Effectiveness of rapid eradication attempts reported using NOTSYS notifications in preventing the spread of *V. v. nigrithorax* in Europe

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Executive summary

The Asian hornet or yellow-legged hornet, *Vespa velutina nigrithorax*, originates from Asia and is thought to have been in Europe since at least 2004, arriving as a stowaway with traded goods transported into south-western France, spreading rapidly into northern Spain (including Mallorca Island), Portugal, Belgium, Italy, the Netherlands, Germany, the UK, the Channel Islands and recently into Luxemburg and Switzerland.

V. v. nigrithorax is an invasive alien species of Union concern and, therefore, national authorities have to establish surveillance and control plans with the requirement to notify all new detections and related eradication measures through the EASIN Notification System, NOTSYS¹. These obligations entered into force on 3 August 2016.

We used modelling approaches to compare spread patterns between countries and assess the effectiveness of the rapid eradication measures in reducing spread of *V. v. nigrithorax* undertaken in Belgium, Germany, the Netherlands, and the UK following implementation of the Regulation (EU) 1143/2014 on Invasive Alien Species. These were the only countries which have submitted notifications of the early detection and rapid eradication of the target species in NOTSYS over the period between the entry into force of the relevant obligation (3 August 2016) and 15 July 2020.

The objective was to assess the effectiveness of the Regulation in addressing the threat of *V. v. nigrithorax* through notification of the early detection and rapid eradication of the target species in EASIN.

Species occurrence data for *V. v. nigrithorax*, comprising 23,190 records on a global scale spanning from 1993 to 2020, were used within a Species Distribution Model (SDM) to assess the environmental suitability for *V. v. nigrithorax* across Europe. Data were obtained from the Biological Records Centre (UK), Inventaire National du Patrimoine Naturel (France), Vespa watch (Belgium), LIFE STOPVESPA (Italy), Waarneming.nl (the Netherlands), Ministry for Ecological Transition and Demographic Challenge - MITECO (Spain), the Global Biodiversity Information Facility (GBIF) and Aktion-Wespenschutz and University of Hamburg (Germany).

Projections from the model highlight areas of high suitability for occurrence of *V. v. nigrithorax* in France, Spain, Portugal, Italy, Belgium, the Netherlands, Denmark, Germany, Croatia, the United Kingdom and the Republic of Ireland.

¹ https://easin.jrc.ec.europa.eu/NOTSYS

The results from the SDM were used to inform a predictive model to project the future spread of *V*. *v. nigrithorax* by identifying the parameters (environmental suitability thresholds and dispersal kernels) that best describe the spread of *V. v. nigrithorax* in France, Italy and Spain, where this species is now widespread. This produced three different scenarios of spread that were used to predict the potential spatial extent of *V. v. nigrithorax* in four countries, in which the species is at an earlier stage of invasion and which have submitted NOTSYS notifications: Belgium, Germany, the Netherlands and the UK. From the table below it can be seen that in all four countries assessed the SDM predicted that *V. v. nigrithorax* should have colonised considerably more sites than has been the case. Perhaps most strikingly is the comparison within the UK where *V. v. nigrithorax* is currently considered absent following eradication and the model indicates that 14-52% of suitable 10 km squares would have been colonised without rapid response.

Proportion of sites (10 km²) and suitable sites (10 km²) in four EU countries² predicted by the SDM to be colonised by V. v. nigrithorax in 2020 and 10 years after initial incursion in the absence of early eradication efforts. Estimates are taken from 100 simulations informed by previous spread in France, Spain and Italy. Table shows highest and lowest estimate across these three spread scenarios. Table also shows approximate (10 km²) area predicted to be occupied based on sites with a high probability of occupancy (>0.9).

	% of 10 predic cole	km squares ted to be onised	% of suit squares p be co	able 10 km redicted to Ionised	Area (km²) predicted to be colonised		
Country	2020	10 years after initial incursion	2020	10 years after initial incursion	2020	10 years after initial incursion	
Belgium	57-82%	69-87%	73-96%	94-98%	13,400 km ²	21,900 km ²	
Germany	0.5-2%	1-18%	6-16%	11-100%	600 km ²	1,900 km ²	
the Netherlands	27-62%	99-100%	27-63%	99-100%	2,700 km ²	35,800 km²	
UK	5-36%	16-52%	14-52%	44-66%	3,700 km ²	37,400 km ²	

In the case of Belgium, rapid containment attempts reported in NOTSYS notifications have not been successful in preventing further spread of *V. v. nigrithorax* (See NOTSYS notification Belgium #2 "measure effectiveness" for details). However, the model outputs suggest that spread may have been reduced anyway since the prediction was that 73-96% of suitable sites were predicted to be colonised by 2020 and this is not the case. The lack of success in containment of *V. v. nigrithorax* in

² UK was an EU Member State over the period analysed.

Belgium may be due to failure to detect established populations or to eradicate established populations, but is most likely due to increased propagule pressure as result of widespread occupancy of *V. v. nigrithorax* in neighbouring France. Our predictive model performed well in explaining the current (as of October 2020) distribution in Belgium following rapid containment attempts reported in 2016 and 2017.

For the UK, Germany and the Netherlands, the model outputs highlight the potential extent of distribution of *V. v. nigrithorax* in the absence of rapid eradication attempts: 14-52%, 6-16%, 27-63% respectively by the end of 2020. Therefore, given this pattern of spread has not been realised, it can be concluded that the rapid eradications reported through NOTSYS notifications have contributed to the success in limiting the spread of *V. v. nigrithorax* in the UK, Germany and the Netherlands. It is important to note that these predictions are based on parameters that perform well in explaining the patterns of invasion observed in France, Italy and Spain, where this species is already widespread.

The modelling approach adopted does not attempt to predict spread as a result of rare long-distance dispersal events including human-mediated dispersal, which has been documented in France and Italy. Therefore, the model is likely to produce a conservative estimate of future spread, meaning that the figures presented above on potential distribution that has not been realised is likely to be an underestimate. The framework of the predictive model could be expanded to include rare long-distance movement of *V. v. nigrithorax* as result of human-mediated dispersal, however, this will most likely reduce the accuracy of predictions due to the difficulty of predicting where in the landscape such events will occur. The model could be extended to incorporate major trade routes of goods, in which *V. v. nigrithorax* queens may stowaway but this would require accurate data on routes by which these goods are traded within and between countries as well as on the probability of invasion success via such trade events. It is important to note that only movement of reproductive queen *V. v. nigrithorax* are relevant in this context. One approach could be to consider scenarios that might increase spread of *V. v. nigrithorax* rather than attempting to derive model outputs given the random nature of such events.

The modelling framework developed uses many common pseudo-absence selection procedures to establish which perform best when predicting environmental suitability for the focal species and allows dispersal parameters to be estimated from previous spread. Therefore, the approach can be applied to assess the potential extent of invasion and future spread of other invasive alien species of Union concern (Regulation (EU) 1143/2014) and inform the evaluation of the effectiveness of measures implemented within the context of Regulation (EU) 1143/2014 such as rapid eradications

reported using NOTSYS notifications but also other measures required under Regulation (EU) 1143/2014. Key inputs facilitating extension of the framework to other species are sufficient data on occurrence and annual spread, ideally from the invaded range in Europe or environmentally similar biogeographic regions, as well as locations of initial introduction and abatement in focal countries. *A priori* knowledge of dispersal and reproduction rates, including human-mediated spread pathways, is also advantageous. We have identified nine species of Union concern for which this modelling framework may be well suited based on availability of datasets on the particular species and understanding of life history traits that would inform the suitability and spread models. Furthermore, in the cases where impacts of invasive alien species could be quantified, the modelling framework could be extended for assessing the associated costs of invasion and related savings following an eradication.

