Received: 16 October 2020 | Accepted: 19 January 2021

DOI: 10.1002/2688-8319.12050

Ecological Solutions and Evidence | BRITISH ECOLOGICAL SOCIETY

PLANT TRANSLOCATIONS AND CLIMATE CHANGE: BIOASSAY, SURVEILLANCE AND SOLUTION TO A GLOBAL THREAT

Research Article

Using macroecological species distribution models to estimate changes in the suitability of sites for threatened species reintroduction

Joe Bellis[1] | Mike Longden[1,2] | Joshua Styles[3,4] | Sarah Dalrymple[1]

[1] School of Biological and Environmental Sciences, Liverpool John Moores University, Liverpool, UK

[2] Lancashire Wildlife Trust, Bolton, UK

[3] Manchester Metropolitan University, Manchester M15 6BH, UK

[4] Cedar House, Chester Zoo, Chester, UK

Correspondence
Joe Bellis, School of Biological and Environmental Sciences, Liverpool John Moores University, Liverpool, L3 3AF, UK.
Email: joebellis7@gmail.com

Handling Editor: Jonas Hagge

[Correction added on 2 July 2021, after first online publication: Conflict of Interest statement has been added.]

Abstract

1. Species reintroductions often aim to establish populations of threatened taxa over the long-term. However, climate change may jeopardize reintroduction efforts by altering the conditions of a recipient site beyond the tolerances of the focal species. To aid the selection of recipient sites that will retain their suitability under climate change, species distribution models (SDMs) have been proposed as a method of locating areas with a greater likelihood of facilitating species persistence.
2. We applied SDMs to predict macroclimatic suitability changes for 13 threatened plant and invertebrate species considered for reintroduction at four lowland raised bog sites undergoing restoration. We estimated suitability based on current and projected future conditions under two greenhouse gas concentration scenarios – one low (RCP2.6) and one high (RCP8.5) – using three general circulation models, for the period 2041–2060.
3. When considering current predicted suitability, our models indicated that nine species were viable candidates for reintroduction to at least one of the restoration sites. But when accounting for potential future changes in suitability, the number of candidates was reduced to seven species, based on the RCP8.5 climate change scenario. While three of the sites received consistently similar predictions of suitability across species and scenarios, the most northerly site, Red Moss, received divergent suitability predictions for some species. This site is predicted to remain suitable for *Metrioptera brachyptera* and *Genista anglica* under at least one scenario despite substantial losses forecast across the rest of their U.K. ranges, suggesting that it could act as a macroclimatic refuge as climate change advances.
4. The findings presented here made a valuable contribution to the reintroduction planning process, by facilitating the prioritization of reintroduction efforts towards species with a greater likelihood of establishing long-term populations at the prospective recipient sites.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2021 The Authors. *Ecological Solutions and Evidence* published by John Wiley & Sons Ltd on behalf of British Ecological Society

KEYWORDS
climate refugia, conservation planning, lowland raised bog, peatland restoration, recipient site selection, translocation

1 | INTRODUCTION

Anthropogenic pressures in the form of climate change, intensive agriculture, pollution, overexploitation and the introduction of invasive species have led to the degradation and loss of habitats worldwide (Díaz et al., 2019). These pressures have caused numerous regional and global extinctions (Pimm et al., 2014). As species are lost from communities, so too are their ecological interactions, which may lead to functional deficits in the ecosystem (Valiente-Banuet et al., 2015).

Ecological restoration focuses on improving degraded ecosystems by restoring structural and functional complexity (Lipsey et al., 2007). While some species will be able to recolonize restoration sites through natural dispersal mechanisms, others will struggle due to an increasingly fragmented landscape (McGuire et al., 2016). To aid the colonization process, reintroductions and other conservation translocations are increasingly utilized (Seddon et al., 2007; Taylor et al., 2017). Reintroductions, in which organisms are translocated into parts of their indigenous range (IUCN, 2013), have contributed to some major conservation successes, such as the reversal of the decline of the Large Blue butterfly *Maculinea arion* in the UK (Thomas et al., 2009). Historically, however, reintroduction attempts of both animals and plants have often failed to establish viable populations (Dalrymple et al., 2012; Fischer & Lindenmayer, 2000).

Abiotic factors at the recipient site are one of the most frequently cited causes of failure in conservation translocations (Bellis et al., 2019). To mitigate the risk of reintroducing organisms to habitats that do not meet their abiotic needs, the Guidelines for Reintroductions and Other Conservation Translocations (IUCN, 2013) recommend that 'the climate requirements of the focal species should be understood and matched to current and/or future climate at the destination site'. Species distribution models (SDMs) offer an approach for identifying sites that meet the environmental requirements of focal species (IUCN, 2013). An SDM is a statistical tool that combines species occurrences with environmental descriptors to produce spatially explicit predictions of suitability. Recipient site suitability predicted using macroclimatic SDMs was shown to be positively associated with the probability of translocation success (Bellis et al., 2020). However, relying solely on SDMs fitted with macroecological variables is insufficient to assess a prospective recipient site fully, as a species selects its habitat at multiple spatial scales (Johnson, 1980). Fine-scale factors, such as the availability of suitable microclimates or the presence of symbionts, are not fully captured by SDMs fitted with macroecological variables (Louthan et al., 2015), thus finer scale surveys should complement SDM predictions to reflect the multiple processes and interactions that deliver a species' niche requirements (Stadtmann & Seddon, 2018).

One common application of SDMs that has received less attention in the reintroduction context (but see Maes et al., 2019) is the prediction of suitability under future anthropogenic climate change (Araújo et al., 2019; Foden et al., 2019). Areas that will retain their suitability over the timeframe required to meet the objectives of a reintroduction project can be identified by projecting SDM outputs onto scenarios of future climate change. However, there are a number of potential limitations associated with using SDMs to project suitability across time, such as assuming that species–climate relationships will remain constant (Pearson & Dawson, 2003), not accounting for extreme weather events (Morán-Ordóñez et al., 2018) and the inherent uncertainty attached to projections of future climatic conditions (Kujala et al., 2013). Despite these limitations, SDMs have accurately predicted plant and animal responses to recent climate change (Dobrowski et al., 2011; Stephens et al., 2016). As climate change-driven local extinctions have already become geographically and taxonomically widespread (Wiens, 2016), the potential benefits of incorporating climate change projections into reintroduction management plans likely outweigh the potential costs.

In this study, we use SDMs to estimate potential suitability changes for 13 species earmarked for, or currently undergoing reintroduction at four lowland raised bog sites undergoing restoration in north west England. Bogs are highly complex ecosystems that form through the gradual accumulation of decaying plant material (often *Sphagnum* spp.; Bragg & Tallis, 2001). They support highly specialized flora and fauna, affording them high conservation value (Buchholz, 2016; Minayeva et al., 2017). However, degradation of bogs through drainage (in order to dry out and improve the land for forestry and farming) and cutting over (harvesting for peat) has resulted in a dramatic decline in the extent of the habitat across Europe, where it is estimated that more than 50% of bogs have been lost (Finlayson & Spiers, 1999; Joosten, 2012), with the largest decreases occurring in the past 75 years (EU, 2007). Because of this, many characteristic bog species are now threatened or already extinct (Hughes et al., 2008; Topić & Stančić, 2006). Moreover, there are concerns about the potential negative impacts of climate change (Gallego-Sala et al., 2010), which may be more pronounced on raised bogs, since the habitat is ombrotrophic and highly sensitive to changes in temperature and evapotranspiration (Aaby, 1976).

