The potential of species distribution modelling for reintroduction projects : the case study of the Chequered Skipper in England

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Title

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Running title

Modelling for reintroduction

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The potential of species distribution modelling for reintroduction projects: the case study of the Chequered Skipper in England

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Abstract

The Chequered Skipper *Carterocephalus palaemon* inhabits a variety of habitats in NW Europe: heathlands, wet grasslands and chalk grasslands, usually at woodland edges and wide rides and glades in different types of woodlands. It mainly uses broadleaved grasses such as *Molinia*, *Calamagrostis* and *Brachypodium* as host plants. The species became extinct in England in 1976 and an earlier reintroduction attempt in 1995-99 was unsuccessful. Using species distribution models, we located potential source regions in NW Europe for its reintroduction to England. To do so, we gathered distribution data of the butterfly and environmental variables (Corine Land Cover and climate data) from four regions in Belgium (Belgian Campine, Fagne-Famenne-Calestienne, Ardenne-Thiérache and Gaume-Lorraine), two in the Netherlands (Achterhoek and Dutch Campine) and one in the United Kingdom (Argyll, Scotland). We calibrated the models in these regions and projected them to the Rockingham Forest landscape, the reintroduction site in England. The Fagne-Famenne-Calestienne and the Gaume-Lorraine model resulted in the highest average probability when projected to the Rockingham Forest landscape. Based on additional expert knowledge on potential host plant abundance and the presence of large source populations, the Fagne-Famenne-Calestienne was selected as the source region for the reintroduction of the Chequered Skipper to England. To assess the possible impact of climate change, we also built a model with present-day climate data in NW Europe and modelled the probability of occurrence in the Rockingham Forest landscape in the year 2070. The species was predicted to increase in the Rockingham Forest landscape under future climate conditions.

Introduction

Species are going extinct at a much faster pace than ever before, both at the global and at the regional scale (Thomas et al. 2004b). Several, often interacting drivers are at the origin of these declines such as habitat loss and fragmentation (Krauss et al. 2010), habitat quality loss through a degrading environmental quality (e.g. increased nitrogen deposition – Mortelliti et al. 2010; WallisDeVries and van Swaay 2017), a lack of appropriate management (New et al. 1995) and/or climate change causing species range shifts that can lead to local extinctions (Travis 2003; Thomas et al. 2004a). Anthropogenic pressures such as intensive agriculture and forestry and industrial pollution, together with urban expansion have brought many species to the brink of extinction, especially in highly industrialised regions (Maes and Van Dyck 2001; Konvička et al. 2006; van Strien et al. 2019). Sedentary species in particular are suffering from a decline in habitat quality (Thomas et al. 2001) and increased fragmentation of metapopulations, which prevent recolonisations (Hanski 1999). When distances between populations or to potentially suitable locations become greater than the dispersal capacity of the species, genetic exchange and natural colonisation is less likely or even impossible (Fahrig and Merriam 1994). In such cases, reintroducing individuals from a sufficiently large source population is often the only solution for its conservation (e.g. Seddon et al. 2007; Chauvenet et al. 2013). Due to habitat fragmentation and changing climatic conditions, species are not always able to track their optimal climatic niche and, therefore, translocation of individuals to climatically suitable areas ("assisted migration/colonisation") can be applied as a species conservation measure (e.g. McLachlan et al. 2007; Willis et al. 2009; Thomas 2011).

Although species distribution models are increasingly used in conservation biology (Hodgson et al. 2009; Guisan et al. 2013; Wood et al.), their applicability is still strongly underestimated (Tulloch et al. 2016). With more and more environmental data available (e.g. land use, climate, soil) at increasingly higher resolutions (e.g. through remote sensing), species distribution modelling is now able to predict potential species occurrences at increasingly finer scales (Ciuti et al.). One of the more recent applications of species distribution modelling is to predict potentially suitable localities for the reintroduction or translocation of species in or to a focal region (e.g. Martinez-Meyer et al. 2006; Anderson et al. 2009; Kalle et al. 2017; Brooker et al.). By using relevant, often broad-scaled variables (land use and climate) in sites where the species is still present, species distribution modelling can explain why they went extinct in certain regions and/or which areas have the highest probability of occurrence in sites that are beyond their dispersal capacities (Hijmans and Graham 2006). One of the limiting factors in species distribution modelling, however, is that important small-scale variables (e.g. microclimate, host plant abundance and condition, level of the ground water table) are usually not available on larger scales (e.g. countries, continents) and cannot be included in such models (IUCN/SSC 2013). Therefore, local expert knowledge about the focal species and its local habitat use are an important additional source of information to decide where to get source individuals from and where to select the reintroduction sites (White et al. 2015).

Butterfly conservation has a long history in the United Kingdom (Heath et al. 1984). With only four out of the 62 resident and regularly breeding butterfly species being classified as Regionally Extinct (i.e. Black-veined White *Aporia crataegi*, Large Copper *Lycaena dispar*, Mazarine Blue *Cyaniris semiargus* and Large Tortoiseshell *Nymphalis polychloros*), the UK has one of the lowest proportions of extinct butterflies among European countries (Fox et al. 2011; Maes et al. 2019). Part of the success of butterfly conservation in the UK can be attributed to reintroduction projects, although not all of them were equally successful (Oates and Warren 1990; Schultz et al. 2008). One of the best known and most successful reintroductions in the United Kingdom is that of the Large Blue *Phengaris arion* (LINNAEUS 1758), a myrmecophilous butterfly that went extinct in 1979, but is now present in several populations in southern England (Thomas et al. 2009). A few years earlier (1976), another butterfly also became extinct in England: the Chequered Skipper *Carterocephalus palaemon* (PALLAS 1771) and the re-introduction of the Chequered Skipper to England was a long held conservation priority for Butterfly Conservation. Studies suggest that single and/or small populations of specialist, rare or endangered butterflies rarely survive longer than a few decades and that metapopulations are needed for the sustainable conservation of such species (e.g. Hanski et al. 1994 ; Harrison et al. 1988; León-Cortés et al. 2003; Thomas and Hanski 1997). The successful application of this metapopulation theory to landscape-scale approaches for the conservation of butterflies and moths (e.g. Small Pearl-bordered Fritillary *Boloria selene* ([DENIS & SCHIFFERMÜLLER], 1775), Duke of Burgundy *Hamearis lucina* (LINNAEUS, 1758) – Ellis et al. 2011) suggested that reintroductions to multiple sites were more likely to succeed than single-site reintroductions. Therefore, Butterfly Conservation aims at reintroducing the Chequered Skipper to several sites within a landscape comprising networks of well-connected woodlands supporting patches of high quality habitat, with the objective of establishing a functional metapopulation. From a genetic point of view, there is no indication that Scottish or Belgian populations of the Chequered Skipper differed from the extinct populations in England. Instead, populations in NW Europe (Belgium, England and Scotland) and southern Scandinavia (Norway) all come from the same post-glacial colonisation route and can, therefore, be regarded as belonging to a similar gene-pool (Joyce and Pullin 2004).

Here, we first apply species distribution modelling using land cover variables in seven regions in Belgium, the Netherlands and Scotland to locate the region that is most suitable as a source for the reintroduction of the Chequered Skipper to the Rockingham Forest landscape in England. Secondly, we use additional ecological knowledge of local experts on host plant use, microclimate and habitat management to determine and confirm the most suitable source region for the reintroduction of the Chequered Skipper to England. Finally, to assess how climate change will affect the suitability for the butterfly in the Rockingham Forest landscape, we also calibrated a climate change model for the whole of NW Europe and projected it to the Rockingham Forest landscape to see how the modelled occurrence probability would change in the future.

Methods

Study species

The Chequered Skipper *Carterocephalus palaemon* (Pallas 1771) is a small brown and yellow butterfly that flies from early May to late June in a variety of biotopes: woodland rides and glades, damp grasslands or heathlands, fens and calcareous grasslands at woodland edges (Bink 1992; Ravenscroft 1994b). Its distribution area ranges from Scotland in the west to Japan in the east and from northern Spain in the south to northern Norway in the north (Bink 1992). The species also occurs in Canada and the United States, where it is known as the Arctic Skipper (Bird et al. 1995). The Chequered Skipper uses a variety of host plants, mostly occurring on certain soil types in each of the regions: Purple Moor-grass *Molinia caerulea* and *Calamagrostis canescens* are the main host plants on sandy and/or acid soils (with the highest abundances in the Campine, Ardenne-Thiérache, Gaume-Lorraine (Belgium), Achterhoek, Campine (Netherlands) and Argyll (Scotland), see below) and False Brome *Brachypodium sylvaticum* and/or Tor-grass *B. pinnatum* on loamy and calcareous soils (with the highest abundances in the Fagne-Famenne-Calestienne region – Lambinon et al. 1998; FLORON 2011; Preston et al. 2002; Ravenscroft and Warren 1992; Van Landuyt et al. 2006)). In the former English populations, the two *Brachypodium* spp. were believed to be the main host plants (Emmet and Heath 1989). Other broad-leaved grasses such as Wood Small-reed *Calamagrostis epigejos*, Purple Small-reed *C. canescens*, Reed Canary Grass *Phalaris arundinacea*, Meadow Foxtail *Alopecurus pratensis*, Giant Fescue *Festuca gigantica*, Meadow fescue *F. pratensis* and Yorkshire Fog Grass *Holcus lanatus* have been reported as host plants as well (Bink 1992; Moore 2004).