Introduction

The Asian hornet or yellow-legged hornet, (Vespa velutina nigrithorax) originates from Asia. The native range of V. v. nigrithorax includes Bhutan, China (including Hong Kong), East Nepal, North-East India and North Vietnam (Villemant et al. 2011, Perrard et al. 2014). It was first recorded in Europe in 2005 arriving as a stowaway with traded goods transported into south-western France from China (Haxaire et al. 2006), but probably the species was already established at least since 2004 (Villemant et al. 2006, Rortais et al. 2008). V. v. nigrithorax has since spread into northern Spain, Portugal, Belgium, Italy, the Netherlands, Germany, Mallorca Island, the Channel Islands (Rome and Villemant 2017, Husemann et al. 2020, Laurino et al. 2020), the UK (Budge et al. 2017) and recently into Luxemburg and Switzerland. It has also been introduced to South Korea (Choi et al. 2012) and Japan (Ueno 2014, Takeuchi et al. 2017). The estimates for the rate of spread for this species does vary between countries with a spread rate of 78km/year in France (Robinet et al. 2017), 18km/year in Italy (Bertolino et al. 2016) and 10-20km/year in South Korea (Choi et al. 2012). There is also evidence of accidental human-mediated transport of founding queens with some nests reported at distances of 200 km ahead of the invasion front (Rome et al. 2011, Robinet et al. 2019). In 2019 an individual of V. v. nigrithorax was found in Hamburg in Northern Germany; this constitutes the most northern record of this species globally (Husemann et al. 2020) and is possibly a consequence of long-distance human-mediated transport. An abandoned nest was subsequently discovered in Hamburg in the spring of 2020 (NOTSYS notification, Germany #3). Climate and landuse are considered important factors influencing the spread of V. v. nigrithorax (Fournier et al. 2017). Up to 13,000 individuals can be present annually in a single colony (with a mean of approximately 6,000 individuals) and several hundred queens of this eusocial insect can be produced in the autumn (Rome et al. 2015) (Figure 1a).

The arrival of *V. v. nigrithorax* in Europe is of concern primarily because it is a voracious predator of insects and shows a preference for pollinating insects including honey bees, wild bees and wasps (Perrard et al. 2009). There are concerns that this invasive alien species will adversely affect beekeeping and honey production (Requier et al. 2019) but also pollination of crop and wild flowers (Rojas-Nossa and Calviño-Cancela 2020). In regions where *V. v. nigrithorax* has established in France beekeepers have estimated losses of honeybee colonies ranging from 5 to 80% (Monceau et al. 2014). Honeybee colonies respond to the presence of a hawking hornet by reducing foraging and so not only is there a direct effect of the hornets through predation of the honey bees but the colony may also be weakened through starvation (Arca et al. 2014, Requier et al. 2019). The impact of *V. v. nigrithorax* on wild pollinators and pollination services has not been quantified extensively but is predicted to exceed the cost of nest destruction (Barbet-Massin et al. 2020).

V. v. nigrithorax is an invasive alien species of Union concern and as such national authorities have to establish surveillance systems with the requirement to notify all new detections and related rapid eradication measures through the EASIN Notification System, NOTSYS³. Rapid eradication and control of *V. v. nigrithorax* is mainly achieved by nest destruction and bait trapping (Monceau et al. 2014). Rapid eradication or management (including eradication or containment of established populations) is most effective if achieved early in the season; before gynes and males are produced and go on to reproduce (Kennedy et al. 2018, Lioy et al. 2019a). Therefore, early-detection and rapid eradication, underpinned by monitoring and surveillance, is critical for the successful management of this invasive alien species. France has the longest invasion history of this species in Europe and models suggest that only about 48% of nests have been detected and destroyed (Keeling et al. 2017). However, there are a number of emerging technologies that could be deployed to improve detection including radio tracking (Kennedy et al. 2018), harmonic radar tracking (Maggiora et al. 2019) and forward looking infrared cameras by ground inspections (Lioy et al. 2020) or attached to drones (Al-doski et al. 2016).

Many countries have developed mass participation citizen science approaches for surveillance of *V. v. nigrithorax* (Table 1). In Belgium an initiative called Vespa-Watch⁴ has been implemented and in Great Britain people are asked to report sightings of concern (Roy et al. 2015) through an on-line recording platform or smart phone application called Asian Hornet Watch⁵. Thousands of suspected (with the vast majority misidentified) sightings of *V. v.nigrithorax* are reported every year in Great Britain (Figure 2); records are verified by an expert and to date there have only been 18 confirmed sightings 9 of which were nests, all of which have been destroyed. In Italy a network has been developed by LIFE STOPVESPA and StopVelutina projects to encourage both beekeepers and others to monitor the presence of *V. v. nigrithorax* using hornet-baited traps or observation in apiaries (Lioy et al. 2019b). The first sighting of *V. v. nigrithorax* in the Netherlands was reported through an online recording platform⁶.

The datasets from these monitoring schemes have been utilised in previous studies to model the environmental suitability for *V. v. nigrithorax* in Europe and the potential dynamics of its spread (Ibáñez-Justicia and Loomans 2011, Villemant et al. 2011, Barbet-Massin et al. 2013, 2018, 2020, Fournier et al. 2017, Keeling et al. 2017, Lioy et al. 2019b). These approaches have been valuable in improving our understanding of the potential extent of invasion by this species and the potential

³ <u>https://easin.jrc.ec.europa.eu/notsys/</u>.

⁴ <u>https://vespawatch.be/identification/</u>

⁵ <u>https://www.brc.ac.uk/apps</u>

⁶ https://waarneming.nl/species/8807/

invasion dynamics. We extend these approaches by utilising a modelling framework that integrates outputs from Species Distribution Models (SDMs) into a mechanistic spread model (Engler and Guisan 2009, Engler et al. 2012), which can be parametrised using data from previous spread in other countries (Figure 1b). Consequently, we can project the future distribution of *V. v. nigrithorax* following introductions whilst incorporating both dispersal constraints and life-history traits as well as environmental suitability across Europe.

Table 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 established. *- There is no recording scheme with records of V. v. nigrithorax in Germany. Records were obtained from Dr Martin Husemann (University of Hamburg). Records were also obtained from Aktion-wespenschutz, a community website set up to advocate protection of social wasps. The website contains records of V. v. nigrithorax in Germany.

COUNTRY	FIRST NEST RECORDED	RECORDING SCHEME	LINK	INTERVENTIONS	STATUS
FRANCE	2004	Frelon asiatique	http://frelonasiatique.mnhn.fr/	Ongoing Management	Established
SPAIN	2010	Avispa Asiatica	https://avispaasiatica.org/espana/	Ongoing Management	Established
PORTUGAL	2011	StopVESPA	http://stopvespa.icnf.pt/	Ongoing Management	Established
NETHERLANDS	2017	Weerneming .nl	https://waarneming.nl/	Local interventions	Recorded
UK	2016	Asian Hornet Watch	App (iPhone or Android) or <u>https://www.brc.ac.uk/risc/alert.php</u> ? species=asian_hornet	Local interventions	Recorded
BELGIUM	2016	VespaWatch	https://vespawatch.be/	Ongoing Management	Established
GERMANY	2014	*	*	Local interventions	Recorded
ITALY	2013	LIFE STOPVESPA & StopVelutina	https://www.vespavelutina.eu & https://www.stopvelutina.it/	Ongoing Management	Established



Figure 1: (A) Life cycle of V. v. nigrithorax with circles showing stages in spread model. (B) Representation of spread model, 1: Queens disperse from occupied sites travelling different distances based on chosen dispersal kernel. 2: Successful establishment at sites is dependent on suitability of site. 3: Life cycle is completed and after a year step 1 and 2 are repeated. Photo: Gilles San Martin CC BY-SA 2.0



Figure 2: Number of reports of suspected Asian hornet sightings in Great Britain over time noting that there have only been 18 confirmed sightings comprising a total of 9 nests, all have been destroyed (https://www.gov.uk/government/publications/asian-hornet-uk-sightings)

b)



We provide an assessment of the effectiveness of the rapid eradication measures on *V. v. nigrithorax* undertaken in Belgium, Germany, the Netherlands and the UK resulting from implementation of the Regulation (EU) 1143/2014 on Invasive Alien Species. We used the developed modelling approach to compare (1) the observed spread of the species and (2) the spread of the species if measures had not have been taken. Species distribution data reported by the Member States and the information on rapid eradication notified through NOTSYS have been included. Specifically, we have:

1. Implemented a modelling approach to assess the effectiveness of rapid eradication measures for the species reported on NOTSYS specifically focussing on Belgium, Germany, the Netherlands and the UK.

2. Provided a comparison of actual extent of *V. v. nigrithorax* and predicted extent in all EU countries in the absence of the rapid eradication measures (undertaken in Belgium, Germany, the Netherlands and the UK only as a result of the implementation of Regulation (EU) 1143/2014).

We have also considered the generic applicability of the modelling framework for other invasive alien species of Union concern (aquatic and terrestrial) that have been subject to different management measures. Furthermore, we suggest ways of extending the models to predict the environmental impacts of specific invasive alien species and assessing the costs of invasion and the savings following a successful eradication.

Methods

Distribution data

Species occurrence data for *V. v. nigrithorax* were obtained from the Biological Records Centre (UK), Inventaire National du Patrimoine Naturel (France), Vespa watch (Belgium), LIFE STOPVESPA (Italy), Waarneming.nl (Netherlands), Ministry for Ecological Transition and Demographic Challenge -MITECO (Spain), the Global Biodiversity Information Facility (GBIF) and Aktion-Wespenschutz and University of Hamburg (Germany). This resulted in 23,190 records on global scale that were used to model the environmental suitability for *V. v. nigrithorax* across Europe (Figure 3).