Our focal taxa consists of nine perennial plant and four insect species that are of local and/or national conservation significance. Some of these species have not been observed at the restoration sites for more than a century, raising concerns over their candidacy for reintroduction due to past and projected future changes in climate. Therefore, our main objective was to assess the suitability of the restoration sites for the 13 reintroduction candidate species, by considering both current and projected future macroecological conditions. To achieve this, we used ensemble forecasting techniques (Araújo & New, 2007), which combine multiple SDMs into a single ensemble model through different averaging criteria. To estimate future suitability, SDMs were

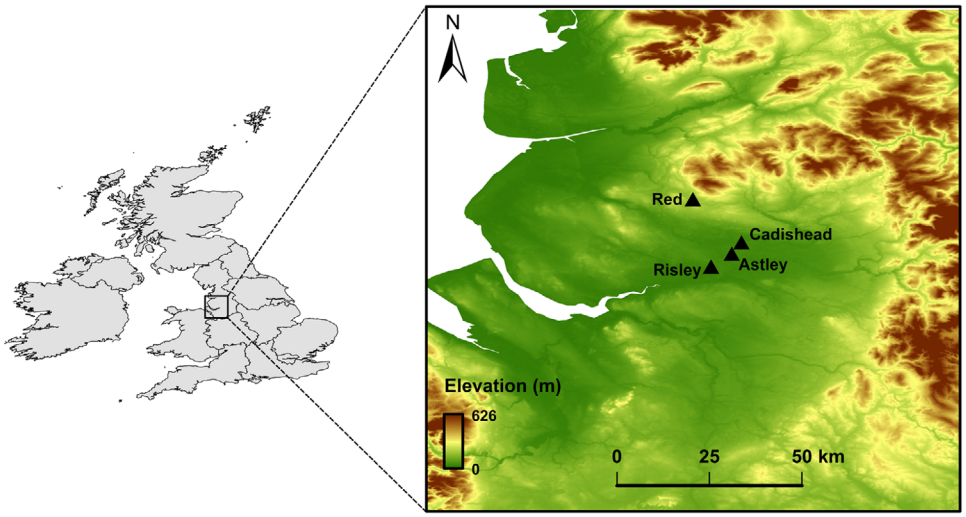


FIGURE 1 Map of the study area and the locations of the four raised bog restoration sites in north west, England, UK

TABLE 1 Taxonomy, life history and Red List statuses (ENG = England, WL = Wales, IRL = Republic of Ireland and GB = Great Britain) of the 13 reintroduction candidate species. The life history traits presented are indicative of plant longevity and insect generational turnover, reflecting the information available for each group

Species	Group	Order	Life history	ENG	WL	IRL	GB
Bog-rosemary *Andromeda polifolia*	Plant	Ericales	Perennial	NT	LC	LC	LC
Great Sundew *Drosera anglica*	Plant	Caryophyllales	Perennial	EN	VU	LC	NT
Oblong-leaved Sundew *Drosera intermedia*	Plant	Caryophyllales	Perennial	VU	VU	LC	LC
Petty Whin *Genista anglica*	Plant	Fabales	Perennial	VU	LC	N/A	NT
Marsh Gentian *Gentiana pneumonanthe*	Plant	Gentianales	Perennial	NT	VU	N/A	LC
Marsh Clubmoss *Lycopodiella inundata*	Plant	Lycopodiales	Perennial	EN	VU	VU	EN
Bog Asphodel *Narthecium ossifragum*	Plant	Dioscoreales	Perennial	LC	LC	LC	LC
White Beak-sedge *Rhynchospora alba*	Plant	Poales	Perennial	NT	LC	LC	LC
Lesser Bladderwort *Utricularia minor*	Plant	Lamiales	Perennial	VU	LC	LC	LC
Manchester Treble-bar *Carsia sororiata*	Insect	Lepidoptera	Univoltine	–	–	CR	–
Large Heath *Coenonympha tullia*	Insect	Lepidoptera	Univoltine	–	–	VU	VU
White-faced Darter *Leucorrhinia dubia*	Insect	Odonata	Semivoltine	–	–	–	EN
Bog Bush Cricket *Metrioptera brachyptera*	Insect	Orthoptera	Semivoltine	–	–	–	LC

projected to 2041–2060, based on two greenhouse gas concentration scenarios and three general circulation models (GCMs). To determine the potential wider contribution of these reintroductions to the conservation of each species, we also estimated distributional changes at the scale of the UK and Ireland.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area is located in north west England (53°27′N, 2°27′W), across the counties of Cheshire, Lancashire, Merseyside and Greater Manchester (Figure 1). Up until the 19th century, the study area consisted of an expansive lowland raised bog. However, due to railway construction, agricultural expansion and sustained peat extraction, just 2% of the raised bog habitat remains, with remnant patches now highly fragmented and many in poor condition. A partnership between NGOs, private organizations and academic institutions is now working to restore some of the lowland raised bog sites. At four of the sites, namely Astley, Cadishead, Red and Risley, there are plans to reintroduce 13 plant and invertebrate species that are of local and/or national conservation concern (Table 1). All of these species are typical of healthy bog habitat representing a range of conditions from bog pools (*Utricularia minor*) through to the drier fringes (*Genista anglica*).

2.2 | Species distribution models

2.2.1 | Data selection

We compiled a database of global occurrences using multiple data repositories where possible for each species. While SDMs constructed from openly available data repositories can achieve accuracy comparable with those constructed from field-sampled data (Jackson et al., 2015), there are a number of potential pitfalls that require consideration (e.g. coordinate imprecision, spatial biases and inclusion of historical records) (Beck et al., 2014). Therefore, we diligently cleaned each species occurrence dataset to maximize spatial and temporal reliability in preparation for modelling (further details are given in Appendix S1 in the Supporting Information).

We considered a combination of nine climatic variables and soil pH as macroecological predictors in our SDMs, based on their ecophysiological relevance to our focal species. Seven climate variables were downloaded from the WorldClim dataset (Version 1.4; www.worldclim.org) (Hijmans et al., 2005). We also generated growing degree days (sum of all monthly temperatures greater than 5°C; Prentice et al., 1992) using the *envirem* package (v2.0; Title & Bemmels, 2018) in R v.3.5.1 (R Core Team, 2018) and soil moisture deficit (difference between annual precipitation and potential evapotranspiration; PET was provided by A. Trabucco; (Trabucco & Zomer, 2009). We downloaded data on soil pH in H_2O at a depth of 15 cm from the web-based global soil information system (SoilGrids; https://soilgrids.org; Hengl et al., 2017). To avoid multicollinearity between the 10 predictors, we removed variables that presented a variance inflation factor of >10 (Dormann et al., 2013; Guisan et al., 2017) using the R package *usdm* (v. 1.1-18) (Naimi, 2015) (Appendix S1).

To estimate future suitability, we used three GCMs to derive projections of the nine climatic variables for the period 2041–2060; these included MPI-SM-LR (Giorgetta et al., 2013), IPSLCM5A-LR (Dufresne et al., 2013) and HadGEM2-ES (Jones et al., 2011). Additionally, we used two representative concentration pathways describing low (RCP2.6) and high (RCP8.5) greenhouse gas concentration scenarios. To assess the degree of extrapolation for each climate projection (i.e. the extent to which projected environmental conditions were outside those represented within the model calibration data; Barbosa et al., 2009; Araújo et al., 2019), we computed a multivariate environmental similarity surface (MESS) with the *dismo* package (v1.1-4; Hijmans et al., 2017) in R (Appendix S1).

2.2.2 | Modelling approach

We used an ensemble of SDM algorithms to minimize the uncertainty associated with single modelling techniques (Buisson et al., 2010). Our ensemble consisted of generalized additive model, multivariate adaptive regression splines (MARS), generalized boosted model, random forest (RF) and Maxent and was implemented in the *biomod2* package (v. 3.3-7) (Thuiller et al., 2016) in R. To measure the agreement between models, we calculated the coefficient of variation (standard deviation/mean). Model performance was evaluated using the receiver operating characteristic to determine an area under the curve (AUC) and the true skill statistic (TSS). As we were reliant on presence-only data, we generated pseudo-absences (PAs) for each SDM based on recommendations in the literature (Barbet-Massin et al., 2012; Chefaoui & Lobo, 2008; VanDerWal et al., 2009). Because we used PAs instead of true absence data and suitability values were not real occurrence probabilities (Guillera-Arroita et al., 2015), to make predictions comparable across species we standardized the predicted climate suitability values to range between 0 and 1 with the following formula: $(x - \min)/(\max - \min)$ (Appendix S1).

To categorize the candidacy of species for reintroduction and to estimate distributional changes based on current and 2041–2060 conditions, we converted continuous outputs to binary predictions using the suitability value that maximized the TSS score. We chose this method because it demonstrated improved reliability over other commonly applied approaches when only present data were available (Liu et al., 2013).