The Chequered Skipper is classified as Endangered in the United Kingdom (Fox et al. 2011), Near Threatened in Flanders (northern Belgium; Maes et al. 2012), Least Concern in Wallonia (southern Belgium; Fichefet et al. 2008) and Vulnerable in the Netherlands (Bos et al. 2006). On a European scale, however, the species is of Least Concern (van Swaay et al. 2010).

The Chequered Skipper was first recorded in England in 1798 and was quite common in woodlands of the East Midlands (mainly Bedfordshire, Cambridgeshire, Huntingdonshire, Lincolnshire and Northamptonshire) until the 1960s. Old records are also known from other parts of England, such as Dartmoor and possibly the Lake District (Figure 1 – Collier 1986; Farrell 1973). Its decline was gradual and hardly noticed but its extinction was sudden. There were about 80 known sites at the beginning of the 1900s, 20 in the 1960s, but only six in 1971 before extinction in 1976 (Ravenscroft 1995). It seems probable that a combination of factors was responsible for its strong decline. Abandoning coppicing practices and associated ride maintenance would have increased shade levels in open space habitat and excluded the species from woodlands (Collier 1986; Warren 1990). Furthermore, the delayed effects of myxomatosis, reducing Rabbit *Oryctolagus cuniculus* numbers and grazing pressure would have resulted in coarse grassland scrubbing over (cf. Thomas and Jones 1993), despite initially improving the habitat for *C. palaemon* (Ravenscroft 1995). Other factors, e.g. the destruction of marginal habitats around woodland, such as hedgerows, may have contributed to the increased isolation of habitats (Ravenscroft 1995). A previous attempt to reintroduce the species in the Bardney Limewoods landscape in Lincolnshire in 1995-99 using individuals from northern France (Forêt de Spincourt, Villecloye, Bois de Rafour, Forêt d'Argonne) and southern Belgium (Chantemelle) failed to establish a viable population due to the lack of sufficient high quality habitat within the whole woodland complex (Warren 1995; Moore 2004).

The reintroduction site: the Rockingham Forest landscape

The Rockingham Forest landscape (Northamptonshire and Cambridgeshire) was the last stronghold of the Chequered Skipper in England (Figure 1; Asher et al. 2001), which was one of the reasons to select it as the reintroduction site. The Rockingham Forest landscape is large (>500 km²) and the amount of suitable habitat for the species (78 km²) was strongly increased by species-specific management measures (in collaboration with the woodland owners). Key practices such as widening the woodland rides to 20-30 m and rotational ride mowing to both provide sufficient nectaring plants during the flight season of the adult butterflies, as well as prevent the grassy margin breeding habitat from becoming scrubbed over. The Rockingham

Forest landscape was also selected because it holds at least 30 potentially suitable woodlands within the dispersal capacity of the Chequered Skipper (Ravenscroft 1994a) , although their ability to support the species is strongly dependent on appropriate habitat restoration.

Species distribution modelling

To model the Chequered Skipper's distribution, we first compiled all available distribution data in NW Europe. We restricted our analysis to Belgium, the Netherlands and Scotland because distribution data were readily available here. Other possible source locations might be present in the north of France, but extensive distribution data were not available from this region. In NW Europe, the Chequered Skipper occurs in four ecological regions in Belgium (Belgian Campine, Ardenne-Thiérache, Fagne-Famenne-Calestienne and Gaume-Lorraine), two in the Netherlands (Achterhoek, Dutch Campine) and one in the United Kingdom (Argyll, Scotland – Figure 1). To compile the calibration data sets for the different ecological regions, we attributed every observation of the Chequered Skipper to a 1 x 1 km^2 grid cell of the European Universal Transverse Mercator (UTM) projection (Table 1a). Observations were obtained from www.waarnemingen.be and the butterfly database of l'Observatoire de la Faune, de la Flore et des Habitats (OFFH) (Belgium), www.waarnemingen.nl and the National Database Flora and Fauna (the Netherlands) and Butterfly Conservation UK (Scotland). Subsequently, for each region, we added a similar number of absences using the best-surveyed grid cells in each ecological region (i.e. grid cells with a minimum number of observed butterfly species, depending on the ecological region, without observations of the Chequered Skipper during the flight period). As environmental variables, we used data from the Corine Land Cover 2012 Version 18.5.1 (http://land.copernicus.eu/pan-european/corine-land-cover/clc-2012). We reduced the Corine Land Cover variables to eleven land cover types (Table 1). For normality, these variables were square root-transformed prior to analysis.

For modelling, we used quadratic Generalised Linear Models (GLM - McCullagh and Nelder 1989) with one interaction level. We used the Akaike Information Criterion (AIC) for variable selection in the Biomod2 package (Thuiller et al. 2009; Thuiller et al. 2012). For each ecological region in which the Chequered Skipper occurs in NW Europe, we applied a separate species distribution model. Per region, we did 20 model runs with a random split in 70% calibration and 30% evaluation. Models were evaluated using the Area under the Curve (AUC) of the Receiver Operating Characteristic (ROC) and models with an AUC ≥ 0.7 were considered acceptable (Huang and Ling 2005; Swets 1988). The average variable importance was obtained by averaging the variable importance of the 20 randomised models in each region. To obtain a final probability per grid cell in each ecological region, we applied ensemble forecasting (Araújo and New 2007) for which only models with an AUC ≥ 0.7 were used in all regions, except in Fagne-Famenne-Calestienne where, due to poorer performance of the models, we used AUC ≥ 0.6. To test the performance of each model projected to its own (calibration) region but also in the six other regions, we used the pROC package (Robin et al. 2011). The latter test was done using grid cells in each of the ecological regions in which at least 10 species were observed. To test for differences between each of the projected probabilities among the seven source regions to the introduction site (the Rockingham Forest landscape), we applied a TukeyHSD post-hoc comparison test using the multcomp package (Hothorn et al. 2008) in R (R Core Team 2018).

In addition to the habitat suitability, we also projected the future climatic suitability of the reintroduction site. Since the seven ecological regions are relatively small (ranging from 935 km² in the Gaume-Lorraine region in Belgium to about 6,000 km² in the Argyll region in Scotland) leading to very restricted ranges of the climate variables, it is not appropriate to include climate variables in each region separately and projecting the outcome of the models to the other regions (Barbet-Massin et al. 2010; Synes and Osborne 2011; Titeux et al. 2017). Therefore, we built a climate model with the data from all seven ecological regions together (Belgium, the Netherlands and the United Kingdom) and projected it to the Rockingham Forest landscape for the present (i.e., the year 2000) and future climate (i.e., the year 2070). This resulted in a wider variation in the calibration set. Apart from land cover variables, we added two climate variables from the WordClim database (Hijmans et al. 2005) to the climate change model: the temperature (Bioclim variable 10) and precipitation of the warmest quarter (Bioclim variable 18 - Table 1b). We used these variables because they potentially have the highest impact on host plant quality with higher temperatures and lower precipitation leading to drought and thus a lower host plant quality (Ravenscroft 1994a). As a possible future climate scenario, we used the CCSM3 scenario (Hijmans et al. 2005). To test for differences between present and future projected probabilities in the Rockingham Forest landscape in the climate change model, we used an analysis of variance model (Chambers et al. 1992).

Results

With an average AUC ranging from 0.790-0.845, most of the calibrated models performed well when projected to their own region. Only the Fagne-Famenne-Calestienne model performed relatively poorly (average AUC = 0.655; Table 2). When projected to other regions, however, the average AUC was usually lower (Table 2). The most important land cover variables that explained the distribution of the Chequered Skipper were the three different woodland types (coniferous, deciduous and mixed woodland) and heathland, which coincides with its biotope preferences (Table 3).