Predicting the future distribution of V. v. nigrithorax in Europe

To better understand how suitability for *V. v. nigrithorax* varies across Europe we used a SDM to project the current environmental suitability for *V. v. nigrithorax* across Europe based on their current distribution (for full methods, including environmental predictors used in the models see Annex 1.1,1.2 & 1.3). Using the results from this suitability model we then used a predictive model to project the future spread of *V. v. nigrithorax* by identifying the parameters (environmental suitability thresholds and dispersal kernels) that best describe the spread of *V. v. nigrithorax* in France, Italy and Spain, where this species is now more widespread. This produced three different scenarios of spread that varied in both estimates of dispersal, and suitability thresholds. These scenarios were used to predict the spread of *V. v. nigrithorax* in the four countries which have submitted through NOTSYS in total 22 notifications, Belgium, Germany, the Netherlands and the UK in the period from 3 August 2016 (entry into force of relevant obligations) until 15 July 2020. There were two records in the United Kingdom that were removed because they only record a single hornet and further surveillance has not resulted in any further records or the discovery of



Figure 3: Occurrence records obtained for V.v. nigrithorax and used in modelling (showing native (blue triangles) and invaded distributions (red circles)).

nests, therefore it is unlikely that these records would have resulted in the establishment and spread of *V*. *v*. *nigrithorax* from these locations.

In Belgium, *V. v. nigrithorax* is no longer considered a notifiable species under Article 16 of Regulation (EU) 1143/2014 but is now considered a widespread species under Article 19 (see NOTSYS notification Belgium #2 "measure effectiveness" for details). Therefore, we used additional records from Belgium to evaluate the ability of outputs to predict the distribution of *V. v. nigrithorax* (for full methods see Annex 1.4).

Results

Suitability for V. v. nigrithorax in Europe

The selected SDM performed well across evaluation metrics and our projections highlight areas of high suitability in France, Spain, Portugal, Italy, Belgium, the Netherlands, Denmark, Germany, Croatia, the United Kingdom and Northern Ireland and the Republic of Ireland (Figure 4). Currently, there are records of *V. v. nigrithorax* in all of these countries, except for Croatia, the Republic of Ireland and Denmark (for full model outputs see Annex 2.1). The predictive model using this suitability output was initialised using NOTSYS notifications of occurrence where eradication attempts had taken place (Figure 5). The projected spread if early eradications had not taken place was established over ten years from the earliest NOTSYS notification, specifically the date of detection and not the date of submission of the notification, using the predictive model.



Figure 4: Suitability for V. v. nigrithorax across Europe.

The first dates of NOTSYS notifications for each country were 18 November 2016 for Belgium, 4 November 2017 for Germany, 17 September 2017 for the Netherlands and 29 September 2016 for the UK.

Projecting the spread of V. v. nigrithorax NOTSYS notifications and early eradication Our projected distribution of V. v. nigrithorax in Belgium, used the three different scenarios of spread parametrised using France, Italy and Spain (that differed in estimated dispersal rates and suitability thresholds). 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 to France and Italy, although the Spain and France scenarios produced similar patterns of spread in Germany. Projections from these three scenarios resulted in a projection that 73 to 96% of suitable sites in Belgium could had been colonised by 2020 (57 to 82% of all 10 km² grid cells across Belgium). Our projection also shows that 94 to 98% of suitable sites could had been occupied by 2026 (69 to 87% of all 10 km² grid cells across Belgium) (Figure 6). Instead, the current distribution of V. v. nigrithorax in Belgium shows that 22% to 27% of suitable sites are currently occupied. When assessing the ability to predict spread based on the mean probability of occupancy per cell across all three spread scenarios, we also found that our predictions of probability of occupancy performed well in explaining the current distribution of *V. v. nigrithorax* in Belgium.

In Germany, approximately 6 to 16% of suitable sites could have been colonised by 2020 (0.5% to 2% of all 10 km² grid cells across Germany) and 11 to 100% of suitable sites are predicted to be colonised by 2027 (1% to 18% of all 10 km² grid cells across Germany) (Figure 7) if there had been no eradication attempts following the first detection of *V. v. nigrithorax*. In the Netherlands, 27 to 63% of suitable sites are predicted to be colonised by 2020 (27% to 62% of all 10 km² grid cells across Netherlands) and 99% to 100% of suitable sites are projected to be colonised by 2027 (99% to 100% of all 10 km² grid cells across Netherlands) (Figure 8). Finally, in the UK, 14 to 52% of suitable sites are predicted to be colonised by 2020 (5% to 36% of all 10 km² grid cells across UK) and 44 to 66% of suitable sites are predicted to be colonised by 2026 (16% to 52% all 10 km² grid cells across UK) (Figure 9).



Figure 5: Suitability for V. v. nigrithorax in (a) Belgium, (b) Germany, (c) the Netherlands and (d) UK. Black circles show locations of NOTSYS notification used to initialise spread models



Figure 6: Predicted probability of occupancy by V. v. nigrithorax across all sites in Belgium using three different spread scenarios. (a) Predicted probability of occupancy in 2020 using mean of three different spread scenarios. (a) Predicted probability of occupancy in 2020 using mean of three different spread scenarios (c) proportion of suitable sites that are predicted to be occupied from 2016 to 2026 (d) proportion of total sites that are predicted to be occupied from 2016 to 2026 if rapid eradication had not been undertaken following first detection of V. v. nigrithorax. Yellow circles show NOTSYS notifications and open black circles show additional records of occurrence used to establish performance of predictions.



Figure 7: Predicted probability of occupancy by V. v. nigrithorax across all sites in Germany using three different spread scenarios. (a) Predicted probability of occupancy in 2020 using mean of three different spread scenarios (c) proportion of suitable sites that are predicted to be occupied from 2017 to 2027 under three different spread scenarios (d) proportion of total sites that are predicted to be occupied from 2017 to 2027. Yellow circles show NOTSYS notifications.



Figure 8: Predicted probability of occupancy by V. v. nigrithorax across all sites in the Netherlands using three different spread scenarios. (a) Predicted probability of occupancy in 2020 using mean of three different spread scenarios (b) predicted probability of occupancy in 2027 using mean of three different spread scenarios (c) proportion of suitable sites that are predicted to be occupied from 2017 to 2027 under three different spread scenarios (d) proportion of total sites that are predicted to be occupied from 2017 to 2027. Yellow circles show NOTSYS notifications.



Figure 9: Predicted probability of occupancy by V. v. nigrithorax across all sites in the UK using three different spread scenarios. (a) Predicted probability of occupancy in 2020 using mean of three different spread scenarios (c) proportion of suitable sites that are predicted to be occupied from 2016 to 2026 under three different spread scenarios (d) proportion of total sites that are predicted to be occupied from 2016 to 2026. Yellow circles show NOTSYS notifications.

Discussion

Suitability for *V. v. nigrithorax* in Europe and effectiveness of early eradication reported in NOTSYS notifications in limiting spread.

Our models show areas of high suitability for V. v. nigrithorax in the Netherlands, Denmark, Germany, Croatia, the United Kingdom and the Republic of Ireland, in addition to the countries where the species is already widespread. Of these countries, Germany, the Netherlands and the United Kingdom have submitted NOTSYS notifications and undertaken early eradication attempts. In the time between data collection (21st July 2020) and completion of the report (21st October 2020) 14 new NOTSYS notifications have been received from the Netherlands (ten notifications), Germany (two notifications) and Luxembourg (two notifications). No new notifications have been received from the UK. The details of 12 of these notifications are still to be clarified, therefore the extent currently occupied by V. v. nigrithorax is difficult to ascertain. However, if each NOTSYS notification reports a single nest, each in a different 10km² site, this could mean that 0.016% of all sites in the Netherlands and <0.01% of all sites in Germany are currently occupied. This is significantly less than the predicted extent of invasion without rapid NOTSYS notifications by 2020 in these countries. Our predictive model suggests that we would expect to see a minimum of 6% (Germany), 27% (Netherlands) and 14% (UK) of suitable sites being colonised in these countries by 2020 (respectively 0.5%, 27% and 5% of all 10 km² sites) in the absence of eradication measures (Table 2). These results suggest that 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: 14-52%, 6-16%, 27-63% respectively by 2020. These predictions are further supported by testing this model in Belgium, a country with initial rapid containment attempts followed by further spread (see NOTSYS notification Belgium #2 "measure effectiveness" for details). In this case, we found that the predictive model initialised with containment attempts (as locations of invaded sites) performed well in explaining the current distribution of V. v. nigrithorax, which is now considered widespread in Belgium.