2.3 | Data analyses

To estimate the future suitability of the recipient sites (and across the whole of the UK and Ireland), we averaged the SDM projections for the three GCMs to produce a consensus prediction of suitability. For the purposes of this paper, we calculated the mean (SD) suitability of the four potential recipient sites and present these as a single value. As the four sites are within close proximity of each other and are predominantly located in lowland habitats, suitability predictions were expected to be similar. However, binary suitability did differ among sites for a small number of species (Table S2.3 in the Supporting Information) and we explore the implications of this in the discussion.

To test the sensitivity of our suitability predictions to single-variable dominance, we re-ran our SDMs without temperature seasonality, while keeping all other parameters constant (though calibration/testing sets differed). Similar approaches have been used previously to test the robustness of SDM predictions to variable selection (Almpanidou et al., 2016). We computed Pearson's correlation coefficients to calculate the strength of correlation between suitability predictions made with and without temperature seasonality for current and projected future climates.

To gain a more comprehensive view of the threat posed by climate change to the UK and Ireland ranges of our focal species (Ohlemüller et al., 2006), we calculated three types of suitability change based on the binary output maps:

1. *Proportional change in overall suitability (assuming full dispersal).* This quantifies the overall predicted change in the number of cells between those classified as suitable currently, and cells classified as suitable in 2041–2060. It assumes that the species can disperse to all suitable cells in the future.

2. *Proportional change in currently suitable cells (no dispersal)*. This quantifies the threat posed by projected climate change in 2041–2060 to cells predicted to be suitable under current conditions. It assumes that the modelled species will be unable to disperse to newly emerging suitable cells.
3. *Proportional change in suitability of occupied cells (no dispersal)*. This quantifies the threat posed by projected climate change in 2041–2060 to currently suitable cells where a species has been recorded as present. It assumes that the species will be dispersal limited to currently occupied cells.

Calculating multiple types of suitability change is advantageous because one type may yield greater insight than another, depending on the species dispersal capacity, the amount of survey effort applied to locating the species and the species detectability. The first two measures are likely to be most informative for communicating the impacts of climate change on species with less well-described distributions, that is species that are more difficult to detect and/or are under-surveyed (e.g. cryptic species such as *Carsia sororiata*). The third measure focuses on areas of confirmed species presence and is likely to be most informative for species that are well-monitored/recorded (e.g. conspicuous species such as *Coenonympha tullia*). This distinction arises because the first two measures use predicted current suitability as a starting point, which may represent a more realistic baseline for some species (e.g. cryptic species) than if the observed distribution was used (see challenges faced by Ballesteros-Mejia et al., 2017).

Previous studies have noted a positive association between the latitudinal centre of species' distributions and the threat posed by climate change (Dyderski et al., 2018; Virkkala & Rajasärkkä, 2011). To investigate the relevance of this association for our focal species, we used the Spearman rank correlation to quantify the strength of association between the mean latitudinal centre of the global distribution and the proportional change in the suitability of occupied cells in the UK and Ireland.

3 | RESULTS

Model discrimination accuracy metrics indicated good performance for all species, with AUC ranging from 0.915 to 0.986 (mean 0.944 ± 0.005) and TSS ranging from 0.649 to 0.866 (0.725 ± 0.016).

The three most consistently high ranking variables in our focal species SDMs were temperature seasonality, growing degree days and soil pH (Table S2.1 in the Supporting Information). Although the relative importance of these variables differed among species, temperature seasonality ranked highest most frequently, being the most important predictor for 10 species.

According to the MESS results, SDMs reported a negligible extrapolation when predicting suitability in future scenarios (Table S2.2 in the Supporting Information). Proportions of the UK and Ireland with some degree of model extrapolation ranged from 0% to 11%, with most species at <3%. For all species, the potential recipient sites were well within the range of values used to run the models.

The average suitability of the potential recipient sites showed a statistically significant difference between time periods for 12 species (Figure 2). For the majority of species ($n = 9$), suitability is predicted to decrease by 2041–2060 under at least one RCP scenario. The largest decline in suitability is predicted for *M. brachyptera*, decreasing by more than 50% under the more pessimistic RCP8.5 scenario. However, for four of the plant species, namely *D. anglica*, *D. intermedia*,

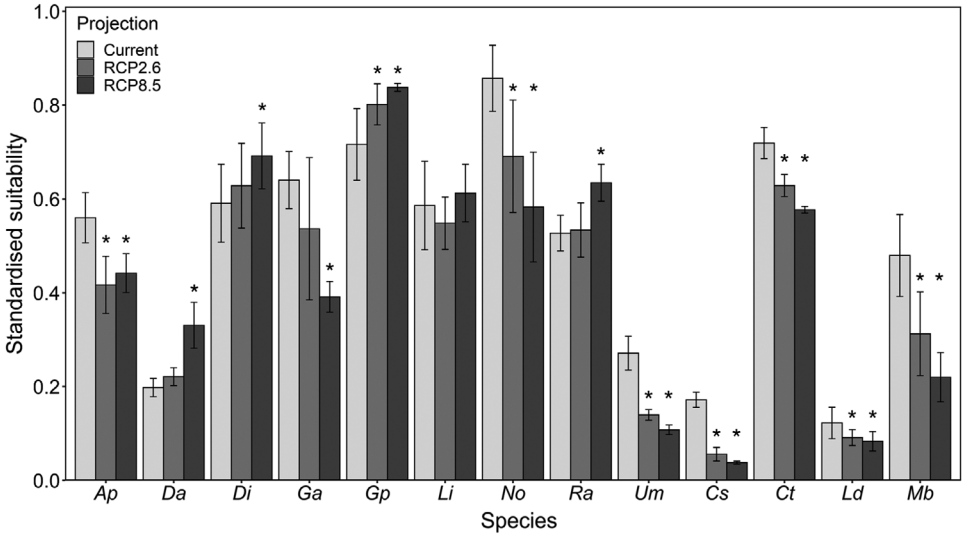


FIGURE 2 Mean (SD) predicted environmental suitability of potential recipient sites for nine plant and four invertebrate species. SD represents the variation in predicted suitability between the four sites. * indicates statistically significant differences between current and future climate suitability according to a Wilcoxon signed-rank test (significance set to $p < 0.05$). Abbreviations are as follows: *Ap*, *Andromeda polifolia*; *Cs*, *Carsia sororiata*; *Ct*, *Coenonympha tullia*; *Da*, *Drosera anglica*; *Di*, *Drosera intermedia*; *Ga*, *Genista anglica*; *Gp*, *Gentiana pneumonanthe*; *Ld*, *Leucorrhinia dubia*; *Li*, *Lycopodiella inundata*; *Mb*, *Metrioptera brachyptera*; *No*, *Narthecium ossifragum*; *Ra*, *Rhynchospora alba*; *Um*, *Utricularia inor*.