The models calibrated in the Fagne-Famenne-Calestienne and the Gaume-Lorraine region in Belgium resulted in the highest average probability in the Rockingham Forest landscape, but as mentioned earlier, the Fagne-Famenne-Calestienne model performed rather poorly. A post-hoc comparison did not show significant differences between these two models, but both were significantly better than all the other models (Figure 2). The projections of the seven different models to the full area of Belgium, the Netherlands and the UK are given in Supplementary Material S1.

Climate change was predicted to have a negative effect on the distribution of the Chequered Skipper in all the seven present-day regions in NW Europe ranging from predicted declines of 38% in the Dutch Campine region (Netherlands) to 68% in the Gaume-Lorraine region in the south of Belgium (Table 4). When projected to the Rockingham Forest landscape, however, probabilities were predicted to increase significantly (+155%) by 2070 compared to the year 2000 (Figure 3).

Discussion

The use of species distribution modelling in addition to detailed local ecological knowledge about the Chequered Skipper and its habitat, allowed us to select the most suitable potential source region for the reintroduction of the Chequered Skipper to the Rockingham Forest landscape in England. The models calibrated in the Fagne-Famenne-Calestienne region and in the Gaume-Lorraine region both resulted in the highest average occurrence probability in the reintroduction site, but the former was selected based on additional expert knowledge about the host plant and habitat similarity between the source region and the reintroduction site. Climate change models for 2070 predicted a decrease of the species in NW Europe, but a strong increase in the Rockingham Forest landscape.

Why a reintroduction in the Rockingham Forest landscape?

The Chequered Skipper is considered a High Priority species for Butterfly Conservation in the UK, particularly within Scotland, where its last remaining populations reside (40 grid squares of 10 x 10 km^2 during the period 2010-2014). It is also included on the Scottish Biodiversity List (species considered of principal importance for biodiversity conservation). Since 1976, its distribution in Scotland has declined by 44% and it is, therefore, considered as threatened in the UK (Fox et al. 2011). Re-establishing a metapopulation in England would represent a significant step forward in increasing the resilience and strengthening the status of the Chequered Skipper in the UK. For this purpose, the Rockingham Forest landscape provides a suitable landscape to establish a local metapopulation of the species either by natural colonisation or by targeted additional reintroductions (cf. Thomas et al. 2009).

Previous management measures for the reintroduction of the Chequered Skipper to the Rockingham Forest landscape will benefit a wide variety of other priority butterflies such as the Dingy Skipper *Erynnis tages* (LINNAEUS, 1758), the Grizzled Skipper *Pyrgus malvae* (LINNAEUS, 1758), the Wood White *Leptidea sinapis* (LINNAEUS, 1758), the White Admiral *Limenitis camilla* (LINNAEUS, 1764) and the White-letter Hairstreak *Satyrium w-album* (KNOCH, 1782). Apart from butterflies, other species groups such as moths (e.g. Concolorous *Chortodes extrema* (HÜBNER, 1809) and Liquorice Piercer *Grapholita pallifrontana* (LIENIG & ZELLER, 1846)), plants (e.g. Basil Thyme *Clinopodium acinos* (L.) KUNTZE), bats (e.g. Brown Long-eared bat *Plecotus auritus* (LINNAEUS, 1758)) and reptiles (e.g. Adder *Vipera berus* (LINNAEUS, 1758)) that are also associated with high quality woodlands will also benefit from the woodland management instigated for this reintroduction (https://naturebftb.co.uk/the-projects/roots-of-rockingham/). The Chequered Skipper may represent a flagship species for additional habitat improvements to the woodlands in the Rockingham Forest landscape initially and to other potential suitable areas in the future. The species distribution models from the different possible source regions in NW Europe could also be used to estimate the potential suitability of other historic strongholds such as Willingham Woods, Market Rasen or Bardney Limewoods (the site where the previous reintroduction attempt was carried out – Supplementary Material S1).

Suitability of the source regions and additional ecological resources

The Fagne-Famenne-Calestienne and the Gaume-Lorraine models resulted in the highest predicted probabilities in the Rockingham Forest landscape and, therefore, appeared to be the most suitable source regions for the reintroduction of the Chequered Skipper in England. An additional consideration for the choice of the source region was host plant distribution. This is an important factor, but was not included in the models, because suitable host plants are present almost everywhere, albeit in very different abundances. The lack of detailed data on their local abundance and quality made it impossible to consider this variable in the models. In the Netherlands and in most regions in Belgium, including Gaume-Lorraine, *Molinia caerulea* and *Calamagrostis canescens* are the primary host plants (Ravenscroft 1994a). Meanwhile, in the Fagne-Famenne-Calestienne region *Brachypodium* spp. are widespread host plants, notably in an extensive network of forest rides and glades which were widened in the framework of a EU Life+ project ("Butterfly Life project", LIFE07NAT/B/000039 - http://www.life-papillons.eu). The Chequered Skipper is probably flexible enough to use the locally available broad-leaved grasses since it is known to accept a wide range of grasses when bred in captivity (Bink 1992; Ravenscroft 1994c). Nevertheless, we conclude from the combination of the species distribution modelling, the similarity in host plant abundance and the availability of large populations of the Chequered Skipper that the Fagne-Famenne-Calestienne region is the most suitable source region. Whether individuals from within the UK, i.e. Argyll (where its main host plant is *Molinia caerulea* – Ravenscroft 1994a) could strengthen the reintroduced population in the Rockingham Forest landscape (where *Brachypodium* spp. are the main host plants) at a later date remains to be studied, although on the basis of the results presented in this paper it is not recommended. This could be experimentally tested by offering *Brachypodium* spp. to females from a *Molinia* population and vice versa and test for acceptance of the host plant (Moore 2004) and for caterpillar survival rate on the host plant. Other important factors for which high resolution data were lacking are, for example, microclimate and water regime of the soil, two major environmental conditions that determine the quality of the host plant (Ravenscroft 1994a; Ravenscroft 1994b).

Genetic diversity and potential impact risk on source populations are two crucial issues in re-introduction projects. According to the data available (from the Lycaena Working Group) and thanks to the Butterfly Life+ project restorations, the forest populations of Fagne-Famenne-Calestienne are now better connected than the ones from the Gaume-Lorraine region. Genetic diversity could, therefore, be larger and the impact risk on source populations lower by sampling individuals from the Fagne-Famenne-Calestienne region (cf. Weeks et al. 2011). This assumption, however, remains to be tested as a possible follow-up project of the reintroduction. To increase genetic diversity in the introduced population in England, we suggest not to restrict the collection of individuals to a single source site, but to collect them from a number of preferably large populations. After the initial reintroduction, restocking is often needed after the first year of establishment to keep the number of individuals in the introduced population sufficiently high (Fischer and Lindenmayer 2000). This also enables individuals to spread to potentially suitable habitats in the vicinity to create a sustainable metapopulation (Hanski et al. 1994; León-Cortés et al. 2003).

Model performance

Apart from the Fagne-Famenne-Calestienne model, all species distribution models performed relatively well when projected to their own region (Table 2). The Fagne-Famenne-Calestienne is an ecological region with a mixture of soil types (limestone, peat, clay and schist), which makes it difficult for a statistical model to calibrate correctly. Building separate models for the Fagne, the Famenne (clay and schist) and the Calestienne (limestone) regions, however, would lead to a too low number of presences to run the models appropriately. Adjacent regions in the north of France could probably also be suitable as source regions (they were used in the 1990s reintroduction), but we did not have access to detailed distribution data of the Chequered Skipper to test how northern France would perform as a potential source region.

As variables in the species distribution models, we used CORINE land cover data instead of national land cover maps of the three countries. CORINE has the advantage that it covers the whole of Europe using the same biotope types, although countries sometimes have different interpretations of these biotopes (Garcia-Alvarez and Olmedo 2017). When using national land cover maps, if at all available, it would have been difficult to transform the different national land cover categories into uniform biotopes for the four countries. The fact that different woodland types and heathlands were selected as the most important variables in most of the models (Table 3) corresponds well with the species' ecology. These broad *biotopes* give an indication of the suitability of a region on a landscape-scale, but additional detailed information on species-specific ecological resources is needed to determine whether the woodlands in the high probability grid cells indeed contain suitable *habitats* for the Chequered Skipper (e.g. wide rides, sufficient host and nectar plants, high water table for optimal host plant quality, etc. – cf. Vanreusel and Van Dyck 2007).