Table 2: Approximate area (in 10 km² sites) predicted to be occupied across all three spread scenarios by 2020 and 10 years after the initial incursion of V. v. nigrithorax in each country if rapid eradication had not been undertaken following first detection of V. v. nigrithorax. Numbers in brackets show three different results based on probability of occupancy at sites. Area occupied based on sites with probability of occupancy greater than 0.9 (>0.9), probability of occupancy greater than 0.8 (>0.8) and probability of occupancy greater than 0.7 (>0.7).

Country	Total area currently occupied	Area occupied by 2020	Area occupied after 10 years
Belgium	8,700 km ²	13,400 km² (>0.9) 16,800 km² (>0.8) 18,600 km² (>0.7)	21,900 km² (>0.9) 22,200 km² (>0.8) 22,700 km² (>0.7)
Germany		600 km ² (>0.9) 1,600 km ² (>0.8) 2,100 km ² (>0.7)	1,900 km² (>0.9) 3,800 km² (>0.8) 5,600 km² (>0.7)
the Netherlands		2,700 km ² (>0.9) 6,100 km ² (>0.8) 8,400 km ² (>0.7)	35,800 km² (>0.9) 35,800 km² (>0.8) 36,100 km² (>0.7)
UK		3,700 km² (>0.9) 8,300 km² (>0.8) 17,800 km² (>0.7)	37,400 km ² (>0.9) 46,700 km ² (>0.8) 56,300 km ² (>0.7)

In the case of Belgium, rapid containment attempts reported in NOTSYS notifications do not appear to be have been successful in preventing the spread of V. v. nigrithorax but model predictions do suggest that this species could have been more widespread by 2020 if there had not been attempts to contain the spread through rapid eradication. This lack of successful containment may be because established populations had gone undetected or containment attempts where not entirely successful but most likely results from high propagule pressure in this area of Belgium due to widespread occupancy of V. v. nigrithorax in neighbouring France. More detailed analysis could have been possible if Member States provided details of ongoing surveillance post-arrival of the invasive alien species and more detailed information about the success of the eradication with NOTSYS notifications. For example, for V. v. nigrithorax, some NOTSYS records are accompanied by notes on whether the queen was killed and whether dispersal had already occurred prior to nest destruction. Integrating this information on the success of the eradication, directly into the dispersal and reproduction rates in the model for a site, could help to support the use of the modelling framework for exploring how failed eradications could influence patterns of invasion. Moreover, this information could be used to guide further surveillance for invaded sites around those eradication sites, where dispersal of the queen may have already occurred. Additionally, mapping the surveillance network in place for the early detection of the focal species in different regions could

enable the models to evaluate how missed eradications may have contributed to the speed of spread. Indeed Regulation (EU) 1143/2014 requires Member States to document the surveillance approaches adopted for the IAS of EU concern and such information could inform the models. Citizen science databases like Asian Hornet Watch provide excellent data on spatial patterns of surveillance within the UK (Figure 2) and could be coupled with data on the spatial locations of other key participants in surveillance networks, such as beekeepers.

Extension to other species of Union Concern

This modelling framework has the benefit of being generalisable and flexible as it considers many common pseudo-absence selection procedures to establish which perform best when predicting suitability for the focal species and allows dispersal parameters to be estimated from snapshots of previous spread. Therefore, the approach could be utilised to look at the effectiveness of rapid eradications outlined in NOTSYS notifications for other invasive alien species of Union concern (Regulation (EU) 1143/2014) and the potential extent of invasion and future spread. Though it should be noted that the use of this modelling framework will require access to *a priori* knowledge on reproductive rates alongside data on initial introductions and 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 species distribution model. The models can be tailored to other species through the selection of relevant climate, land-use and trait variables to inform the SDM and the spread model.

To assess the suitability of using the framework for other species of Union concern we used the number of GBIF records available globally and in Europe as proxy to determine those species for which this modelling approach may be applicable (Table 3). We would expect the potential niche to be better predicted for species that are well-recorded in the native and introduced range, as the data represent a more complete picture of suitable climate and land cover. Some of the invasive alien species of Union concern for which this modelling framework may be well suited based on availability of records in both the native range and the EU include Alopochen aegyptiaca, Lagarosiphon major, Ludwigia peploides, Muntiacus reevesi, Myocastor coypus, Oxyura jamaicensis, Procambarus clarkii, Procyon lotor and Threskiornis aethiopicus (Table 3). However, some species of Union concern may be more difficult to model using this approach. For example, species such as Procambarus fallax f. virginalis, Heracleum persicum, Perccottus 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 3). In cases where sufficient numbers of records are available outside of Europe and no records of spread are available in invaded countries, projections of suitability in Europe could be estimated using this framework and dispersal parameters could be estimated using the literature or expert elicitation to provide an estimate of

future spread. However, these factors would need to be taken into account when interpreting the output from models.

Accurately predicting spread patterns in the invaded range may also be influenced by the relative roles of natural dispersal processes and human-mediated dispersal events (see Limitations section for further discussion). For example, species able to stowaway on boats and other recreational equipment moved between waterways could be under-predicted compared to those species whose dispersal is predominantly natural after the point of introduction. Classifying species by their pathways of spread may be a useful exercise to evaluate the transferability of the current models to other species of Union Concern. In order for human-mediated long-distance dispersal to be integrated into this framework, it is important to examine whether spatial proxies can be found for the propagule pressure arising from particular spread pathways connecting different parts of the landscape. An innovative recent approach for freshwater species mapped the human-mediated propagule pressure from freshwater invasive alien species due to recreational use of UK lakes and rivers (Chapman et al. 2020).

The modelling framework was developed to evaluate potential patterns of spread in the absence of rapid eradication. However, the framework could also be applicable to species that have been managed using alternative measures, provided that the locations of these interventions are available. For example, containment may have been attempted through local management or public awareness campaigns may have been launched to slow the spread of species. In these cases, the models could be used to compare observed patterns of spread with those predicted in the absence of those interventions, or to compare among regions with and without these measures in place.

Limitations

As with any modelling approach, there are limitations. Firstly, our modelling framework uses a SDM 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 and Pearson 2005, Gallien et al. 2012). The stage of invasion may therefore influence the ability of SDMs to predict potential habitat prone to invasion. SDMs may under predict the extent of invasion at the early stages invasion compared to later stages of invasion, where a species would be closer to equilibrium (Václavík and 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 none-the-less the SDM 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 (Gallien et al. 2012, Barbet-Massin et al. 2018). Moreover, the SDM approach used here does attempt to account for non-equilibrium through the pseudo-absence selection process, which chooses absences only from accessible, but unsuitable regions. This gives the modelling framework flexibility to incorporate detailed biological information about the focal species, where available, which can go some way to mitigating this limitation (Chapman et al. 2019).

Secondly, some of the records used in the SDM may not necessarily result in successful 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 a SDM, 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 at 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 and Villeemant 2017) which make up the majority of records used in the SDM (79.5%). However, none of the other data sets used in this study allow 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 SDM are from sites that may not be suitable for *V. v. nigrithorax*.

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 fresh water non-native 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. It is important to note that only movement of reproductive queen *V. v. nigrithorax* are relevant in this context. One further approach could be to consider descriptive scenarios that might increase spread of *V. v. nigrithorax* rather than attempting to derive model outputs given the random nature of such events.

Potential extensions to the modelling framework

In addition to understanding the potential spread of *V. v. nigrithorax* in Europe, this modelling approach could potentially be extended to evaluate different scenarios of surveillance and management. For example, spatial patterns in eradication attempts could be modelled to inform and prioritise management strategies where complete eradication within a Member State would not be practical. There are also possibilities to link this framework with other approaches to better understand the potential impact of *V. v. nigrithorax*, for example, on native pollinators and honey bees.

Informing surveillance and eradication

By optimising the surveillance and eradication effort for invasive alien species the costs incurred for surveillance, eradication and damage can be substantially reduced (Bogich et al. 2008, Hauser and McCarthy 2009, Moore et al. 2011, Epanchin-Niell et al. 2012). The modelling framework presented here could be extended to address questions regarding the spatial allocation of management and surveillance of invasive alien species (Lioy et al. 2019b). This could be done by incorporating the removal of occupied sites into model simulations 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 (Cacho et al. 2010, Giljohann et al. 2011, Baker 2017). The spread component of the models is also amenable to simulations, which could 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 all cases, model accuracy and simulation tools are reliant on robust data and as such surveillance systems that maximise the gathering of information on the occurrence of the invasive alien species but also on management interventions as near to real time as possible would be advantageous. Of course it is also important that such information is shared openly and rapidly amongst Member States using a standardised data structure.

