands, and the UK by 2020 and 10 years following the first introduction based on spread scenarios from France, Italy, and Spain. Black dots show the locations of NOTSYS notifications used to initialise spread models.



Non-Native Species Strategy as an example of successful eradication. Additionally, the framework may help identify areas of concern for the implementation of Art. 14 on surveillance. Similarly, this modelling framework may also be useful to assess the potential spread of priority pests outlined by the European Food Safety Authority (EFSA), hence contributing to assessing the effectiveness of measures implemented within other policy sectors and legislation.

Where surveillance and rapid eradication are not already ongoing for specific invasive alien species, providing a relatively rapid assessment of the likely extent and speed of biological invasion can generate valuable information that can then be used to assess the likely impacts of invasive alien species and aid in targeting surveillance and management. This can help to counteract any justification for a 'wait and see' approach given the uncertainty in spread rates and the extent of spread (Epanchin-Niell, 2017). It also provides an opportunity to optimise surveillance and eradication efforts for invasive alien species, identify key areas of concern, and substantially reduce the potential costs incurred for surveillance, eradication and damage (Bogich et al., 2008; Epanchin-Niell et al., 2012; Hauser & McCarthy, 2009; Moore et al., 2011). The modelling framework presented here could feasibly be extended to address questions regarding the spatial allocation of management and surveillance of invasive alien species (Lioy et al., 2019). This could be done by incorporating the removal of occupied sites into the modelling framework to understand the effects of different surveillance and eradication scenarios on patterns of spread. For instance, by testing different scenarios of surveillance (i.e. active vs. passive surveillance) or eradication effort it may be possible to determine how the area occupied by a focal invasive alien species may change and provide estimates of how potential costs of management would also be affected (Bonneau et al., 2017; Cacho et al., 2010; Faccoli & Gatto, 2016; Giljohann et al., 2011). It is important that such scenarios and models are framed and shared openly and rapidly with

key stakeholders (Dunn & Laing, 2017; Marzano et al., 2015). These approaches could also be used to develop interactive tools for practitioners to explore the implications of different levels of surveillance and eradication effort in a given region in real time.

It should be noted, however, that the use of this modelling framework will require access to a priori knowledge of reproductive rates alongside data on initial introductions and patterns of previous spread to parameterise dispersal rates, as well as a sufficient number of records from the invaded and/or native range to fit a robust ENM. We would expect the potential niche to be better predicted for species that are well-recorded in the native and introduced range, for which the data represent a more complete picture of suitable environmental conditions. For example, considering the implementation of Regulation (EU) No 1143/2014, it is clear that there are many invasive alien species of Union concern for which this modelling framework may be well suited based on the availability of records in both the native range and the EU including, for example, *Alopochen aegyptiaca*, *Lagarosiphon major*, *Ludwigia peploides*, *Muntingia reevesii*, *Myocastor coypus*, *Oxyura jamaicensis*, *Procambarus clarkii*, *Procyon lotor*, and *Threskiornis aethiopicus* (Table S5). It is possible that the effectiveness of interventions for these species could also be assessed, as well as likely scenarios of future spread. However, some species of Union concern may be more difficult to model using this framework. For example, species such as *Procambarus fallax f. virginalis*, *Heracleum persicum*, *Percocottus glenii*, *Gymnocoronis spilanthoides*, *Humulus scandens*, *Plotosus lineatus*, and *Persicaria perfoliata* all have either limited records at global scale or limited records within the EU (Table S5). In cases where sufficient numbers of records are available in the native range but no records of spread are available in invaded countries, projections of suitability could be estimated using this framework, and dispersal parameters could be estimated using the literature or expert elicitation.