As shown in Table 2, model performance was always highest when projected to the region in which the model was calibrated. When transferred to other regions, model performance decreased considerably. Transferability of species distribution models to other regions is usually better when the source and the receiver regions are more similar in the variables used for calibration (Randin et al. 2006; Vanreusel et al. 2007). Although there are differences among the ecological regions to calibrate the models on the one hand and the Rockingham Forest landscape on the other, they were sufficiently comparable to assume that models were transferable among regions (Table 1).

Climate change

Given the fact that climate will become warmer and drier in the future, the climate change model predicts a relatively strong decline in species occurrence probability in NW European regions under future climate conditions (Table 4), which agrees with the predictions by Settele et al. (2008). Translocation of species to climatically suitable areas is, therefore, a conservation measure that has been increasingly advocated (cf. Thomas 2011). The Chequered Skipper is a species of humid and relatively cool climates (Ravenscroft 1994b) for which future climates in lowland regions are predicted to become less suitable in the future. The Ardenne-Thiérache and the Argyll regions are at present cooler than the Rockingham Forest landscape. Nonetheless, the combination of a predicted moderate temperature rise and the strong predicted increase in precipitation in both regions (in comparison with a modest predicted increase in the Rockingham Forest landscape - Table 4), might cause a potential strong decline in biotope suitability for the Chequered Skipper in NW Europe in the future.

Epilogue: the actual reintroduction

On 22-23 May 2018, 42 individuals of the Chequered Skippers (32 females and 10 males) were caught in five different populations in the Fagne-Famenne-Calestienne region in Belgium (Matagne-la-Grande, Doische, Hazalles, Petit-Han and Fronville). Butterfly Conservation and partners released them in the Rockingham forest landscape on 24 May 2018 as part of the Back from the Brink project.

Future prospects of the Chequered Skipper in England

By reintroducing the Chequered Skipper to the Rockingham Forest landscape, we hope to establish a viable metapopulation in its former national stronghold in England. Different reasons strengthen our assumption that this reintroduction can be successful:

1. The reintroduction of a genetically diverse initial population, coming from five different locations in the Fagne-Famenne-Calestienne region in Belgium, should prevent problems of inbreeding;
2. The conservation management to maintain and/or increase the suitability of the Rockingham Forest landscape and the number of potentially suitable habitat patches present for the Chequered Skipper is assured by several local partners, such as the Forestry Commission, the Wildlife Trust for Bedfordshire, Cambridgeshire & Northamptonshire and private landowners under the guidance of Butterfly Conservation UK;
3. Climate change is predicted to have a positive effect on the presence of the Chequered Skipper in the Rockingham Forest landscape. Since micro-climate and local water level conditions could not be used in the landscape-scale model, this result should be interpreted with care.

Conclusion

Based on species distribution modelling, the Fagne-Famenne-Calestienne and the Gaume-Lorraine appeared to be the best source regions for the reintroduction of the Chequered Skipper to England. Additional local expert knowledge about host plant use in the possible source regions and the abundance of host plants in the reintroduction site and the presence of large and well-connected forest populations of the target species, the Fagne-Famenne-Calestienne was recommend as the source region for the reintroduction to England. Reintroduction of the species in England will likely contribute to the overall persistence of the Chequered Skipper under future climate change.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All procedures performed involving animals were in accordance with the ethical standards of the Disease Risk Management and Post-Release Health Surveillance.

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Table 1a Land cover variables used and average area (in ha) per grid cell in the different regions. Only grid cells >50% land are used. Belgium: CB = Campine, FFC = Fagne-Famenne-Calestienne, AT = Ardenne-Thiérache, GL = Gaume-Lorraine; the Netherlands: AH = Achterhoek, CN = Campine; United Kingdom: Ar = Argyll, RFL = Rockingham Forest landscape.

Country	Belgium				Netherlands		United Kingdom	
Ecological region	CB	FFC	AT	GL	AH	CN	Ar	RFL
Grid cells with *C. palaemon*	431	159	259	64	134	395	165	-
Agriculture	26.67	29.78	14.03	22.62	25.18	52.99	-	61.37
Coniferous woodland	9.22	1.04	15.98	2.55	5.27	12.24	14.33	0.73
Deciduous woodland	2.63	21.19	11.55	24.37	0.6	1.2	8.75	6.63
Grassland	6.31	0.23	4.1	-	7.46	0.42	14.73	-
Heathland	1.56	-	1.29	0.52	1.44	2.02	30.32	-
Marshes	0.41	0.02	7.35	9.88	2.58	9.66	-	-
Mixed woodland	5.48	16.31	27.08	10.95	4.1	3.68	1.58	2.95
Pasture	12.85	16.57	18.24	25.53	37.38	5.67	8.54	14.49
Agricultural grassland	9.69	5.91	4.51	5.93	16.23	3.6	0.36	-
Shrub	1.04	-	1.84	0.37	1.79	6.23	2.80	0.62
Water	1.16	0.44	0.11	-	0.1	0.43	3.79	0.41

Table 1b Average temperature (in °C) and mean precipitation (in mm) in the warmest quarter in 2000 and in 2070 for grid cells in which the Chequered Skipper is present since the year 2010 in the different regions and in the Rockingham Forest landscape (source for the CCSM3 climate model: Hijmans et al. 2005).

	Temperature			Precipitation		
	2000	2070	diff	2000	2070	diff
Campine (B)	16.61	18.27	+1.66 (10%)	210.82	207.18	-3.64 (2%)
Fagne-Famenne-Calestienne (B)	16.52	18.05	+1.53 (9%)	241.45	274.75	+33.3 (14%)
Ardenne-Thiérache (B)	14.77	16.32	+1.55 (10%)	269.80	309.26	+39.46 (15%)
Gaume-Lorraine (B)	16.24	17.78	+1.54 (9%)	238.43	268.98	+30.55 (13%)
Achterhoek (NL)	16.26	17.93	+1.67 (10%)	221.79	214.93	-6.86 (3%)
Campine (NL)	16.50	18.19	+1.69 (10%)	211.90	202.12	-9.78 (5%)
Argyll (UK)	14.05	16.16	+2.11 (15%)	333.31	364.75	+31.44 (9%)
Rockingham Forest landscape (UK)	16.03	17.89	+1.86 (12%)	159.78	164.52	+4.74 (3%)

Table 2 AUC per model projected to its own region (in bold) and to the other regions. Belgium: C = Campine, FFC = Fagne-Famenne-Calestienne, AT = Ardenne-Thiérache, GL = Gaume-Lorraine; the Netherlands: AH = Achterhoek, C = Campine; United Kingdom: Ar = Argyll.

Country	Belgium				Netherlands		United Kingdom
Model built in	AT	CB	FFC	GL	AH	CNL	Ar
From							
AT	**0.790**	0.646	0.598	0.718	0.650	0.691	0.734
CB	0.719	**0.845**	0.604	0.743	0.727	0.794	0.535
FFC	0.682	0.576	**0.655**	0.735	0.677	0.599	0.554
GL	0.679	0.734	0.574	**0.792**	0.615	0.677	0.608
AH	0.535	0.692	0.606	0.683	**0.836**	0.776	0.520
CNL	0.655	0.722	0.555	0.699	0.742	**0.838**	0.585
Ar	0.498	0.704	0.610	0.711	0.656	0.662	**0.776**

Table 3 Average variable importance in the calibration models in the different ecological regions. Variable importance > 0.100 that are positively correlated with the presence of the Chequered Skipper are given in bold. Belgium: C = Campine, FFC = Fagne-Famenne-Calestienne, AT = Ardenne-Thiérache, GL = Gaume-Lorraine; the Netherlands: AH = Achterhoek, C = Campine; United Kingdom: Ar = Argyll. #+ = number of times the variable had an importance above 0.1 and was positively correlated with the presence of the Chequered Skipper.

Country	Belgium				Netherlands		United Kingdom	
Variable	CB	FFC	AT	GL	AH	CNL	Ar	#+
Deciduous woodland	**0.151**	**0.304**	**0.117**	0.085	**0.192**	**0.199**	**0.562**	6
Coniferous woodland	**0.548**	0.091	0.003	**0.119**	**0.452**	**0.683**	**0.296**	5
Mixed woodland	**0.329**	**0.120**	0.003	**0.139**	**0.507**	**0.244**	0.094	5
Heathland	**0.178**	0.069	**0.587**	0.099	**0.336**	**0.473**	0.049	4
Shrub	0.032	0.064	**0.158**	**0.166**	0.006	0.024	0.097	2
Marshes	0.093	0.022	0.012	**0.117**	0.003	0.037	-	1
Agricultural grassland	0.017	0.005	-	0.118	**0.464**	0.145	0.002	1
Agriculture	0.077	0.069	0.088	0.056	0.160	0.305	-	-
Grassland	0.002	0.210	-	-	-	0.077	**0.309**	-
Pasture	0.003	0.157	0.021	0.218	0.361	0.069	0.041	-
Water	0.051	0.011	0.011	-	0.003	0.044	-	-

Table 4 Average predicted probability (multiplied by 1000 for readability) in the years 2000 and 2070 in the grid cells in which the Chequered Skipper is actually present and in the Rockingham Forest landscape. Diff: difference in percentage compared to the year 2000 together with the significance of an ANOVA-test (+++ p<0.001, ++ p<0.01).