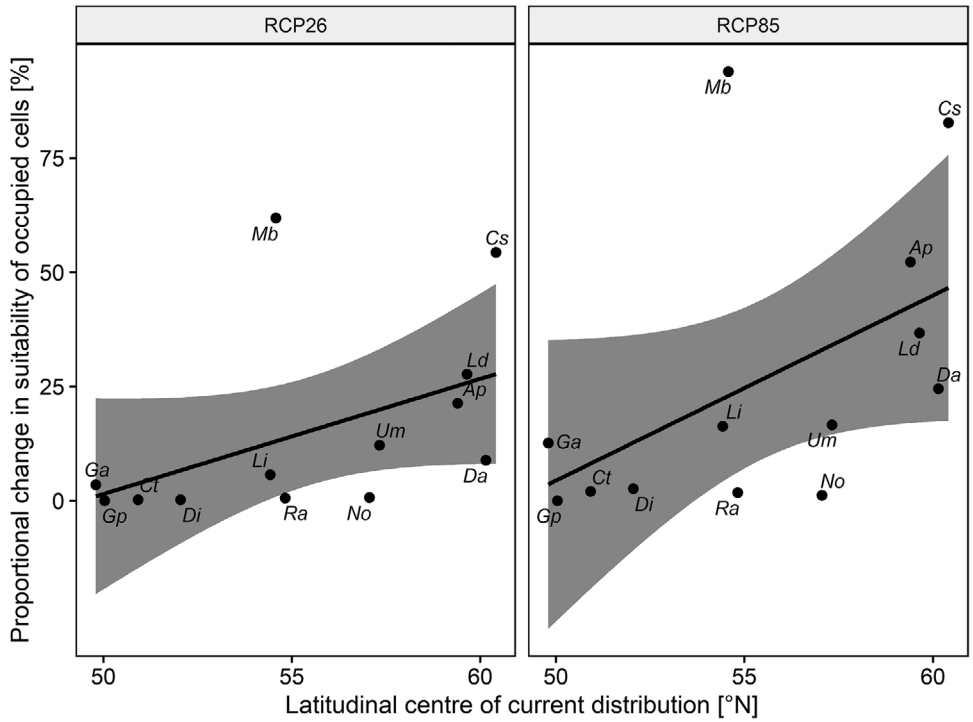


FIGURE 3 Association between mean latitude of global distribution and proportion of threatened occupied area in the UK and Ireland. Left panel is based on RCP2.6 and right panel RCP8.5. The shaded areas represent 95% confidence intervals. Abbreviations are as follows: *Ap*, *Andromeda polifolia*; *Cs*, *Carsia sororiata*; *Ct*, *Coenonympha tullia*; *Da*, *Drosera anglica*; *Di*, *Drosera intermedia*; *Ga*, *Genista anglica*; *Gp* , *Gentiana pneumonanthe*; *Ld*, *Leucorrhinia dubia*; *Li*, *Lycopodiella inundata*; *Mb*, *Metrioptera brachyptera*; *No*, *Narthecium ossifragum*; *Ra*, *Rhynchospora alba*; *Um*, *Utricularia minor*.

G. pneumonanthe, and *R. alba*, climate change is actually forecast to improve the suitability of the potential recipient sites by a statistically significant amount (Figure 2).

Under current conditions, at least one of the sites was categorized as suitable for nine species (Table S2.3 in the Supporting Information). Under the RCP2.6 climate change scenario, this was reduced to eight, and under the RCP8.5 scenario this was reduced to seven. Generally, there was consistency in predicted suitability between Astley Moss, Cadishead Moss and Risley Moss, but suitability at Red Moss differed for some species (Table S2.3 in the Supporting Information). According to the RCP2.6 scenario, all sites were categorized as unsuitable for *M. brachyptera* except Red Moss, which remained above the binary threshold. Similarly, Red Moss was the only site predicted to remain suitable for *G. anglica* under the RCP8.5 scenario (Table S2.3 in the Supporting Information), indicating that reintroduction efforts would not be impaired by projected climate change for this species.

The agreement between SDM predictions (measured using the coefficient of variation) at recipient sites was relatively high for species with more favourable suitability predictions (Table S2.4 in the Supporting Information). Agreement was much lower for species that received unsuitable predictions at the recipient sites, such as *C. sororiata* and *L. dubia*. Furthermore, divergence between SDM predictions increased when models were projected onto the future climate change scenarios. When comparing the agreement between the different GCMs, values were not as extreme as for SDMs, but followed a similar trend in that agreement was higher for species that received favourable suitability predictions.

At the wider UK and Ireland scale, the projected threat of climate change to occupied area was highest under the RCP8.5 scenario. Three of the four species predicted to lose >20% of currently occupied area under both climate change scenarios were invertebrates. Of these species, the most extreme losses were predicted for *C. sororiata* (Figure 3) and *M. brachyptera* (Figure S2.1 in the Supporting Information), which are predicted to lose 54.3% and 61.9% under the RCP2.6 scenario, and 82.7% and 93.9% under the RCP8.5 scenario, respectively (Figure 3). For plants, the biggest losses of currently occupied area were predicted for *A. polifolia*, with SDMs forecasting a 21.3% loss under RCP2.6 and 52.3% under the more severe RCP8.5 scenario. In contrast, the currently occupied cells of *D. intermedia*, *G. pneumonanthe*, *N. ossifragum*, *R. alba* and *C. tullia* were barely threatened (<3%) by projected climate change. *G. pneumonanthe* represents the best example of this (Figure 3) and is actually forecast to experience a large increase in climatically suitable area (>120%) across the UK and Ireland by 2041–2060 (Figure 4).

Climate change presented a greater risk to species with more northerly distributions (Figure 3), and there was a statistically significant positive correlation between proportion of threatened occupied area and the mean latitudinal centre of current distribution under both RCP2.6 (rho = 0.676, $p = 0.014$) and RCP8.5 (rho = 0.599, $p = 0.034$) (Figure 3). However, *M. brachyptera* was an outlier to this

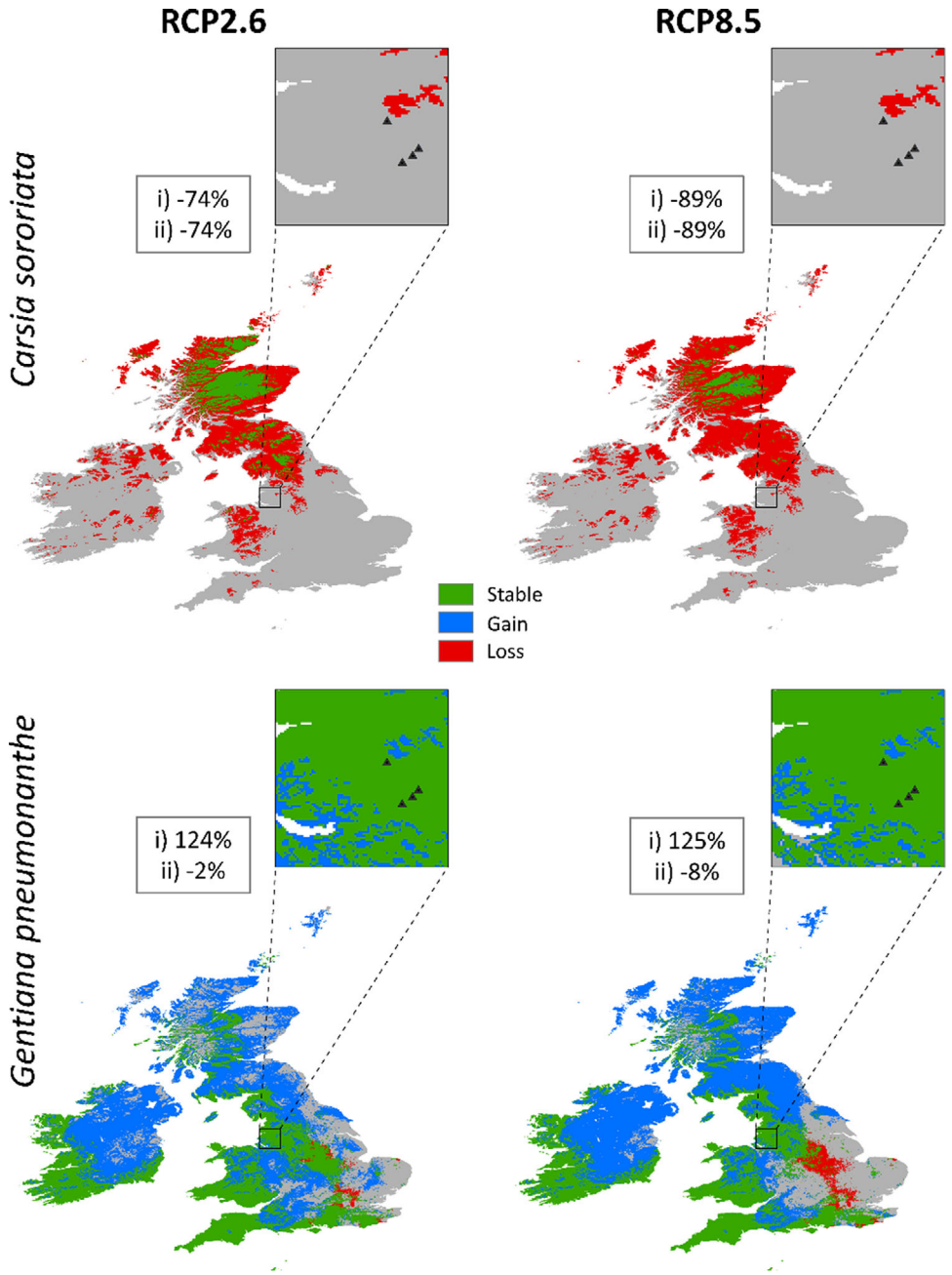


FIGURE 4 Predicted changes in suitable area across the UK and Ireland for*Carsia sororiata* and *Gentiana pneumonanthe* by 2041–2060 under RCP2.6 and RCP8.5. The proportional change in overall suitability (i) and the proportional change in currently suitable cells (ii), which are described in more detail in the Materials and Methods, are also presented. Species presented here represent the extremes of negative and positive projections. Suitability change maps for other species are available in Figure S2.1 in the Supporting Information.

trend, with a large proportion of its current UK range threatened by climate change despite having a relatively low mean latitudinal centre.