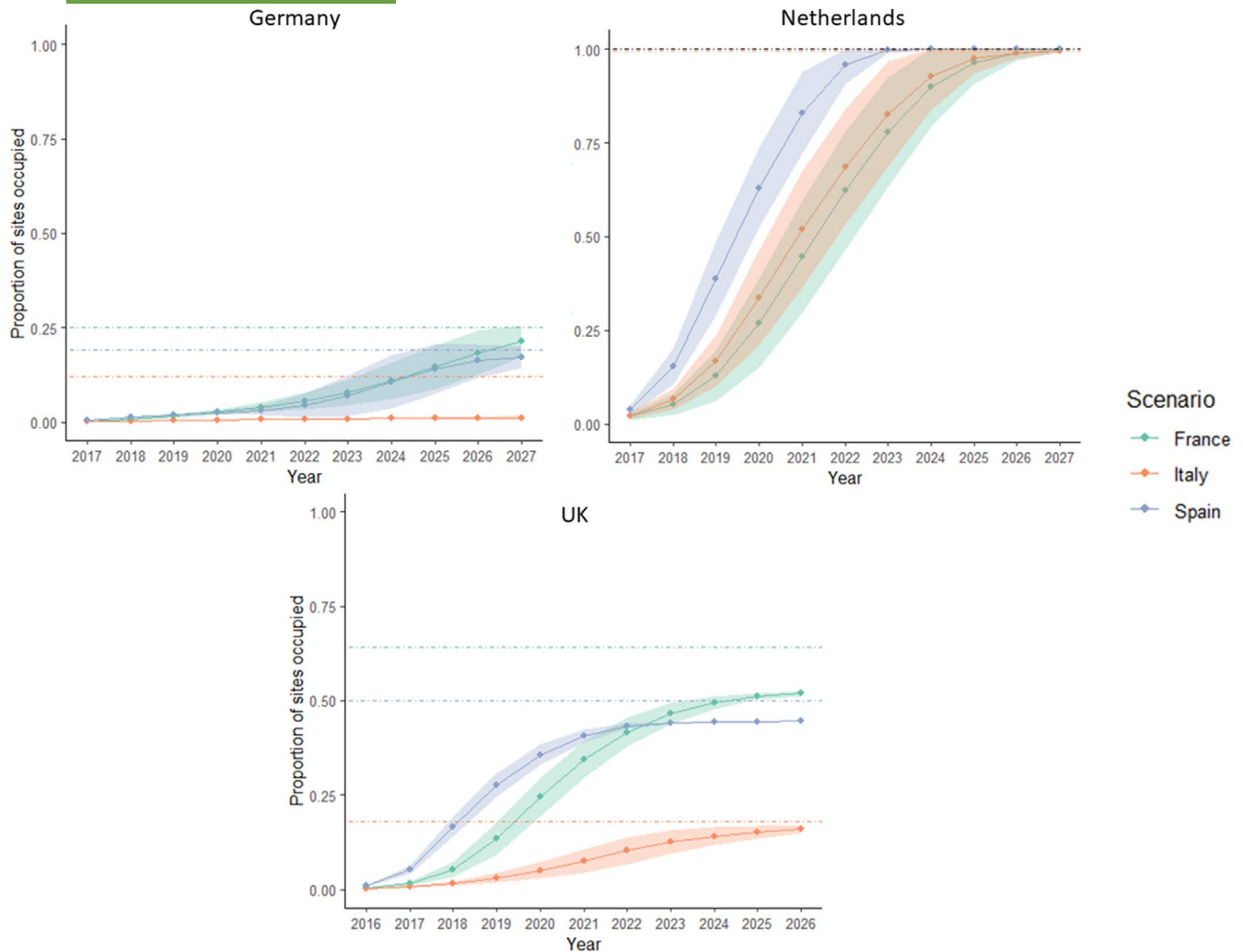


FIGURE 5 Predicted temporal trend in the number of sites predicted to be occupied in Germany, The Netherlands, and the UK using spread scenarios derived from patterns of spread observed in France, Italy, and Spain. Dashed lines indicate the proportion of sites predicted to be suitable using suitability thresholds from each spread scenario. For the Netherlands, the proportion of sites predicted to be suitable was 1 using thresholds from the France and Spain spread scenarios (black dashed line) and 0.995 using threshold from Italy spread scenarios.