Region	2000	2070	Diff (in %)
Campine (B)	665 ± 8	382 ± 8	-43^{+++}
Fagne-Famenne-Calestienne (B)	443 ± 14	152 ± 5	-66^{+++}
Ardenne-Thiérache (B)	479 ± 11	217 ± 6	-55^{+++}
Gaume-Lorraine (B)	574 ± 23	182 ± 7	-68^{+++}
Achterhoek (NL)	496 ± 15	294 ± 11	-41^{+++}
Campine (NL)	625 ± 9	389 ± 8	-38^{+++}
Argyll (UK)	352 ± 13	163 ± 4	-54^{+++}
Rockingham Forest landscape (UK)	304 ± 3	776 ± 6	$+155^{++}$

Figures

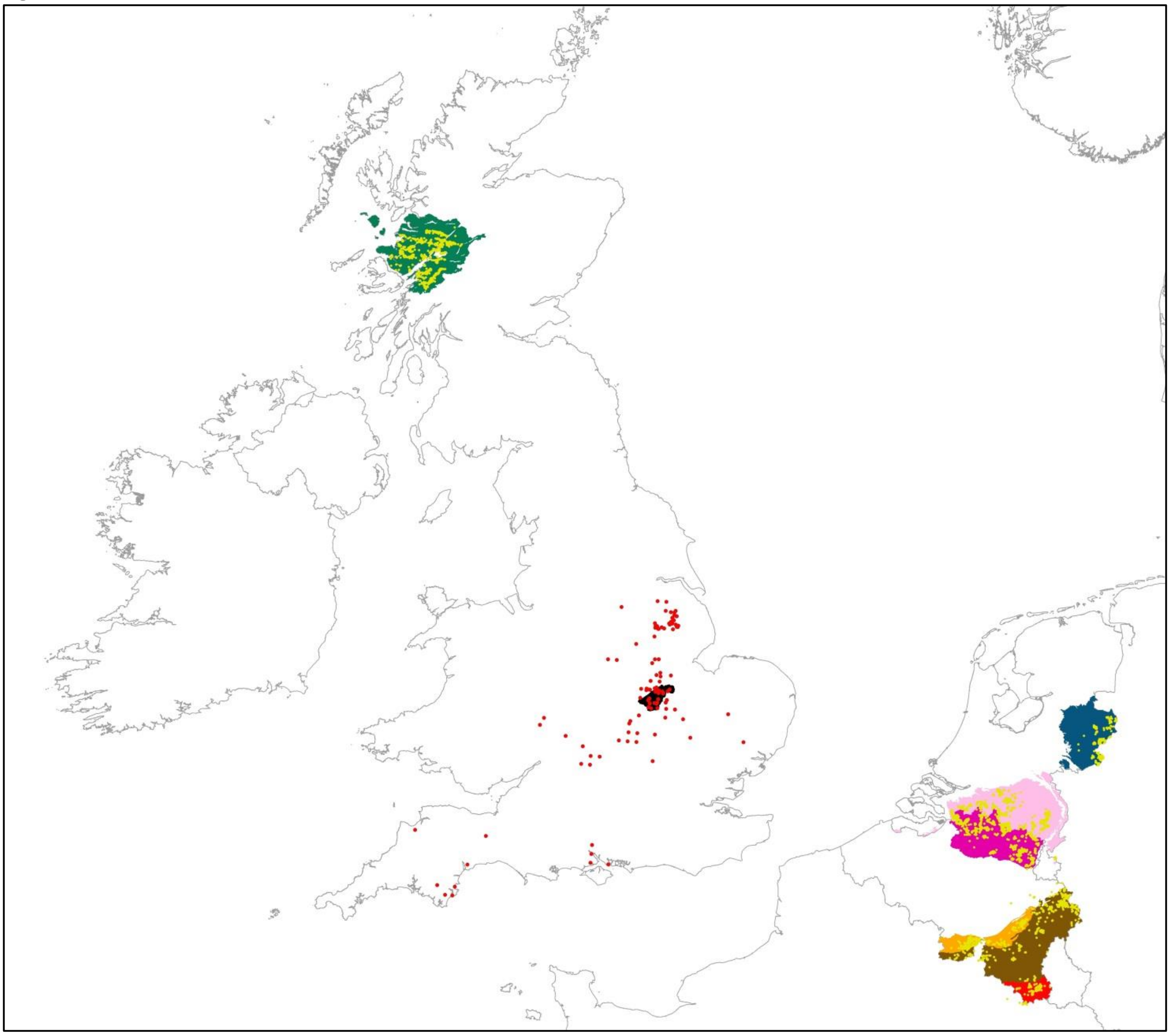


Figure 1 Ecological regions in the Netherlands (blue: Achterhoek, pink: Dutch Campine), Belgium (purple: Belgian Campine, orange: Fagne-Famenne-Calestienne, brown: Ardenne-Thiérache, red: Gaume-Lorraine) and the United Kingdom (dark green: Argyll, black: Rockingham Forest landscape). The actual observations of *Carterocephalus palaemon* in the different regions are shown in yellow; the historical records in England are shown in red.

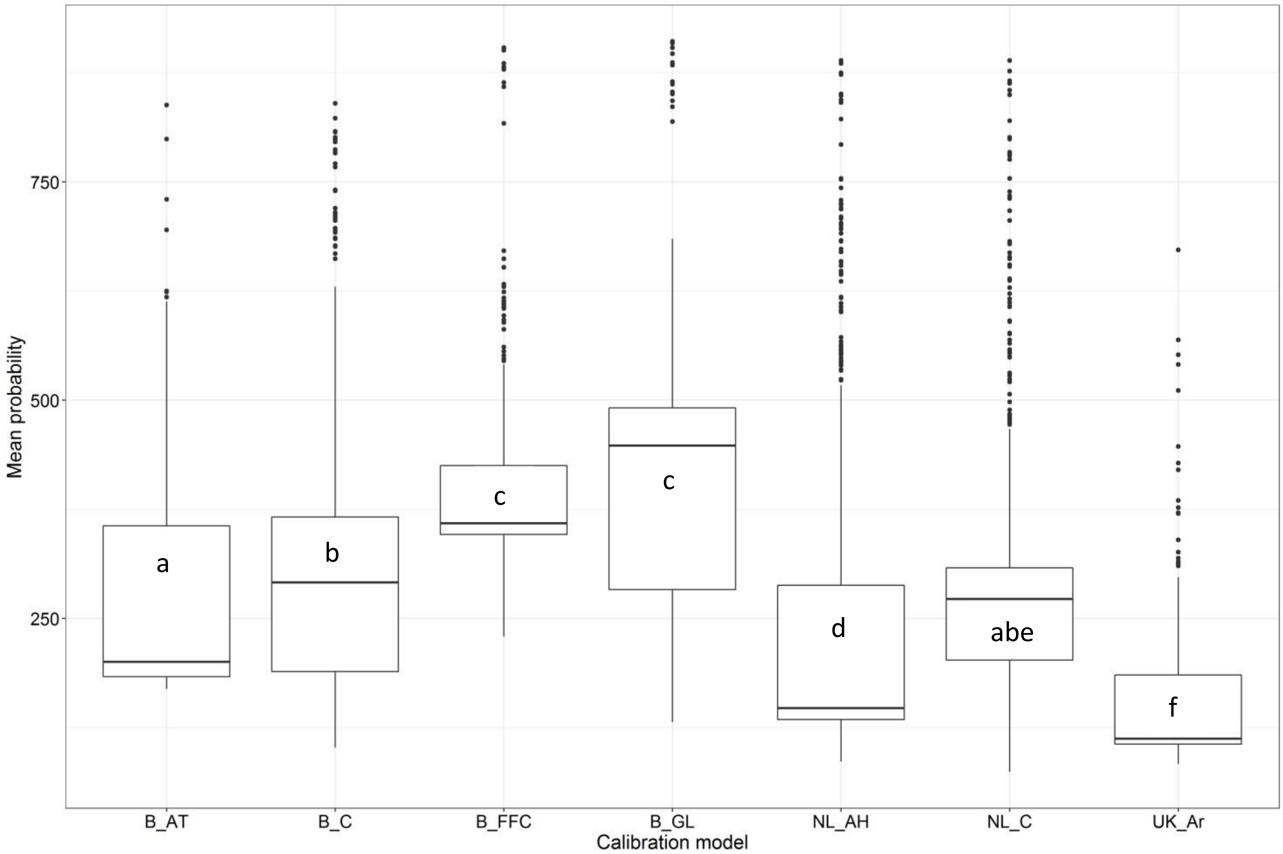


Figure 2 Median predicted probability (horizontal black bar, multiplied by 1,000 for readability) with the standard deviation (white box) (y-axis) in the Rockingham Forest landscape depending on the origin of the calibration data set (x-axis). B_AT = Ardenne-Thiérache (Belgium); B_C = Campine (Belgium); B_FFC = Fagne-Famenne-Calestienne (Belgium); B_GL = Gaume-Lorraine (Belgium); NL_AH = Achterhoek (Netherlands); NL_C = Campine (Netherlands); Ar = Argyll (United Kingdom). Different letters indicate significant differences between the probabilities from the different models when projected to the Rockingham Forest landscape.