4 | DISCUSSION

According to current macroecological conditions, the potential recipient sites are suitable for nine species. However, conditions are forecast to deteriorate for most species by 2041–2060, which would reduce the number of reintroduction candidates to seven if climate change follows the trajectory projected in RCP8.5. While suitability between sites was often similar, the most northerly restoration site, Red Moss, received divergent suitability predictions for some species. For example, this site is predicted to remain suitable for *M. brachyptera* and *G. anglica* under at least one scenario despite substantial losses forecast across the rest of their UK ranges, suggesting that it could act as a macroclimatic refuge for these species under future climate change.

With SDMs constructed at the global scale, the ecological relevance of site-level suitability predictions may be diminished if focal populations are locally adapted to regional environmental conditions.

Regional SDMs, that is models built with occurrences from a restricted portion of the species range, have been suggested as an approach to account for potential local adaptations (Hällfors et al., 2016). However, delimiting the area from which to select occurrences for a regional SDM is difficult to justify without evidence from experimental studies that indicate intraspecific differences in physiological tolerances (Chardon et al., 2020). Furthermore, regionally restricting the construction of SDMs risks misrepresenting the potential suitability of an area by producing biased and truncated estimates of a species niche (Sánchez-Fernández et al., 2011; Titeux et al., 2017), the consequences of which are amplified when projecting to novel time periods (Barbet-Massin et al., 2010). Because future predictions of suitability were required to determine if each species could persist at the potential recipient sites under climate change, we focused on the species' global ranges in order to capture the full extent of potential climatic adaptations that may facilitate long-term persistence of reintroduced populations (Barbet-Massin et al., 2010).

Recipient site suitability was estimated with variables recorded at the macroecological scale, however, fine-scale factors (e.g. interspecific interactions, availability of suitable microclimates and the presence of symbionts) also influence the environmental suitability of a site for a species (Louthan et al., 2015) and, if beneficial, may buffer populations against macroclimatic change (Suggitt et al., 2018). Although fine-scale processes can also be influenced by the global macroclimate (Louthan et al., 2015), it is inevitable that macroecological SDMs will overlook some critical microhabitat features. For example, the larvae of *C. tullia* require stands of hare's-tail cottongrass *Eriophorum vaginatum*, their overwintering hostplant, on surfaces that are high enough for the larvae to avoid prolonged submersion during periods of winter flooding (Joy & Pullin, 1997). To ensure that the resource needs of reintroduction candidates are met at multiple spatial scales (Michel et al., 2008), the model outputs presented in this study are to be used in conjunction with fine-scale habitat surveys and expert opinion when assessing the habitat suitability of recipient sites.

For two of the focal species, *G. anglica* and *M. brachyptera*, suitability are favourable under current conditions (above binary threshold) but iare forecasted to decline significantly by 2041–2060 at three of the potential recipient sites (Table S2.3 in the Supporting Information; Figure 2). When exposed to unsuitable environmental conditions, a population must either disperse, adapt in situ, or face extinction (Urban, 2015). Dispersal to suitable habitat beyond the recipient sites (e.g. to higher latitudes or elevations) is unlikely due to the anthropogenic dominance of the surrounding landscape. Therefore, reintroduced populations would need to evolutionarily adapt in situ if they are to avoid climate change-driven local extinction. Given that *G. anglica* and *M. brachyptera* are both relatively widespread species, they are more likely to have high levels of genetic variation for traits involved in climatic adaptation (e.g. Balanyá et al., 2006; Jump et al., 2008). However, large effective population sizes are required for maintaining genetic variation and evolutionary potential (Willi & Hoffmann, 2009) and there are multiple factors likely to constrain the size of the populations post-reintroduction, such as the limited number of individuals available for reintroduction (e.g. Jamieson, 2011), the limited potential for gene flow with other populations (e.g. Thompson et al., 2013), and neither species having a rapid reproductive strategy (e.g. Bay et al., 2018).

We converted the continuous SDM outputs to binary predictions of suitability in order to categorize the candidacy of species for reintroduction and to estimate future distributional changes. While binary predictions are frequently used for biogeographical and conservation applications (Cerasoli et al., 2020; Dyderski et al., 2018; Maiorano et al., 2019), research has shown that discretizing SDM outputs is often done unjustifiably and may diminish important information (Guillera-Arroita et al., 2015). In our study and the wider context of reintroduction site selection, it is useful to classify sites as suitable or not, thus binary conversion may be justified provided issues relating to the underlying structure of the occurrence data have been addressed (e.g. sampling bias; Guillera-Arroita et al., 2015). However, when selecting from multiple potential recipient sites, as in our study, the continuous SDM outputs can help to identify the most optimal site(s), thus, both forms of prediction present value in reintroduction decision-making.

4.1 | Trends in SDM outputs

In the Northern Hemisphere, the climate is changing more rapidly at higher latitudes (IPCC, 2014). This was reflected in our predictions of suitability change; species with more northerly distributions were generally more threatened by climate change (Figure 3). However, *M. brachyptera* was an outlier to this trend, with >80% of currently occupied cells in the UK projected to become unsuitable by 2041–2060 under the RCP8.5 scenario, despite a mean latitudinal centre comparable to species that are projected to lose significantly less climate space (<20%). We postulate two reasons for this. First, *M. brachyptera* has one of the smallest distributions of the species considered in our analysis, indicating that it may have less climatic adaptations that could facilitate persistence in the threatened parts of its current range (Slatyer et al., 2013) (supported by the UK distribution of *M. brachyptera* having the largest proportion of non-analogue future climates; Table S2.2 in the Supporting Information). Second, although *M. brachyptera* is found across a variety of elevations in Europe, in the southern parts of its range (below a decimal latitude of 48°N), it is mainly located in mountainous areas, such as the Alps, Jura Mountains and Massif Central, where temperatures are comparable to those at much higher latitudes (Jump et al., 2009).

Temperature seasonality dominated variable importance in the SDMs, ranking as the most important predictor for 10 species (Table S2.1 in the Supporting Information). Although previous modelling studies have also found temperature seasonality to be an important variable in the structuring of species' distributions (e.g. Barbet-Massin & Jetz, 2014; Cerasoli et al., 2020; Zhang et al., 2018), this result was somewhat unexpected. VanDerWal et al. (2009) suggests that variable importance can become increasingly dominated by a small number of variables as the PA selection extent increases. To account for this, PA selection extents are often constrained by, for example, restricting records to ecologically relevant biogeographical regions (e.g. biomes

or ecoregions; Bellis et al., 2020; Csergő et al., 2017). Due to the vast extent of some of the ecoregions occupied by our focal species, we chose to refine this approach further by selecting PAs from a 2-degree buffer drawn around each species' distribution. Although this approach reduced single-variable dominance (based on comparisons with initial exploratory models), we tested the sensitivity of our results to the inclusion of temperature seasonality by re-running our SDMs without it (Almpanidou et al.,2016), while keeping all other parameters unchanged. We found that our results were robust to the inclusion of temperature seasonality, with strong and statistically significant correlations detected across recipient site suitability predictions between SDMs calibrated with and without temperature seasonality (current: $r = 0.90$, $p < 0.001$; RCP2.6: $r = 0.95$, $p < 0.001$; RCP8.5: $r = 0.94$, $p < 0.001$).