As with any modelling approach, there are limitations to the framework outlined in this study. Firstly, our modelling framework uses an ENM to identify areas that are likely to be suitable for this species across Europe- based environmental covariates. *V. v. nigrithorax* cannot be considered at equilibrium with the environment in its invaded range, as with many invasive alien species (Araújo & Pearson, 2005; Gallien et al., 2012). The stage of biological invasion may therefore influence the ability of ENMs to predict potential habitats prone to invasion. ENMs may under predict the extent of biological invasion at the early stages of invasion compared with later stages of invasion, where a species would be closer to equilibrium (Václavík & Meentemeyer, 2012). *V. v. nigrithorax* has now spread across most of France and into Italy, Spain, Portugal, and Belgium, so it could be argued that this species is no longer at the early stages of invasion but nonetheless, the ENM used may not predict the full extent of potential invasion in Europe. Despite these limitations, these models are still useful in informing the management of invasive alien species by improving our understanding of

the geographical areas that are likely to be invaded in the near future (Barbet-Massin et al., 2018; Gallien et al., 2012). Moreover, the ENM approach used here does attempt to account for non-equilibrium through the pseudo-absence selection process, which chooses absences only from accessible regions.

Secondly, some of the records used in the ENM may not necessarily result in successful onward establishment at a site and propagule production. This is an issue that could arise particularly for *V. v. nigrithorax*, due to the multiple types of observations that records could encompass: founder queens, embryo nests, developed nests, workers, and males. Of these types of observations, only developed nests and workers found after June should be included in an ENM, since their position confirms that the species could establish with success in a site and produce reproductive individuals. On the contrary, males could be found several kilometres of distance from the position of the nests, and founder queens and embryo nests may not necessarily survive until the development phase of the colonies. Ideally, records should be differentiated by individual attributes and type of nest, as has been

done with the INPN data from France (Rome & Villeemant, 2017), which make up the majority of records used in the ENM (79.5%). However, none of the other data sets used in this study allowed us to differentiate between individuals or differentiate between nests making such validation difficult to achieve at the European scale with the data currently available. This could mean that some records included in the ENM are from sites that may not be suitable for *V. v. nigrithorax* to establish. Therefore, we suggest that reporting from EU Member States in NOTSYS is adjusted to require information on individuals captured or observed and nest type and timing of detection and destruction to understand the viability of an introduction.

Thirdly, this modelling approach does not take into account rare long-distance natural dispersal events (beyond the 100km maximum dispersal range captured by the dispersal kernels we used) or human-mediated dispersal, and therefore, is likely to produce a more conservative estimate of future spread. Indeed, we used hierarchical clustering in an effort to exclude human-mediated dispersal events when estimating dispersal kernels as this will most likely reduce the accuracy of predictions due to the stochasticity of this process. This has previously been found to be the case in a spread model used to understand the spread of *V. v. nigrithorax* in France, which also suggests that much of the expansion of *V. v. nigrithorax* is driven by natural dispersal events (Robinet et al., 2017). In cases where human-mediated dispersal does significantly influence the range expansion of invasive alien species, the use of this predictive modelling framework may not be well suited to accurately predict the potential distribution of these species. However, future work could investigate the use of connectivity analyses, such as those used to assess the influence of human activity on the species richness of freshwater alien species (Chapman et al., 2020), which may help to improve the accuracy of predictions by explicitly estimating those areas that are at a higher risk of introduction by human-mediated dispersal.