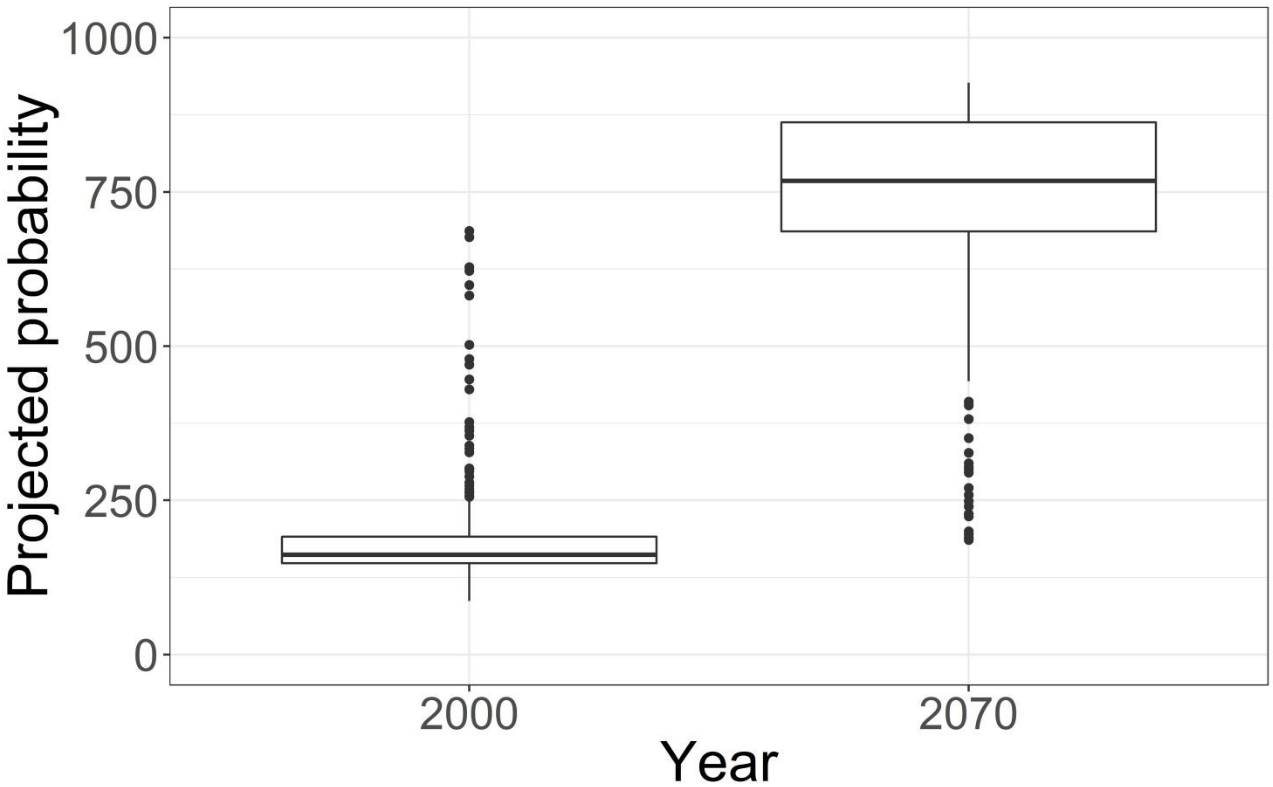
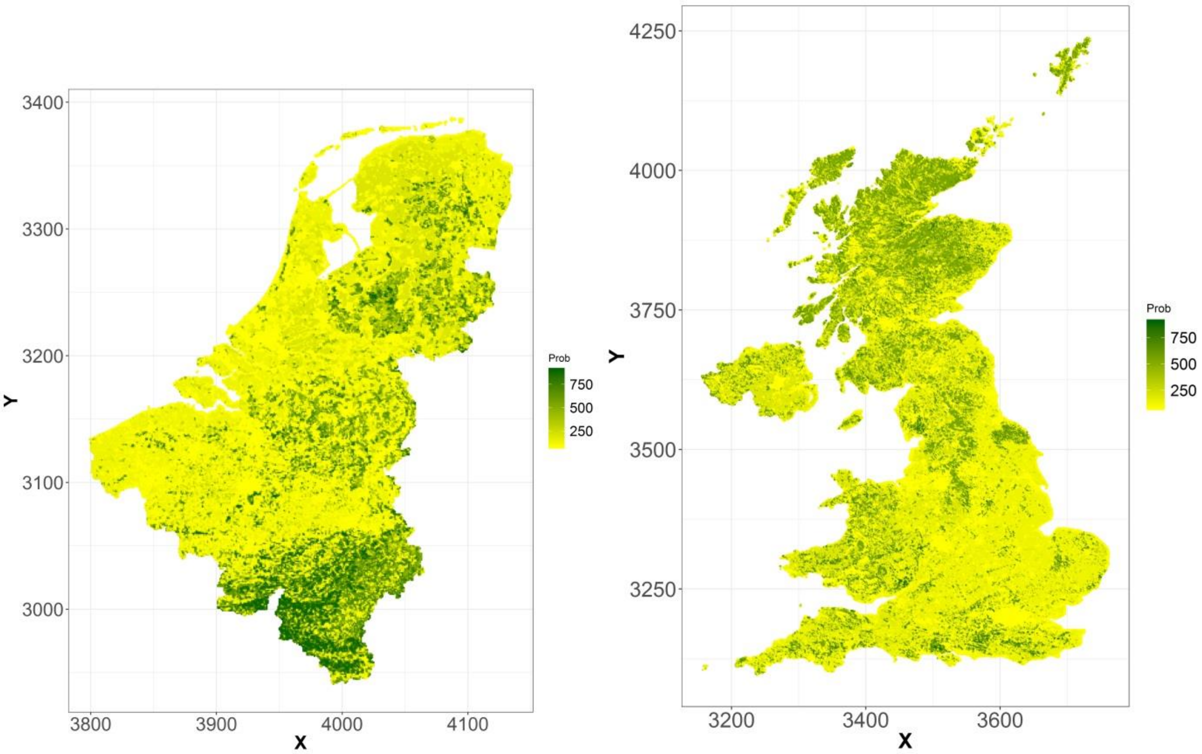


Figure 3 Median projected probability (horizontal black bar, multiplied by 1,000 for readability) with the standard deviation (white box) in the Rockingham Forest landscape under present (2000) and future climate conditions (2070). Results of the statistical analyses are given in Table 4.