This study primarily focused on suitability change at cells currently occupied by each species, but alternative suitability change metrics were also computed (Ohlemüller et al., 2006) to account for different levels of species detection and dispersal capacity. The proportional change in overall suitability metric elucidates the opportunities available to our focal species if they can successfully colonize newly emerging suitable climates (e.g. Figure 3; Figure S2.1 in the Supporting Information). However, suitable climate does not always translate to suitable land cover, or biotic composition (Fournier et al., 2017). Moreover, much of the natural landscape in the UK has become highly fragmented by human infrastructure (Hooftman & Bullock, 2012; Young & Jarvis, 2001), reducing the connectivity of remnant patches of suitable habitat and limiting the ability of species to colonize newly suitable areas (Haddad et al., 2015). Therefore, although suitable new climate space is projected to emerge in the future, accessing this space through natural dispersal mechanisms is likely to be constrained for our focal species, making a limited dispersal scenario more probable.

4.2 | Conservation/management implications

The potential of SDMs to inform reintroduction decision-making has been widely discussed (IUCN, 2013; Krause & Pennington, 2012; Osborne & Seddon, 2012). By considering both current and future suitability, the SDM outputs presented in this study enabled the identification of species with a greater likelihood of establishing a long-term population and therefore can assist with decisions on when reintroductions are likely to be beneficial. For example, *L. inundata* is perhaps the most threatened species considered for reintroduction (Table 1), and although the predicted losses of currently occupied cells are concerning, the fact that suitability at the restoration sites will not be affected by projected climate change commends reintroduction as a positive action in the conservation of the species. Additionally, the SDM outputs provide a rationale for which species to prioritize for ex situ cultivation (i.e. high predicted suitability with increasing trend; *D. intermedia* and *G. pneumonanthe*), because the feasibility of obtaining sufficient source material for the plant reintroductions is currently dependent on a small ex situ facility. The SDM outputs also indicated which species may be less likely to establish viable populations (e.g. *C. sororiata* and *D. anglica*), prompting the exploration of alternative management options such as the selection of recipient sites with higher and more stable suitability (e.g. further north).

Due to the four potential recipient sites being located relatively close to each other, we expected suitability predictions and the resulting management implications to be similar. However, suitability predictions at the Red Moss site diverged for some species (Table S2.3 in the Supporting Information), with SDMs predicting this site to be suitable and the other sites unsuitable. Red Moss is located approximately 14 km north (Euclidean distance) of the other three sites, sitting at the foot of the West Pennine Moors at an altitude of around 100 m above sea level (ASL); an elevation of two to three times higher than the other sites (which range from ca. 30 to 50 m ASL) (see Figure 1). These factors likely contribute to the colder and wetter conditions at Red Moss (see (Jump et al., 2009) and explain why this site is the only one predicted to be suitable site for *G. anglica* (under RCP2.6) and *M. brachyptera* by 2041–2060 (Poniatowski & Fartmann, 2010). With both species projected to lose currently occupied area across the rest of the UK, Red Moss could act as a macroclimatic refuge for these species as the climate changes (Ashcroft, 2010), potentially making an important contribution to their national conservation.

ACKNOWLEDGEMENTS

We would like to thank all of the individuals who have contributed to the Chat Moss Project. We also thank D. Bourke for helpful discussions during the design phase of the study and the two anonymous reviewers for their constructive comments on an earlier version of the manuscript.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

J.B., M.L., J.S. and S.D. conceived the ideas and designed the work. J.B. collected and analysed the data. J.B. led the writing of the manuscript. All authors contributed to every draft and approved the final version for publication.

DATA AVAILABILITY STATEMENT

Download links to species and environmental data used in this study are available at http://opendata.ljmu.ac.uk/ (Bellis, Longden, Styles, & Dalrymple, 2021).

ORCID

Joe Bellis https://orcid.org/0000-0003-2787-3736

Sarah Dalrymple https://orcid.org/0000-0002-6806-855X

REFERENCES

Aaby, B. (1976). Cyclic climatic variations in climate over the past 5,500 yr reflected in raised bogs. *Nature*, *263*, 281–284. https://doi.org/10.1038/263281a0

Almpanidou, V., Schofield, G., Kallimanis, A. S., Türkozan, O., Hays, G. C., & Mazaris, A. D. (2016). Using climatic suitability thresholds to identify past, present and future population viability. *Ecological Indicators*, *71*, 551–556. https://doi.org/10.1016/j.ecolind.2016.07.038

Araújo, M. B., Anderson, R. P., Barbosa, A. M., Beale, C. M., Dormann, C. F., Early, R., Garcia, R. A., Guisan, A., Maiorano, L., Naimi, B., O'Hara, R. B., Zimmermann, N. E., & Rahbek, C. (2019). Standards for distribution models in biodiversity assessments. *Science Advances*, *5*(1), 1–12. https://doi.org/10.1126/sciadv.aat4858

Araújo, M. B., & New, M. (2007). Ensemble forecasting of species distributions. *Trends in Ecology and Evolution*, *22*(1), 42–47. https://doi.org/10.1016/j.tree.2006.09.010

Ashcroft, M. B. (2010). Identifying refugia from climate change. *Journal of Biogeography*, *37*(8), 1407–1413. https://doi.org/10.1111/j.1365-2699.2010.02300.x

Balanyá, J., Oller, J. M., Huey, R. B., Gilchrist, G. W., & Serra, L. (2006). Global genetic change tracks global climate warming in Drosophila subobscura. *Science*, *313*(5794), 1773–1775. https://doi.org/10.1126/science.1131002

Ballesteros-Mejia, L., Kitching, I. J., Jetz, W., & Beck, J. (2017). Putting insects on the map: Near-global variation in sphingid moth richness along spatial and environmental gradients. *Ecography*, *40*(6), 698–708. https://doi.org/10.1111/ecog.02438

Barbet-Massin, M., & Jetz, W. (2014). A 40-year, continent-wide, multispecies assessment of relevant climate predictors for species distribution modelling. *Diversity and Distributions*, *20*(11), 1285–1295. https://doi.org/10.1111/ddi.12229

Barbet-Massin, M., Jiguet, F., Albert, C. H., & Thuiller, W. (2012). Selecting pseudo-absences for species distribution models: How, where and how many? *Methods in Ecology and Evolution*, *3*(2), 327–338. https://doi.org/10.1111/j.2041-210X.2011.00172.x

Barbet-Massin, M., Thuiller, W., & Jiguet, F. (2010). How much do we overestimate future local extinction rates when restricting the range of occurrence data in climate suitability models? *Ecography*, *33*(5), 878–886. https://doi.org/10.1111/j.1600-0587.2010.06181.x

Barbosa, A., Real, R., & Vargas, J. (2009). Transferability of environmental favourability models in geographic space: The case of the Iberian desman (*Galemys pyrenaicus*) in Portugal and Spain. *Ecological Modelling*, *220*(5), 747–754. https://doi.org/10.1016/j.ecolmodel.2008.12.004

Bay, R. A., Harrigan, R. J., Le Underwood, V., Gibbs, H. L., Smith, T. B., & Ruegg, K. (2018). Genomic signals of selection predict climate-driven population declines in a migratory bird. *Science*, *359*(6401), 83–86. https://doi.org/10.1126/science.aan4380

Beck, J., Böller, M., Erhardt, A., & Schwanghart, W. (2014). Spatial bias in the GBIF database and its effect on modeling species' geographic distributions. *Ecological Informatics*, *19*, 10–15. https://doi.org/10.1016/j.ecoinf.2013.11.002

Bellis, J., Bourke, D., Maschinski, J., Heineman, K., & Dalrymple, S. (2020). Climate suitability as a predictor of conservation translocation failure. *Conservation Biology*, *34*(6), 1473–1481. https://doi.org/10.1111/cobi.13518

Bellis, J., Bourke, D., Williams, C., & Dalrymple, S. (2019). Identifying factors associated with the success and failure of terrestrial insect translocations. *Biological Conservation*, *236*, 29–36. https://doi.org/10.1016/j.biocon.2019.05.008

Bellis, J., Longden, M., Styles, J., & Dalrymple, S. (2021). Data from: Using macroecological species distribution models to estimate changes in the suitability of sites for threatened species reintroduction. *LJMU Data Repository*, https://doi.org/10.24377/LJMU.d.00000088

Bragg, O. M., & Tallis, J. H. (2001). The sensitivity of peat-covered upland landscapes. *Catena*, *42*(2–4), 345–360. https://doi.org/10.1016/S0341-8162(00)00146-6

Buchholz, S. (2016). Natural peat bog remnants promote distinct spider assemblages and habitat specific traits. *Ecological Indicators*, *60*, 774–780. https://doi.org/10.1016/j.ecolind.2015.08.025

Buisson, L., Thuiller, W., Casajus, N., Lek, S., & Genouillet, G. (2010). Uncertainty in ensemble forecasting of species distribution. *Global Change Biology*, *16*(4), 1145–1157. https://doi.org/10.1111/j.1365-2486.2009.02000.x.