Despite these limitations, this modelling framework still provides a promising approach for assessing the effectiveness of interventions and rapidly assessing the potential extent and speed of biological invasions. Critically, it provides an evidence base to justify early action in the case of new biological invasions, which is often crucial in limiting impact (Dunn & Laing, 2017; Jones & Kleczkowski, 2020). As demonstrated in this study, information from predictions can be a useful means to update decision-makers and other stakeholders on the success or failures of current management approaches, and this framework has been used to report on the Implementation of Regulation 1143/2014 on Invasive Alien Species to the European Commission and the effectiveness of management approaches for Invasive Alien Species in the UK to the Department of Environmental Food and Rural Affairs (DEFRA) (Defra et al., 2023; Hassall et al., 2020).

AUTHOR CONTRIBUTIONS

Richard M. J. Hassall, Bethan V. Purse, Louise Barwell, Olaf Booy, and Helen E. Roy all contributed to the conception of using the modelling approaches to assess the efficacy of interventions in limiting the spread of invasive alien species. Richard M. J. Hassall, Simone

Lioy, and Stephanie Rorke contributed to the acquisition and curation of data. Richard M. J. Hassall, Bethan V. Purse, and Louise Barwell developed the methodology for the modelling framework. Richard M. J. Hassall carried out the analysis and interpretation of data. Richard M. J. Hassall, Bethan V. Purse, Louise Barwell, and Helen E. Roy drafted the article. Olaf Booy, Simone Lioy, Stephanie Rorke, Kevin Smith, and Riccardo Scalera provided critical feedback throughout the project and contributed to revising the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data used in this study is available from Zenodo <https://doi.org/10.5281/zenodo.14025849> (Hassall et al., 2024).

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- established.
- Table S1.2:** Sources of records used in this study.
- Table S2:** Summary of evaluation metrics for *V. v. nigrithorax* models with each of the pseudo-absence selection methods using different backgrounds and weighting by recording effort.
- Table S3:** Summary of variable importance of the fitted model algorithms and the ensemble models from best performing algorithms for *V. v. nigrithorax*.
- Table S4:** Results from best performing dispersal kernels for *V. v. nigrithorax*.
- Table S5:** Criteria for evaluating the applicability of the modelling framework to other invasive alien species of Union Concern.
- Figure S1.1:** Occurrence records obtained for *V. v. nigrithorax* and used in modelling (showing native (blue triangles) and invaded distributions (red circles)).
- Figure S1.2:** Recording density of Insecta on GBIF, which was used as a proxy for recording effort (log10 transformed for plotting).
- Figure S2:** Hierarchical clustering of abiotic variables based on distance using 1–Pearson's *r*. Red line shows distance threshold of 0.3 below which variables are considered highly correlated.
- Figure S4:** *V. v. nigrithorax* dispersal kernels used in MIGCLIM model.
- Figure S5:** Maps showing *V. v. nigrithorax* clusters identified in (a) France, (b) Spain and (c) Italy using hierarchical clustering of records with a threshold of 100 km.
- Figure S6:** Results from evaluation of best performing SDM with Boyce Index showing change predicted/expected ratio across environmental suitability values for *V. v. nigrithorax*.
- Figure S7:** Partial response plots from fitted models for *V. v. nigrithorax*.
- Figure S8:** Visualisation of predicted colonised cells after running best performing dispersal kernel for 50 simulations from year of first records (yellow circles) used as initial distribution in the model in (a) France, (b) Spain and (c) Italy.
- Figure S9:** Dispersal kernels that best describe the distribution of *V. v. nigrithorax* in France, Italy and Spain.
- Figure S10:** Results from evaluation of best performing dispersal kernels for *V. v. nigrithorax* with Boyce Index showing change predicted/expected ratio across Predicted probability of occupancy values. (a) Spain, (b) France, (c) Italy.
- Figure S11:** Results of the evaluation of the *V. v. nigrithorax* Belgium spread model with Boyce Index showing change predicted/expected ratio across environmental suitability values.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1.1: Table outlining countries where *V. v. nigrithorax* has been recorded, year of first record of a nest, recording schemes, type of interventions currently underway and whether *V. v. nigrithorax* is

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