Approaches to quantifying impacts of V. v. nigrithorax on honey bees

The potential threat of V. v. nigrithorax to honeybee colonies and wild pollinators has led to the conclusion that uncontrolled spread would be disastrous (Keeling et al. 2017). However, empirical evidence of impacts is currently lacking. A recent study highlighted the effects of V. v. nigrithorax on honeybee health demonstrating activation of honeybee antioxidant systems in the presence of the invasive hornet (Leza et al. 2019). Indeed predation by hawking V. v. nigrithorax on honey bees is suspected to weaken honeybee colonies before the winter season in western Europe (Requier et al. 2019). Furthermore, studies comparing the life-history traits of the European hornet, Vespa crabro and V. v. nigrithorax, which share a similar ecological niche, have revealed an overlap of trophic preference, thus the possibility of competition with the native hornet (Cini et al. 2018). The queens of V. v. nigrithorax have higher exploitative tendencies than V. crabro queens and so have an advantage during colony formation. Additionally, the higher abundance of foraging V. v. nigrithorax than V. crabro patrolling and defending food sources during summer and autumn could also lead to displacement of V. crabro as it is outcompeted by the invading hornet (Cini et al. 2018), although a recent analysis on interspecific hierarchies revealed that V. crabro is able to outperform V. v. nigrithorax (Kwon and Choi 2019). Approaches could be developed to link spread models with other relevant datasets such as distribution of honey bee colonies to derive risk maps.

Approaches to quantifying impacts of V. v. nigrithorax on wild pollinators

A number of studies have reported declines in pollinating insects (Potts et al. 2010, Powney et al. 2019). Honey bees and wild pollinators are at threat from climate and land-use change, pollution and invasive alien species. Indeed a recent guide to managing invasive alien species to protect wild pollinators highlights *V. v. nigrithorax* alongside a number of other invasive alien species, including other Hymenoptera, as a threat to pollinating insects and pollination services (IUCN 2020). Bayesian modelling approaches have been developed to assess the effects of large-scale drivers of change on biodiversity, for example large-scale declines on wild bees in oilseed rape has been attributed to neonicotinoid applications (Woodcock et al. 2016). Similar modelling approaches could be used to assess the effects of *V. v. nigrithorax* on wild bees and other pollinating insects. Such approaches could be refined to consider the risk to protected areas or regions where priority (e.g. Red Listed) species occur. The robustness of the models would depend on availability of distribution data and information on relevant life-history traits. Furthermore, given the importance of propagule pressure (total number of individuals introduced to a specific location) in determining the outcomes of biological invasions (Lockwood et al. 2009) but recognising the scarcity of raw data, it would be advantageous to consider proxies to include abundance as a parameter within the models.

Combining spread models and outcomes of impact assessments for invasive alien species of Union concern

The Environmental Impact Classification of Alien Taxa (EICAT)⁷ is a simple and objective way to classify the impacts of alien species into one of categories according to the magnitude of adverse environmental impacts (Volery et al. in press, Blackburn et al. 2014). EICAT could be used alongside spread models for all invasive alien species of EU concern to present a biodiversity indicator of the impacts of the invasive alien species of EU concern.

Furthermore, if the costs associated with an invasive alien species can be quantified (e.g. costs on human activities, costs related to the implementation of long-term management strategies), these can be forecasted before invasion to predict the costs that a Member state could incur in the future for limiting its impacts. At the same time, if an eradication attempt prevents the future spread of the species, savings could be estimated by comparing the predicted invasion scenario.

Conclusions

The modelling approaches described can inform evaluation of the effectiveness of measures implemented within the context of Regulation (EU) 1143/2014 such as rapid eradications reported using NOTSYS notifications but also other measures required under Regulation (EU) 1143/2014. It is evident that for all the Member States that had reported *V. v. nigrithorax* incursions and subsequent interventions, specifically rapid eradication, within NOTSYS the spread of *V. v. nigrithorax* has been limited. In the case of the UK *V. v. nigrithorax* is considered absent following rapid eradication of all observed incursions In Germany and the Netherlands the spread has been substantially reduced. Although in Belgium *V. v. nigrithorax* is now considered established, however, the model predictions indicate that this invasive alien species could have been even more widespread than is currently the case. It would be feasible to extend the modelling framework to other invasive alien species of Union concern and also to adopt approaches to consider the impacts of biological invasions on other species, ecosystem services and human activities.

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⁷ https://www.iucn.org/sites/dev/files/content/documents/eicat_guidelines_v1.1.pdf

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Species of Union Concern	English name	Total GBIF records*	Native range	GBIF records in native range*	Number of EU Member States in which established	GBIF records in EU*	NOTSYS eradication notifications (as of 15/07/2020)	Anthropogenic pathways (CBD classification)
V. v. nigrithorax	Asian hornet	31343	Asia	38	5: Belgium, France, Italy, Spain, Portugal	31299	24	Transportation of habitat material
Acacia saligna (Acacia cyanophylla)	Golden wreath wattle	6743	South-western Western Australia	4131	8: Croatia, Cyprus, France, Greece, Italy, Malta, Portugal, Spain	1406	0	
Ailanthus altissima	Tree of heaven	52408	China	382	Austria, Belgium, Croatia, Czech Republic, France, Germany, Greece, Hungary, Italy, Malta, the Netherlands, Portugal, Slovenia, Spain, the United Kingdom	38579	0	
Alternanthera philoxeroides	Alligator weed	23242	Brazil	215	2: France and Italy	211	2	Pet / Aquarium / Terrarium, Ornamental purposes other than horticulture, Contaminant on plants, Angling and fishing, hitchhikers on ship/boats, Transportation of habitat material
Andropogon virginicus	Broomsedg e bluestem	5944	Northern, central and southern	1640		17	0	

			America and Caribbean					
Asclepias syriaca	Common milkweed	21700	North America	19491	 13: Austria, Czech Republic, Bulgaria, Denmark, France, Croatia, Hungary, Italy, Lithuania, the Netherlands, Poland, Romania and Slovakia 	1934	0	Ornamental purposes other than horticulture, Transportation of habitat material
Baccharis halimifolia	Eastern baccharis	6501	North America	2135	5: Belgium, France, Italy, Spain and the United Kingdom	3373	0	Ornamental purposes other than horticulture
Cabomba caroliniana	Fanwort	2139	southern Brazil, Paraguay, Uruguay and northeast Argentina	120	9: Austria, Belgium, Denmark, France, Hungary, the Netherlands, Poland, Sweden and the United Kingdom	333	3	Pet / Aquarium / Terrarium, Ornamental purposes other than horticulture, Contaminant on plants, Angling and fishing, hitchhikers on ship/boats, Transportation of habitat material, Machinery
Cardiospermum grandiflorum	Balloon vine	2923	South America	606		112	0	
Cortaderia jubata	Purple pampas grass	9429	South America	128		0	0	
Eichhornia crassipes	Water hyacinth	18894	Amazon basin	592	4: France, Italy, Portugal and Spain	640	2	Pet / Aquarium / Terrarium, Ornamental purposes other than horticulture

Elodea nuttallii	Nuttall's waterweed	70387	temperate regions of North America	597	 17: Austria, Belgium, Bulgaria, Denmark, France, Germany, Hungary, Ireland, Italy, Luxembourg, the Netherlands, Poland, Romania, Slovakia, Slovenia, Sweden, and the United Kingdom 	69432	0	Pet / Aquarium / Terrarium, Ornamental purposes other than horticulture, Contaminant on plants, Angling and fishing, hitchhikers on ship/boats, Transportation of habitat material, Machinery
Ehrharta calycina	Perrenial veldt grass	9132	South Africa	1113		16	0	
Gunnera tinctoria	Chilean rhubarb	2377	South America	188	5: France, Ireland, Portugal (Azores), Spain and the United Kingdom	1940	0	Ornamental purposes other than horticulture
Gymnocoronis spilanthoides	Senegal tea plant	571	South America	242		1	1	
Heracleum mantegazzianum	Giant hogweed	62363	Western Greater Caucasus	49	 20: Austria, Belgium, Croatia, the Czech Republic, Denmark, Estonia, Finland, France, Germany, Hungary, Ireland, Italy, Latvia, Luxembourg, Poland, the Netherlands, Slovakia, Slovenia, Sweden and the United Kingdom 	52792	0	Ornamental purposes other than horticulture, Transportation of habitat material