Cerasoli, F., Thuiller, W., Guéguen, M., Renaud, J., D'Alessandro, P., & Biondi, M. (2020). The role of climate and biotic factors in shaping current distributions and potential future shifts of European Neocrepidodera (Coleoptera, Chrysomelidae). *Insect Conservation and Diversity*, *13*(1), 47–62. https://doi.org/10.1111/icad.12376

Chardon, N. I., Pironon, S., Peterson, M. L., & Doak, D. F. (2020). Incorporating intraspecific variation into species distribution models improves distribution predictions, but cannot predict species traits for a widespread plant species. *Ecography*, *43*(1), 60–74. https://doi.org/10.1111/ecog.04630

Chefaoui, R. M., & Lobo, J. M. (2008). Assessing the effects of pseudo-absences on predictive distribution model performance. *Ecological Modelling*, *210*(4), 478–486. https://doi.org/10.1016/j.ecolmodel.2007.08.010

Csergő, A. M., Salguero-Gómez, R., Broennimann, O., Coutts, S. R., Guisan, A., Angert, A. L., Welk, E., Stott, I., Enquist, B. J., McGill, B.,Svenning, J. -C., Violle, C., & Buckley, Y. M. (2017). Less favourable climates constrain demographic strategies in plants. *Ecology Letters*, *20*(8), 969–980. https://doi.org/10.1111/ele.12794

Dalrymple, S. E., Banks, E., Stewart, G. B., & Pullin, A. S. (2012). A meta-analysis of threatened plant reintroductions from across the globe. In J. Maschinski, K. Haskins, & P. Raven (Eds.), *Plant reintroduction in a changing climate* (pp. 31–52). Springer. https://doi.org/10.5822/978-1-61091-183-2_3

Díaz, S. M., Settele, J., Brondízio, E., … Chan, K. (2019). *The global assessment report on biodiversity and ecosystem services: Summary for policy makers*. IPBES.

Dobrowski, S. Z., Thorne, J. H., Greenberg, J. A., Safford, H. D., Mynsberge, A. R., Crimmins, S. M., & Swanson, A. K. (2011). Modeling plant ranges over 75 years of climate change in California, USA: Temporal transferability and species traits. *Ecological Monographs*, *81*(2), 241–257. https://doi.org/10.1890/10-1325.1

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*(1), 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Dufresne, J. L., Foujols, M. A., Denvil, S., Caubel, A., Marti, O., Aumont, O., Balkanski, Y., Bekki, S., Bellenger, H., Benshila, R., Bony, S., Bopp, L., Braconnot, P., Brockmann, P., Cadule, P, Cheruy, F., Codron, F., Cozic, A., Cugnet, D., … Vuichard, N. (2013). Climate change projections using the IPSL-CM5 earth system model: From CMIP3 to CMIP5. *Climate Dynamics*, *40*(9-10), 2123–2165. https://doi.org/10.1007/s00382-012-1636-1

Dyderski, M. K., Paź, S., Frelich, L. E., & Jagodziński, A. M. (2018). How much does climate change threaten European forest tree species distributions? *Global Change Biology*, *24*(3), 1150–1163. https://doi.org/10.1111/gcb.13925

EU. (2007). *LIFE and Europe's wetlands. Restoring a vital ecosystem*. Office for Official Publications of the European Communities.

Finlayson, C. M., & Spiers, A. G. (1999). *Global review of wetland resources and priorities for wetland inventory*. Wetlands International Publication.

Fischer, J., & Lindenmayer, D. B. (2000). An assessment of the published results of animal relocations. *Biological Conservation*, *96*(1), 1–11. https://doi.org/10.1016/S0006-3207(00)00048-3

Foden, W. B., Young, B. E., Akçakaya, H. R., Garcia, R. A., Hoffmann, A. A., Stein, B. A., Thomas, C. D., Wheatley, C. J., Bickford, D., Carr, J. A., Hole, D. G.., Martin, T. G., Pacifici, M., Pearce-Higgins, J. W., Platts, P. J., Visconti, P., Watson, J. E. M., & Huntley, B. (2019). Climate change vulnerability assessment of species. *Wiley Interdisciplinary Reviews: Climate Change*, *10*(1), 1–36. https://doi.org/10.1002/wcc.551

Fournier, A., Barbet-Massin, M., Rome, Q., & Courchamp, F. (2017). Predicting species distribution combining multi-scale drivers. *Global Ecology*

and Conservation, *12*, 215–226. https://doi.org/10.1016/j.gecco.2017.11.002

Gallego-Sala, A. V., Clark, J. M., House, J. I., Orr, H. G., Prentice, I. C., Smith, P., Farewell, T., & Chapman, S. J. (2010). Bioclimatic envelope model of climate change impacts on blanket peatland distribution in Great Britain. *Climate Research*, *45*(1), 151–162. https://doi.org/10.3354/cr00911

Giorgetta, M. A., Jungclaus, J., Reick, C. H., Legutke. S., Bader, J., Böttinger, M., Brovkin, V., Crueger, T., Esch, M., Fieg, K., Glushak, K., Gayler, V., Haak, H., Hollweg, H. - D., Ilyina, T., Kinne, S., Kornblueh, L., Matei, D., Mauritsen, T., … Stevens, B. (2013). Climate and carbon cycle changes from 1850 to 2100 in MPI-ESM simulations for the Coupled Model Intercomparison Project phase 5. *Journal of Advances in Modeling Earth Systems*, *5*(3), 572–597. https://doi.org/10.1002/jame.20038

Guillera-Arroita, G., Lahoz-Monfort, J. J., Elith, J., Gordon, A. Kujala, H., Lentini, P. E., McCarthy, M. A., Tingley, R., & Wintle, B. A. (2015). Is my species distribution model fit for purpose? Matching data and models to applications. *Global Ecology and Biogeography*, *24*(3), 276–292. https://doi.org/10.1111/geb.12268

Guisan, A., Thuiller, W., & Zimmermann, N. E. (2017). *Habitat suitability and distribution models: With applications in R*. Cambridge University Press.

Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., Lovejoy, T. E., Sexton, J. O., Austin, M. P., Collins, C. D. & Cook, W. M. (2015). Habitat fragmentation and its lasting impact on earth's ecosystems. *Science Advances*, *1*(2)e, 1500052. https://doi.org/10.1126/sciadv.1500052

Hällfors, M. H., Liao, J., Dzurisin, J., Grundel, R., Hyvärinen, M., Towle, K., Wu, G. C., & Hellmann, J. J. (2016). Addressing potential local adaptation in species distribution models: Implications for conservation under climate change. *Ecological Applications*, *26*(4), 1154–1169. https://doi.org/10.1890/15-0926

Hengl, T., De Jesus, J. M., Heuvelink, G. B. M., Gonzalez, M. R., Kilibarda, M., Blagotić, A., Shangguan, W., Wright, M. N., Geng, X., Bauer-Marschallinger, B., Guevara, M. A., Vargas, R., MacMillan, R. A., Batjes, N. H., Leenaars, J. G. B, Ribeiro, E., Wheeler, I., Mantel, S., & Kempen, B.. (2017). SoilGrids250m: Global gridded soil information based on machine learning. *PLoS ONE*, *12*(2), e0169748. https://doi.org/10.1371/journal.pone.0169748

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*(15), 1965–1978. https://doi.org/10.1002/joc.1276

Hijmans, R., Phillips, S., Leathwick, J., & Elith, J., & Hijmans, M. (2017). Package "dismo". *Circles*, *9*(1), 1–68.