Supplementary Material S1



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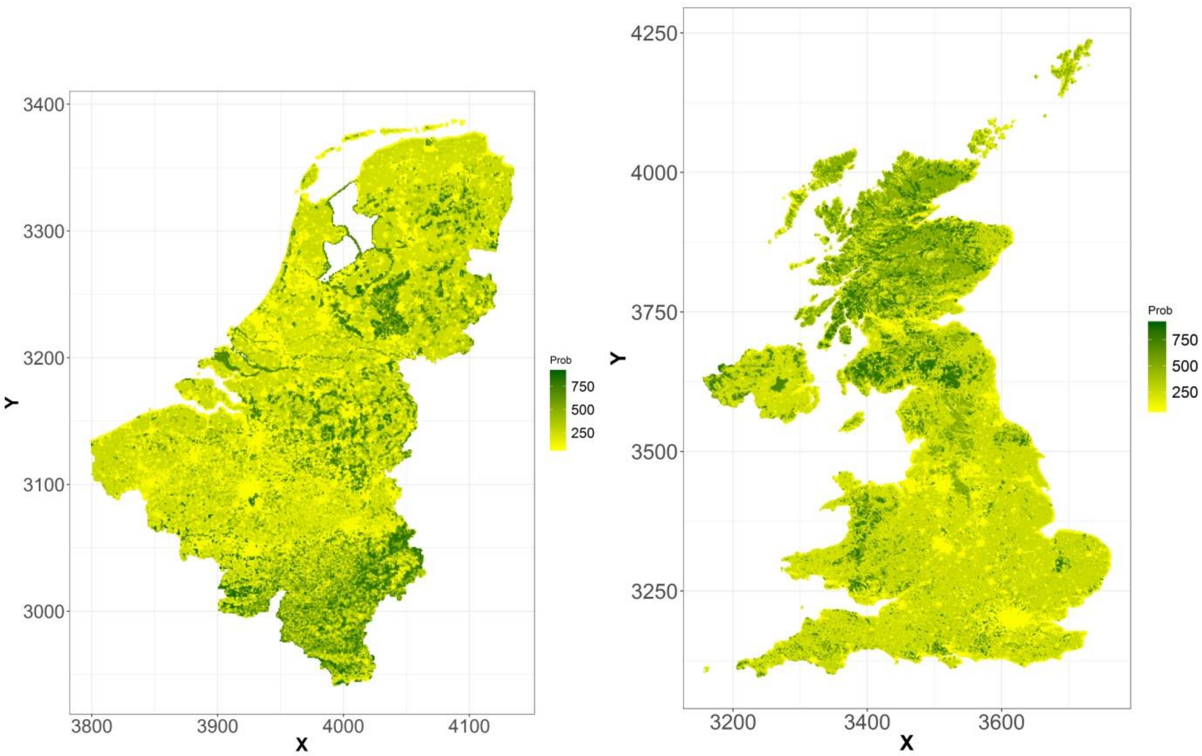

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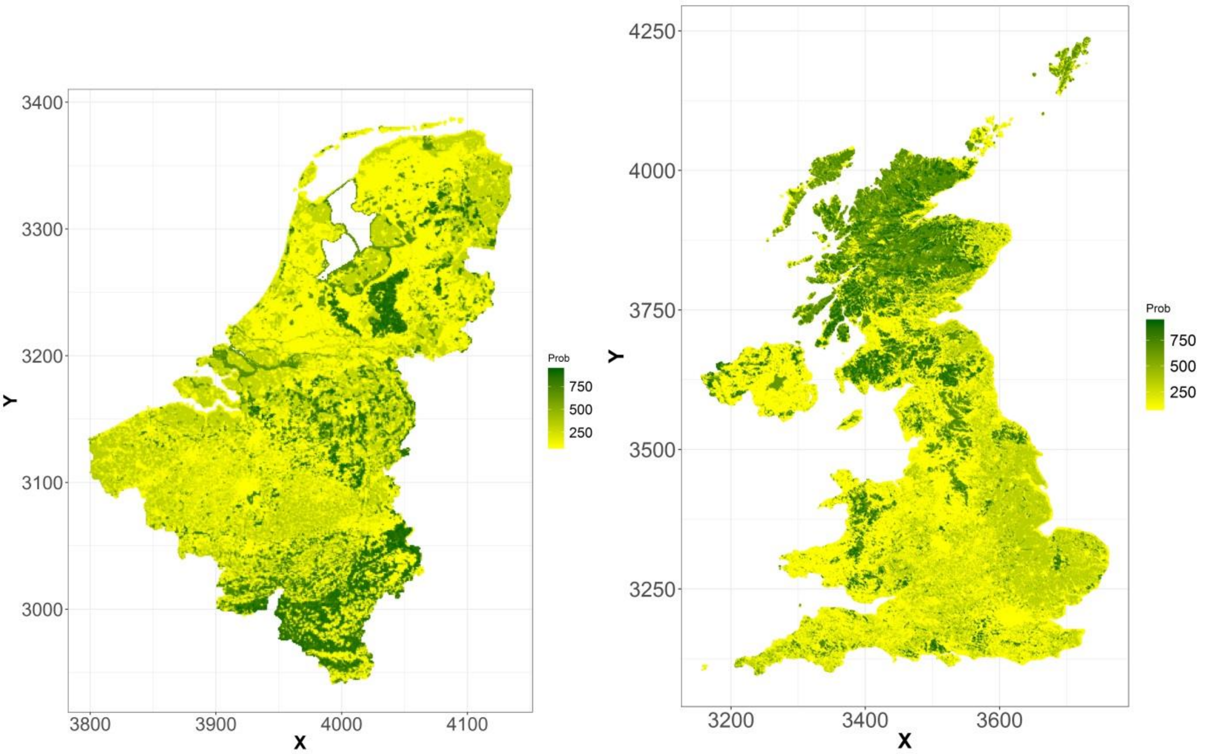

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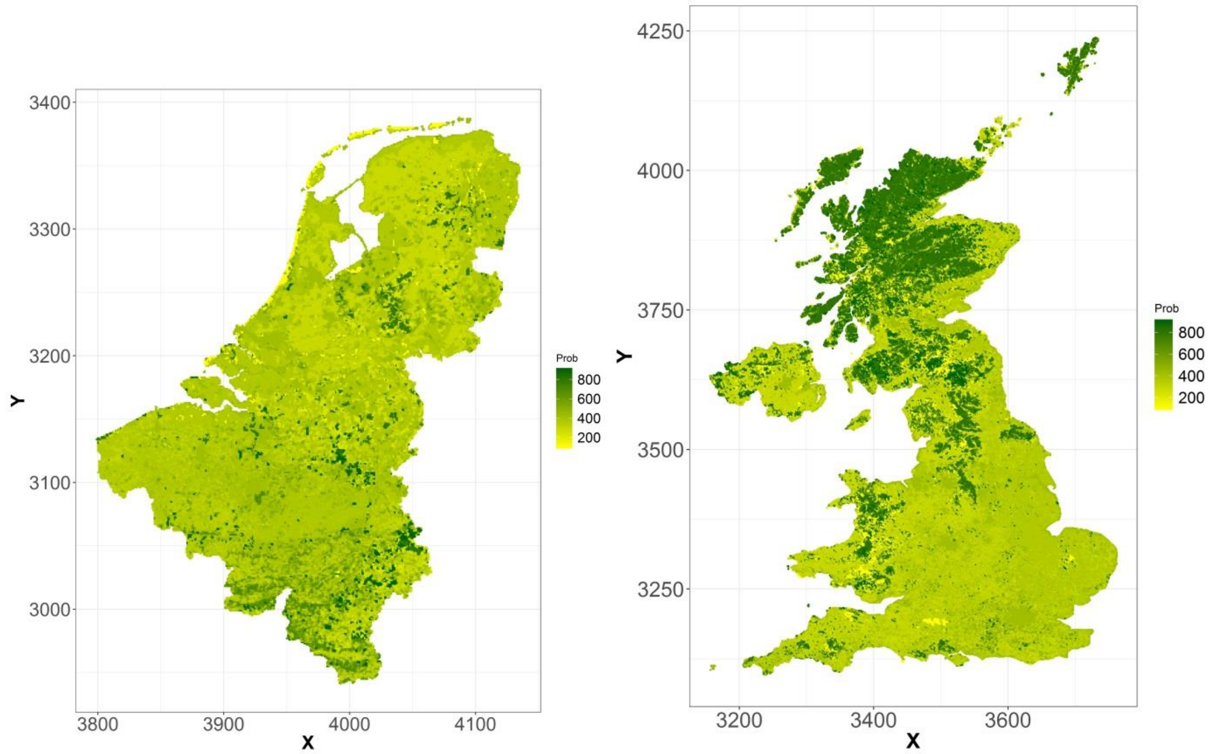