Heracleum persicum Heracleum sosnowskyi	Persian hogweed Sosnowsky 's hogweed	241	Turkey, Iraq and Iran Caucasus, Transcaucasia and North-East	18	 6: Czech Republic, Denmark, Estonia, Finland, Sweden and the United Kingdom 7: Denmark, Estonia, Finland, Hungary, Latvia, Lithuania, 	214	0	Transportation of habitat material, Machinery Transportation of habitat material, Machinery
Humulus scandens	Japanese hop	920	Turkey	NA	Poland	4	0	Transportation of habitat material,
Hydrocotyle ranunculoides	Floating pennywort	7328	North, Central and South America	704	6: Belgium, France, Germany, Hungary, Italy, the Netherlands, Portugal, Spain and the United Kingdom	5631	1	Pet / Aquarium / Terrarium, Ornamental purposes other than horticulture, Contaminant on plants, Angling and fishing, hitchhikers on ship/boats, Transportation of habitat material, Machinery
Impatiens glandulifera	Himalayan balsam	185281	north-west Pakistan to northern India	115	25: all except Greece, Malta and Cyprus	171041	0	Ornamental purposes other than horticulture, Contaminant on plants, Transportation of habitat material, Machinery
Lagarosiphon major	Curly waterweed	2846	South Africa	83	11: Austria, Belgium, France, Germany,	1894	2	Pet / Aquarium / Terrarium, Ornamental purposes other than horticulture, Contaminant on plants,

Lespedeza cuneata (Lespedeza juncea var. sericea)	Chinese bushclover	5209		NA	Hungary, Ireland, Italy, the Netherlands, Portugal, Spain, and the United Kingdom	0	0	Angling and fishing, hitchhikers on ship/boats, Transportation of habitat material, Machinery
Ludwigia grandiflora	Water- primrose	11117	American continent	2572	9: Belgium, France, Germany, Hungary, Ireland, Italy, the Netherlands, Spain and the United Kingdom	8526	0	Pet / Aquarium / Terrarium, Ornamental purposes other than horticulture, Contaminant on plants, Angling and fishing, hitchhikers on ship/boats, Transportation of habitat material, Machinery
Ludwigia peploides	Floating primrose- willow	12585	American continent	9826	6: Belgium, France, Greece, Italy, the Netherlands and Spain	4001	3	Pet / Aquarium / Terrarium, Ornamental purposes other than horticulture, Contaminant on plants, Angling and fishing, hitchhikers on ship/boats, Transportation of habitat material, Machinery

Lygodium japonicum	Vine-like fern	6357		4402		3	0	
Lysichiton americanus	American skunk cabbage	7436	North America	NA	9: Belgium, Denmark, Finland, France, Germany, Ireland, the Netherlands, Sweden and the United Kingdom	4046	1	Ornamental purposes other than horticulture
Microstegium vimineum	Japanese stiltgrass	4594	Asia	1775	0: but established in Turkey	0	0	Machinery
Myriophyllum aquaticum	Parrot's feather	9456	South America	115	 13: Austria, Belgium, France, Germany, Hungary, Ireland, Italy, Luxembourg, the Netherlands, Portugal, Romania, Spain and the United Kingdom 	4211	1	Pet / Aquarium / Terrarium, Ornamental purposes other than horticulture, Contaminant on plants, Angling and fishing, hitchhikers on ship/boats, Transportation of habitat material, Machinery
Myriophyllum heterophyllum	Broadleaf watermilfoi l	1590	Eastern United States	1174	7: Austria, Belgium, Germany, Spain, France, Hungary and the Netherlands	367	0	Pet / Aquarium / Terrarium, Ornamental purposes other than horticulture, Contaminant on plants, Angling and fishing, hitchhikers on ship/boats, Transportation of habitat material, Machinery
Parthenium hysterophorus	Whitetop weed	8681	subtropics	4199	0, but present in Belgium	11	0	Contaminant on plants, Transportation of habitat material,

			of North and South America					Machinery
Pennisetum setaceum	Crimson fountaingra ss	4481	Northern Africa	112	5: Spain, France, Italy, Malta and Portugal	762	0	Ornamental purposes other than horticulture, contaminant on animals, Transportation of habitat material, Machinery
Persicaria perfoliata	Asiatic tearthumb	2902	Asia	1501	0: but established in US and elsewhere	0	2	Transportation of habitat material
Prosopis juliflora	Mesquite	3372	Mexico, Central and northern South America	1073		1	0	
Pueraria lobata	Kudzu vine	1581	Eastern Asia	1304	1: Italy (and Switzerland)	4	0	Ornamental purposes other than horticulture
Salvinia molesta (Salvinia adnata)	Salvinia moss	3091		NA		66	0	
Triadica sebifera (Sapium sebiferum)	Chinese tallow	6274	China, Japan, Taiwan and Vietnam	1386		4	0	
Acridotheres tristis	Common myna	1185953	central and southern Asia	447740		2155	0	
Alopochen aegyptiaca	Egyptian goose	869812	Africa	297763	8: United Kingdom, the Netherlands, Belgium, Germany, Sweden, Cyprus, Denmark and Poland	511093	2	Pet / Aquarium / Terrarium
Arthurdendyus triangulatus	New Zealand flatworm	3374	New Zealand	8	NA	3361	0	

Callosciurus erythraeus	Pallas' squirrel	1861	South East Asia	1448	4: Belgium, France, Italy and the Netherlands	221	0	Pet / Aquarium / Terrarium
Corvus splendens	Indian house crow	446003	Indian sub- continent	402443	1: Netherlands	38	1	
Eriocheir sinensis	Chinese mittencrab	12427	eastern Asia	30	 18: Belgium, Czech Republic, Finland, France, Germany, Hungary, Ireland, Italy, Latvia, Lithuania, Luxembourg, the Netherlands, Poland, Portugal, Romania, Slovakia, Spain and the United Kingdom 	12261	1	live food and live bait
Herpestes javanicus	Small Asian mongoose	7820	Iran, northern India and Indochina	121	1: Croatia, but also a major pest elsewhere	11	0	Pet / Aquarium / Terrarium
Lepomis gibbosus	Pumpkinse ed	74846	North America	48918		25701	0	
Lithobates catesbeianus	American bullfrog	40719	North America	34728	7: Belgium, France, Germany, Greece, Italy, Slovenia and the United Kingdom	4699	1	Pet / Aquarium / Terrarium, contaminant on animals
Muntiacus reevesi	Muntjac deer	14713	south Asia	384	6: Belgium, Denmark, Germany, Ireland, the Netherlands and the United Kingdom	14301	8	Pet / Aquarium / Terrarium

Myocastor coypus	Соури	43920	South America	698	19: Austria, Belgium, Bulgaria,Croatia, Czech Republic, Denmark, France, Germany,Greece, Hungary, 	39989	7	
Nasua nasua	Coati	1738	South America	1519	1: Spain (Mallorca)	1	4	Pet / Aquarium / Terrarium
Nyctereutes procyonoides	Raccoon dog	10695	Eastern Asia	7678	 14: Bulgaria, the Czech Republic, Denmark, Estonia, Finland, France, Germany, Hungary, Latvia, Lithuania, Poland, Romania, Sweden and Slovakia 	3002	1	Pet / Aquarium / Terrarium
Ondatra zibethicus	Muskrat	139444	North America	13508	 19: Austria, Belgium, Bulgaria, Croatia, Czech Republic, Estonia, Finland, France, Germany, Hungary, Italy, Latvia, Lithuania, Luxembourg, Netherlands, Poland, Romania, 	125028	0	

					Spain, Sweden			
Orconectes limosus	Spiny- cheek crayfish	4319	North America	383	 19: Austria, Belgium, Bulgaria, Croatia, the Czech Republic, France, Germany, Hungary, Italy, Latvia, Lithuania, Luxemburg, the Netherlands, Poland, Romania, Slovakia, Slovenia, Spain and the United Kingdom 	3935	0	Pet / Aquarium / Terrarium, Angling and fishing, live food and live bait, contaminant on animals
Orconectes virilis	Virile crayfish	2838	North America	2662	2: the Netherlands and the United Kingdom	164	0	Pet / Aquarium / Terrarium, Angling and fishing, live food and live bait, contaminant on animals
Oxyura jamaicensis	Ruddy duck	1497647	North America	2793547	12: Austria, Belgium, the Czech Republic, Finland, France, Germany, Hungary, Ireland, Italy, the Netherlands, Portugal and the United Kingdom	37173	7	Pet / Aquarium / Terrarium
Pacifastacus leniusculus	Signal crayfish	25600	North-Western US and Canada	687	23: Austria, Belgium, Croatia, the Czech Republic, Denmark, Estonia, Finland, France, Germany, Greece, Hungary,	24896	1	Pet / Aquarium / Terrarium, Angling and fishing, live food and live bait, contaminant on animals

					Italy, Latvia, Lithuania, Luxemburg, the Netherlands, Poland, Portugal, Slovakia, Slovenia, Spain, Sweden, and the United Kingdom			
Perccottus glenii	Amur sleeper	562	North Korea and far eastern Russia	258	9: Bulgaria, Croatia, Estonia, Germany, Hungary, Lithuania, Poland, Romania and Slovakia	166	0	Pet / Aquarium / Terrarium, live food and live bait, contaminant on animals
Plotosus lineatus	Striped eel catfish	1994	unknown	NA		0	0	Pet / Aquarium / Terrarium
Procambarus clarkii	Red swamp crayfish	12272	South-Eastern USA	2430	10: Austria, Belgium, Cyprus, France, Germany, Italy, the Netherlands, Portugal, Spain, and the United Kingdom	9305	2	Pet / Aquarium / Terrarium, Angling and fishing, live food and live bait, contaminant on animals
Procambarus fallax f. virginalis	Marbled crayfish	5	unknown	NA	6: Croatia, the Czech Republic, Germany,Italy, the Netherlands, and Slovakia	5	3	Pet / Aquarium / Terrarium, Angling and fishing, live food and live bait, contaminant on animals
Procyon lotor	Raccoon	37046	North America	28008	16: Austria, Belgium, Croatia, the Czech Republic, Denmark, France, Germany, Hungary,	7568	4	Pet / Aquarium / Terrarium

					Ireland, Italy, Luxemburg, Poland, Romania, Slovakia, Slovenia and Spain			
Pseudorasbora parva	Stone moroko	25773	Eastern Asia	4638	19: Austria, Belgium, Bulgaria, Croatia, the Czech Republic, Denmark, France, Germany, Greece, Hungary, Italy, Luxemburg, the Netherlands, Poland, Romania, Slovakia, Slovenia, Spain, and the United Kingdom	20825	0	Pet / Aquarium / Terrarium, Angling and fishing, live food and live bait, contaminant on animals
Sciurus carolinensis	Grey squirrel	166579	North America	35884	3: Italy, Ireland and the United Kingdom	124001	1	Pet / Aquarium / Terrarium
Sciurus niger	Fox squirrel	27557	North America	27422	0	37	0	Pet / Aquarium / Terrarium
Tamias sibiricus	Siberian chipmunk	3790	Siberian taiga	1384	6: Belgium, France, Germany, Ireland, Italy and the Netherlands	2400	1	Pet / Aquarium / Terrarium
Threskiornis aethiopicus	Sacred ibis	224923	sub-Saharan Africa	184291	8: Belgium, France, Greece, Italy, Latvia, Lithuania, Portugal and Spain	6779	6	Pet / Aquarium / Terrarium
Trachemys scripta	Red-eared, yellow- bellied and Cumberlan d sliders	50891	Eastern and Central US	29552	22: Austria, Belgium, Bulgaria, Croatia, Cyprus, the Czech Republic, Denmark, Finland, France, Germany, Greece, Hungary, Ireland, Italy, Latvia, Luxembourg, Poland, Portugal, Romania,	18248	0	Pet / Aquarium / Terrarium

		Slovakia, Slovenia and		
		Spain		

* includes only georeferenced records, prior to any data cleaning steps

Annex

1. Methods

1.1 Occurrence data

Species occurrence data for *V. v. nigrithorax*, comprising 23,190 records on a global scale were used within a Species Distribution Model (SDM) to assess the environmental suitability for *V. v. nigrithorax* across Europe. Data were obtained from the Biological Records Centre (UK), Inventaire National du Patrimoine Naturel (France), Vespa watch (Belgium), LIFE STOPVESPA (Italy), Waarneming.nl (Netherlands), MITECO (Spain), the Global Biodiversity Information Facility (GBIF) and Aktion-Wespenschutz and University of Hamburg (Germany).

Problematic records, such as records from 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 10 km were also excluded. The remaining 23,190 records (Figure 3 (Main Text)) were gridded at 5 arcminute resolution (0.083 x 0.083 degrees of longitude/latitude) yielding 3805 grid cells with occurrences. As a proxy for recording effort, the number of *Insecta* records held by GBIF was also complied on the same grid (Figure A1).



Figure A1: Recording density of Insecta on GBIF, which was used as a proxy for recording effort (log10 transformed for plotting).

1.2 Abiotic variables used for Species Distribution Model

Climatic variables were obtained from WorldClim version 2.1. Variables used to represent current climactic conditions were taken from historical data (1970-2000) (Fick and Hijmans 2017). The climate variables used in this study were the same as those used in a previous SDM used to project habitat for V. v. nigrithorax in France (Fournier et al. 2017). This study and other studies have also found that V. v. nigrithorax tended to favour nesting in anthropogenically disturbed areas in France (Rome et al. 2015, Fournier et al. 2017) and Italy (Lioy et al. 2019b). Therefore, the Global Human influence index (HII) was included as another abiotic variable (Wildlife Conservation Society - WCS & Center for International Earth Science Information Network - CIESIN - Columbia University, 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 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 A2). Therefore, we selected a single variable from each pair of highly correlated variables. Given the long 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 climactic conditions in a single quarter. Therefore, annual mean temperature (BIO 1) was included instead of 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.



Figure A2: Hierarchical clustering of abiotic variables for V. v. nigrithorax based on distance using 1- Pearson's r. Red line shows distance threshold of 0.3 below which variables are considered highly correlated.

1.3 Projecting environmental suitability

To project the environmental suitability in each cell for V. v. nigrithorax based on abiotic variables outlined above, we fitted a selection of species distribution models (SDMs) both globally and only for Europe. For both sets of models we used six different pseudo-absence selection procedures (i) random pseudo-absence selection across the focal area using BIOMOD2 (n=10000) (Thuiller et al. 2009, Barbet-Massin et al. 2012), (ii) selection of pseudo-absences outside of the climatically suitable areas defined using the "SRE" method in BIOMOD2 (n=10000) (Thuiller et al. 2009, Barbet-Massin et al. 2012), (iii) random selection of pseudo-absences within an accessible area defined by using a 30km buffer around occurrences in invaded regions and 100km buffers around occurrences in native regions (n=3803) (Barbet-Massin et al. 2012, Senay et al. 2013, Chapman et al. 2019), (iv) selection of pseudo-absences within the accessible area weighted by recording effort (number of Insecta records) (n=3803) (Phillips et al. 2009, Chapman et al. 2019), (v) pseudo-absence selection from both accessible and climatically unsuitable areas, with sampling weighted by recording effort in the accessible area (n=6803) (Chapman et al. 2019) and (vi) random pseudo-absence selection from both accessible and climatically unsuitable areas (n=6803). To evaluate how well our SDM predicted species occurrences, we used the Boyce Index and retained 1000 randomly sampled occurrence records from Europe for model evaluation prior to fitting models. The data used for modelling was randomly split, using 70% of 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 (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 and Grenouillet 2013, Liu et al. 2013). For each model, an ensemble model was fitted using BIOMOD ('Biomod2' R package V3.3-7) 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). Selection of best performing algorithms for the final ensemble model was based on modified Z-scores (Iglewicz and Hoaglin 1993, Chapman et al. 2019). 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.

1.4 Projecting future distribution of V. v. nigrithorax

To predict the future distribution of *V. v. nigrithorax* in the countries that have given NOTSYS notifications based on dispersal constraints, environmental suitability and time to reproduction, we utilised the MIGCLIM model ('MigClim' package in R) (Engler and Guisan 2009, Engler et al. 2012).

This model allows the use of suitability maps projected using BIOMOD to project the future distribution of species using current distribution, dispersal constraints and time to propagule production.

To assess which dispersal kernel would be best suited to predict the distribution of *V. v. nigrithorax* in the countries with NOTSYS notifications, we used existing distribution data in Spain (2010-2016), Italy (2013-2019) and France (2004-2014) to determine the average dispersal kernel that best describes the distribution of *V. v. nigrithorax* in each of these three countries. To do this we ran the MigClim model for 50 simulations, each time using a different dispersal kernel generated using gaussian, negative exponential and power law equations (eq 1,2,3; Figure A3). We also used three different thresholds to classify cells as suitable and unsuitable for *V. v. nigrithorax* by using the "minROCdist", "Default" and "Max Sens +Spec" methods in the PresenceAbsence package in R (Freeman and Moisen 2008). In an effort 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) to establish which clusters were segregated by a distance greater than 100km. This resulted in multiple clusters of records in each country. The cluster containing the earliest records in each country was used to establish the best suited dispersal kernel (Cluster 1 in Figure A3 (a), (b) and (c)).