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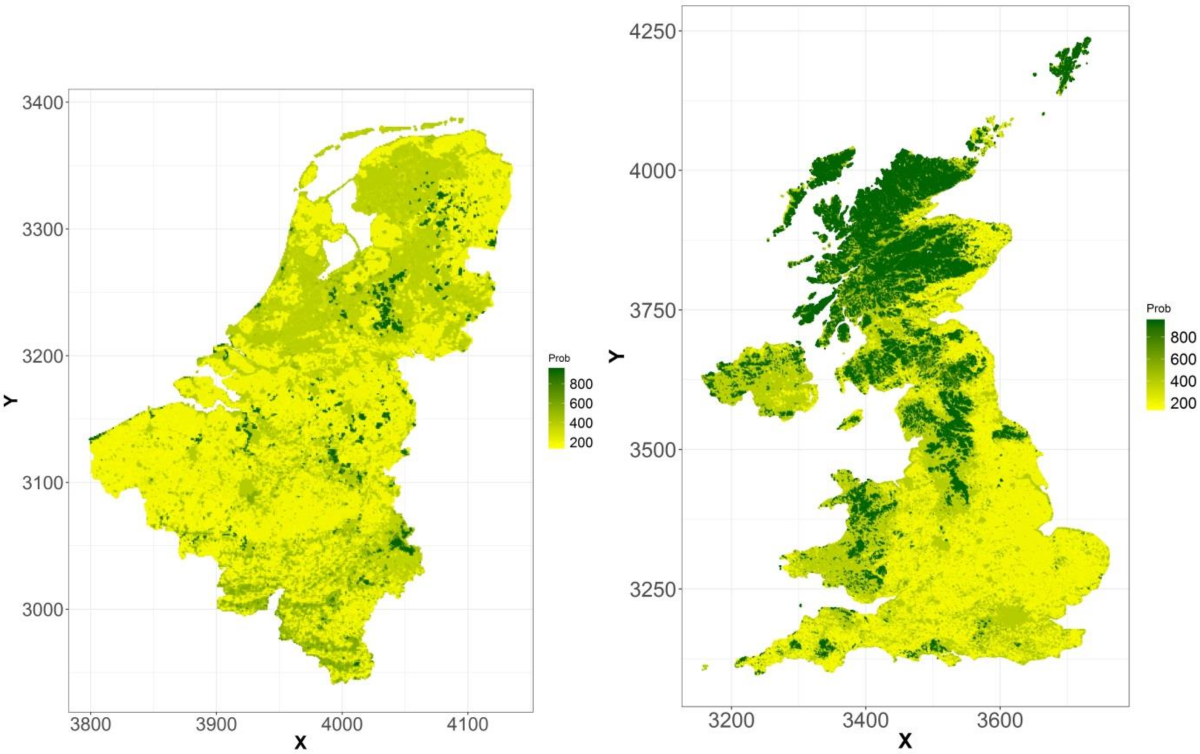
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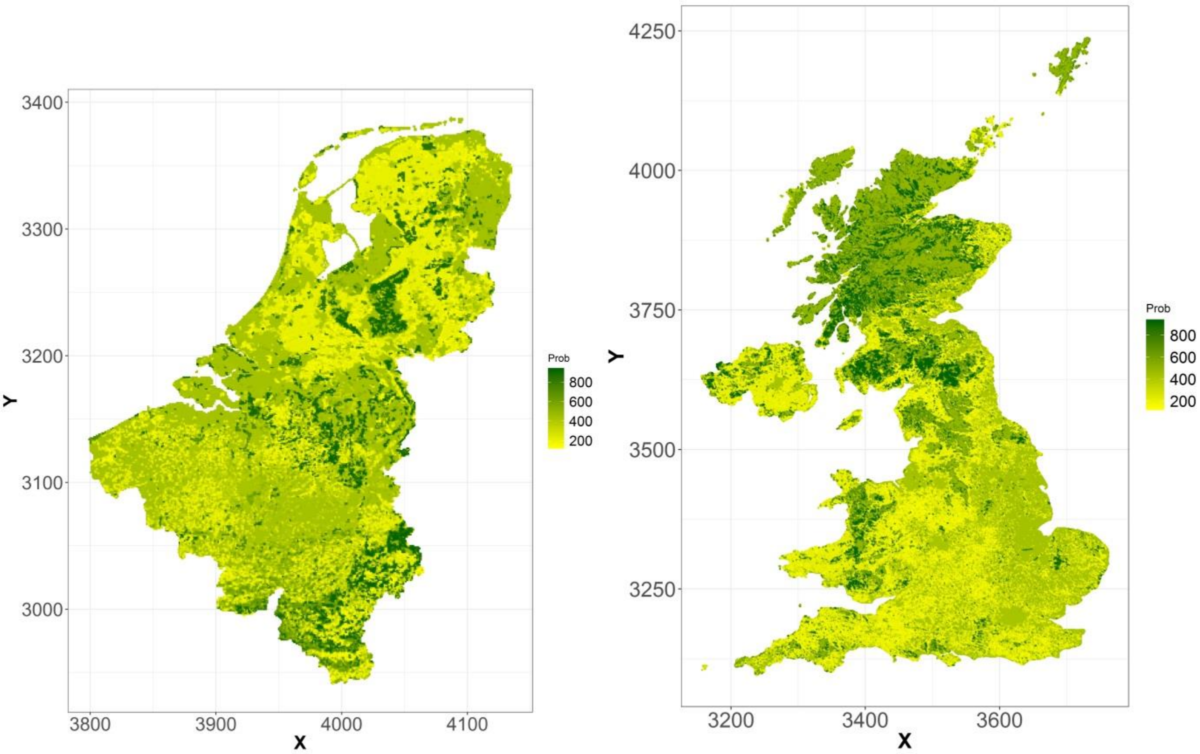
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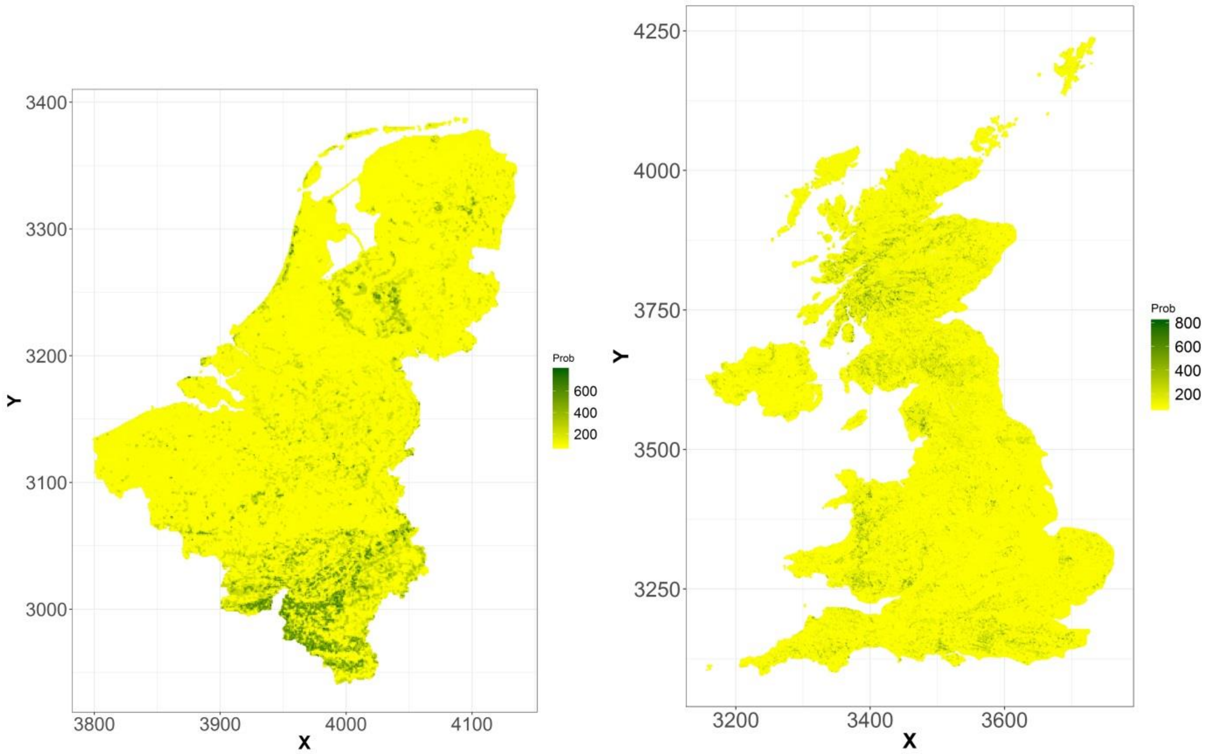

g)

S1 Predictions in Belgium and the Netherlands (left) and the United Kingdom (right) according to the origin of the calibration model ranging from yellow (low probability) to green (high probability). Maps are in ETRS89 projection and the scale is given on the x- and y-axis (in kilometers). a = Achterhoek (NL), b = Dutch Campine (NL), c = Belgian Campine (B), d = Fagne-Famenne-Calestienne (B), e = Ardenne-Thiérache (B), f = Gaume-Lorraine (B), g = Argyll (UK).