For each model cells were set to produce propagules after a single year as *V. v. nigrithorax* takes a single year to complete its life cycle and produce new queens (Monceau et al. 2014). The probability of cell becoming colonised is determined by the dispersal kernel and whether the cell is classified as suitable or unsuitable using the selected threshold. For each run we determined the probability that each site would be occupied by determining the number of simulations in which each site was occupied at the end of each run. We then calculated the AUC and Boyce Index for each run using this probability of occupancy (number of simulations occupied/total number of simulations) and available records to determine which model performed best at predicting occurrences and discriminating between occupied and unoccupied sites in each country. When calculating the AUC, the same number of unoccupied sites and occupied sites were used by randomly sampling from all unoccupied sites. We used the first recorded introductions in each country as a starting point in each model.

For the model in the Belgium, Germany, the Netherlands and the UK we used the best performing combination of dispersal kernel and threshold value from the MIGCLIM model for France, Spain and Italy as three different scenarios of spread in each country with NOTSYS notifications.



Figure A3: 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. Cluster 1 in each country is the cluster containing earliest records and other clusters were removed when estimating dispersal kernels to reduce the potential influence of human-mediated dispersal events.

Instead of using a single initial distribution, we adapt this approach to incorporate records of nest removal in 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 additional NOTSYS notifications in later years. The MIGCLIM model for each country with NOTSYS notifications was run for 100 simulations using each of the three different spread scenarios from the first NOTSYS notification in each country for 10 years. To produce a spatial map of probability of occupancy in each country with NOTSYS notifications we calculated the mean probability of occupancy in across the three different spread scenarios.

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 difference spread scenarios predicted the spread of *V. v. nigrithorax* in Belgium

Box A1

We used four functions to define dispersal kernels that were then used to explore the spread of *V. v. nigrithorax* in France. Exponential (eq1), gaussian (eq2) and power law equations (eq 3).

eq1.
$$P_{i,j} = \exp\left(-\frac{dist_{i,j}}{a}\right)$$
 $a = 2 \text{ to } 20$

eq2.
$$P_{i,j} = \exp\left(-\frac{dist_{i,j}^2}{a^2}\right)$$
 $a = 2 \text{ to } 20$

eq3. $P_{i,j} = \left(1 + \frac{dist_{i,j}}{a}\right)^{-b}$ a = 0.5 to 10 b = 1.5 and 2

Where, the probability of colonisation(P) between a source cell (i) and a suitable cell (j) is determined by the distance in km between cells ($dist_{i,j}$) and two scaling parameters (a and b). Resulting dispersal kernels from each equation and different scaling parameters are shown in Figure A3.



Figure A4: V. v. nigrithorax dispersal kernels used in MIGCLIM model. Probability of a cell being colonised declines as a function of distance from the source cell. Alpha parameter used for each kernel is shown in the legend.

2. Results

2.1 Suitability in Europe

Of all fitted models, the model using accessible regions pseudo-absence selection method had the best performance across all evaluation metrics (Table A1, Figure A5). Using this pseudo-absence selection procedure, our ensemble model suggests that suitability for *V. v. nigrithorax* is most strongly influenced by precipitation and temperature seasonality, which together accounted for 82% (64% and 18%) of the variation explained. This is followed by mean annual temperature seasonality, which explained 14% of the variation. Annual precipitation explained 2% of variation, and anthropogenic influence explained 2% of the variation (Table A2).

Table A1: 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. cAUC= Calibrated AUC, TSS= True skill statistic, Boyce = Boyce index and Mean across metrics = mean of all evaluation metrics.

Background	Focal Area	Recording Effort	cAUC	TSS	Воусе	Index across metrics
Accessible	Global	No	0.59	0.88	0.96	0.81
Unsuitable	Global	No	0.49	0.97	0.94	0.80
Unsuitable & Accessible	Global	No	0.49	0.92	0.94	0.78
Unsuitable	Europe	No	0.50	0.88	0.95	0.78
Random	Europe	No	0.50	0.88	0.92	0.77
Random	Global	No	0.35	0.97	0.86	0.73
Accessible	Europe	Yes	0.61	0.62	0.98	0.73
Accessible	Global	Yes	0.59	0.63	0.99	0.72
Accessible	Europe	No	0.57	0.59	0.99	0.72
Unsuitable & Accessible	Europe	Yes	0.46	0.71	0.98	0.71
Unsuitable & Accessible	Global	Yes	0.46	0.73	0.98	0.71
Unsuitable & Accessible	Europe	No	0.45	0.69	0.98	0.70

Table A2: Summary of variable importance of the fitted model algorithms and the ensemble models from best preforming algorithms for V. v. nigrithorax. Results are average of models fitted to ten different background samples of the data.

Algorithm	Selected for Ensemble	Mean Annual Temperature	Temperature Seasonality	Annual Precipitation	Precipitation Seasonality	Global Human Influence Index
GLM	No	0.17	0.22	0.01	0.59	0.01
GAM	Yes	0.15	0.22	0.01	0.60	0.01
ANN	Yes	0.10	0.20	0.02	0.65	0.03
GBM	Yes	0.10	0.17	0.01	0.71	0.02
MARS	Yes	0.13	0.09	0.00	0.78	0.01
RF	Yes	0.17	0.19	0.06	0.52	0.06
Ensemble	-	0.14	0.18	0.02	0.64	0.02



Figure A5: Results from evaluation of best preforming SDM with Boyce Index showing change predicted/expected ratio across environmental suitability values for V. v. nigrithorax.

Environmental suitability varied across Europe, with areas of high suitability in France, Spain, Portugal, Italy, Belgium, the Netherlands, Denmark, Germany, the United Kingdom and Northern Ireland and the Republic of Ireland (Figure A6). Regions with an annual mean temperature of approximately 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 A7).

2.2 Predicting future spread

By evaluating different dispersal kernels using the MIGCLIM model in France, Spain and Italy, we found that the best performing dispersal differed in each country (Figure A8, Figure A9, Figure A10). This resulted in three scenarios of spread that were used to determine the potential future distribution on *V. v. nigrithorax* in Belgium, Germany, the Netherlands and the UK assuming that there had not been rapid eradication measures implemented for this species.

2.3 Projections and spread in Belgium

Our projected distribution of *V. v. nigrithorax* in the Belgium using the three different scenarios resulted in a projection that 73 to 96% of suitable sites in Belgium could be colonised by 2020 (Lowest CI= 57%; highest CI=98%). Our projection also shows that 94 to 98% of suitable sites could be occupied by 2026 (Lowest CI= 96%; highest CI=99%). 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 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 probability of occupancy performed well in explaining the current distribution of *V. v. nigrithorax* (AUC=0.88; Boyce Index=0.86) (Figure A11).

2.4 Projections of spread in other NOTSYS countries

In Germany, 6 to 16% of suitable sites are predicted to be colonised by 2020 (Lowest CI= 4%; highest CI=18%) and 11 to 100% of suitable sites are predicted to be colonised by 2027 (Lowest CI= 6%; highest CI=100%). In the Netherlands, 27 to 63% of suitable sites are predicted to be colonised by 2020 (Lowest CI= 15%; highest CI=73%) and 99% to 100% of suitable sites are projected to be colonised by 2027 (Lowest CI= 97%; highest CI=100%). Finally in the UK, 14 to 52% of suitable sites are predicted to be colonised by 2020 (Lowest CI= 8%; highest CI=56%) and 44 to 66% of suitable sites are 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.



Figure A6: a) Projected suitability for V. v. nigrithorax in the Europe under current climatic conditions. b) Uncertainty in the suitability projections for current climatic conditions, expressed as the among-algorithm standard deviation in predicted suitability, averaged across ten datasets.



Figure A7: Partial response plots from fitted models for V. v. nigrithorax. Thin coloured lines show responses from the algorithms in the ensemble. The thick black line is their ensemble. In each plot, other model variables are held at their median value in the training data. Bio1 = Annual mean temperature, Bio4 = temperature seasonality, Bio12= Annual precipitation, Bio15= Precipitation seasonality and HII= Global Human Influence Index

Table A3: Results from best preforming dispersal kernels for V. v. nigrithorax. AUC and Boyce index based on predicted probability of occupancy using each dispersal kernel. Also, proportion of records in cells with a predicted probability of occupancy of zero.

<u>Country</u>	<u>Threshold</u>	<u>AUC</u>	<u>Boyce</u>	Proportion of records
France	0.5	0.86	0.91	0.05
Italy	0.72	0.93	0.89	0
Spain	0.59	0.97	0.95	0.005



Figure A8: Visualisation of predicted colonised cells after running best preforming 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. Maps show the percentage of simulations in which each cell was predicted to be occupied and open black circles are all records in following years.



Figure A9: Dispersal kernels that best describe the distribution of V. v. nigrithorax *in France, Italy and Spain.*



Figure A10: Results from evaluation of best preforming 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 A11: Results of the evaluation of the V.v. nigrithorax Belgium spread model with Boyce Index showing change predicted/expected ratio across environmental suitability values.

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