Hooftman, D. A. P., & Bullock, J. M. (2012). Mapping to inform conservation: A case study of changes in semi-natural habitats and their connectivity over 70years. *Biological Conservation*, *145*(1), 30–38. https://doi.org/10.1016/j.biocon.2011.09.015

Hughes, P. D. M., Lomas-Clarke, S. H., Schulz, J., & Barber, K. E. (2008). Decline and localized extinction of a major raised bog species across the British Isles: Evidence for associated land-use intensification. *Holocene*, *18*(7), 1033–1043. https://doi.org/10.1177/0959683608095574

IPCC. (2014). *Climate change 2014: Synthesis report. contribution of working groups i, ii and iii to the fifth assessment report of the Intergovernmental Panel on Climate Change* [Core Writing Team, Pachauri. R. K, and Meyer L. A., (Eds.). IPCC.

IUCN. (2013). *Guidelines for reintroductions and other conservation translocations. version 1.0*. IUCN.

Jackson, M. M., Gergel, S. E., & Martin, K. (2015). Citizen science and field survey observations provide comparable results for mapping Vancouver Island white-tailed ptarmigan (*Lagopus leucura saxatilis*) distributions. *Biological Conservation*, *181*, 162–172. https://doi.org/10.1016/j.biocon.2014.11.010

Jamieson, I. G. (2011). Founder effects, inbreeding, and loss of genetic diversity in four avian reintroduction programs. *Conservation Biology*, *25*(1), 115–123. https://doi.org/10.1111/j.1523-1739.2010.01574.x

Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, *61*(1), 65–71. https://doi.org/10.2307/1937156

Jones, C. D., Hughes, J. K., Bellouin, N., Hardiman, S. C., Jones, G. S. , Knight, J., Liddicoat, S., O'Connor, F. M., Andres, R. J., Bell, C., Boo, K.-O., Bozzo, A., Butchart, N., Cadule, P., Corbin, K. D., Doutriaux-Boucher, M., Friedlingstein, P., Gornall, J., Gray, L., … Zerroukat, M. (2011). The HadGEM2-ES implementation of CMIP5 centennial simulations. *Geoscientific Model Development*, *4*(3), 543–570. https://doi.org/10.5194/gmd-4-543-2011

Joosten, H. (2012). Status and prospects of global peatlands. *Natur Und Landschaft*, *87*, 50–55.

Joy, J., & Pullin, A. S. (1997). The effects of flooding on the survival and behaviour of overwintering large Heath butterfly *Coenonympha tullia* larvae. *Biological Conservation*, *82*(1), 61–66. https://doi.org/10.1016/S0006-3207(97)00006-2

Jump, A. S., Mátyás, C., & Peñuelas, J. (2009). The altitude-for-latitude disparity in the range retractions of woody species. *Trends in Ecology and Evolution*, *24*(12), 694–701. https://doi.org/10.1016/j.tree.2009.06.007

Jump, A. S., Peñuelas, J., Rico, L., Ramallo, E., Estiarte, M., Martínez-Izquierdo, J. A., & Lloret, F. (2008). Simulated climate change provokes rapid genetic change in the Mediterranean shrub *Fumana thymifolia*. *Global Change Biology*, *14*(3), 637–643. https://doi.org/10.1111/j.1365-2486.2007.01521.x

Krause, C., & Pennington, D. (2012). Strategic decisions in conservation: Using species distribution modeling to match ecological requirements to available habitat. In J. Maschinski, K. Haskins, & P. Raven (Eds.), *Plant reintroduction in a changing climate* (pp. 131–153). Island Press.

Kujala, H., Moilanen, A., Araújo, M. B., & Cabeza, M. (2013). Conservation planning with uncertain climate change projections. *PLoS ONE*, *8*(2), e53315. https://doi.org/10.1371/journal.pone.0053315

Lipsey, M. K., Child, M. F., Seddon, P. J., Armstrong, D. P., & Maloney, R. F. (2007). Combining the fields of reintroduction biology and restoration ecology. *Conservation Biology*, *21*(6), 1387–1390. https://doi.org/10.1111/j.1523-1739.2007.00806.x

Liu, C., White, M., & Newell, G. (2013). Selecting thresholds for the prediction of species occurrence with presence-only data. *Journal of Biogeography*, *40*(4), 778–789. https://doi.org/10.1111/jbi.12058

Louthan, A. M., Doak, D. F., & Angert, A. L. (2015). Where and when do species interactions set range limits? *Trends in Ecology and Evolution*, *30*(12), 780–792. https://doi.org/10.1016/j.tree.2015.09.011

Maes, D., Ellis, S., Goffart, P., Cruickshanks, K. L., van Swaay, C. A. M., Cors, R., Herremans, M., Swinnen, K. R. R., Wils, C., Verhulst, S., De Bruyn, L., Matthysen, E., O'Riordan, S., Hoare, D. J., & Bourn, N. A. D. (2019). The potential of species distribution modelling for reintroduction projects: The case study of the Chequered Skipper in England. *Journal of Insect Conservation*, *23*(2), 419–431. https://doi.org/10.1007/s10841-019-00154-w

Maiorano, L., Chiaverini, L., Falco, M., & Ciucci, P. (2019). Combining multi-state species distribution models, mortality estimates, and landscape connectivity to model potential species distribution for endangered species in human dominated landscapes. *Biological Conservation*, *237*(3), 19–27. https://doi.org/10.1016/j.biocon.2019.06.014

McGuire, J. L., Lawler, J. J., McRae, B. H., Nuñez, T. A., & Theobald, D. M. (2016). Achieving climate connectivity in a fragmented landscape. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(26), 7195–7200. https://doi.org/10.1073/pnas.1602817113

Michel, P., Dickinson, K. J. M., Barratt, B. I. P., & Jamieson, I. G. (2008). Multi-scale habitat models for reintroduced bird populations: A case study of South Island saddlebacks on Motuara Island. *New Zealand Journal of Ecology*, *32*(1), 18–33.

Minayeva, T. Y., Bragg, O. M., & Sirin, A. A. (2017). Towards ecosystem-based restoration of peatland biodiversity. *Mires and Peat*, *19*(1), 1–36. https://doi.org/10.19189/MaP.2013.OMB.150

Morán-Ordóñez, A., Briscoe, N. J., & Wintle, B. A. (2018). Modelling species responses to extreme weather provides new insights into constraints on

range and likely climate change impacts for Australian mammals. *Ecography*, *41*(2), 308–320. https://doi.org/10.1111/ecog.02850

Naimi, B. (2015). usdm: Uncertainty analysis for species distribution models. R package version, 1, 1–12.

Ohlemüller, R., Gritti, E. S., Sykes, M. T., & Thomas, C. D. (2006). Quantifying components of risk for European woody species under climate change. *Global Change Biology*, *12*(9), 1788–1799. https://doi.org/10.1111/j.1365-2486.2006.01231.x

Osborne, P. E., & Seddon, P. J. (2012). Selecting suitable habitats for reintroductions: Variation, change and the role of species distribution modelling. In J. G. Ewen, D. P. Armstrong, K. A. Parker, & P. J. Seddon (Eds.), Reintroduction biology: Integrating science and management (pp. 73–104). Wiley-Blackwell. https://doi.org/10.1002/9781444355833.ch3

Pearson, R. G., & Dawson, T. P. (2003). Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Global Ecology and Biogeography*, *12*(5), 361–371. https://doi.org/10.1046/j.1466-822X.2003.00042.x

Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., & Sexton, J. O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, *344*(6187), 1246752. https://doi.org/10.1126/science.1246752

Poniatowski, D., & Fartmann, T. (2010). What determines the distribution of a flightless bush-cricket (*Metrioptera brachyptera*) in a fragmented landscape? *Journal of Insect Conservation*, *14*(6), 637–645. https://doi.org/10.1007/s10841-010-9293-3

Prentice, I. C., Cramer, W., Harrison, S. P., Leemans, R., Robert, A., & Solomon, A. M. (1992). Special Paper: A global biome model based on plant physiology and dominance, soil properties and climate. *Journal of Biogeography*, *19*(2), 117–134.

R Core Team. (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Sánchez-Fernández, D., Lobo, J. M., & Hernández-Manrique, O. L. (2011). Species distribution models that do not incorporate global data misrepresent potential distributions: A case study using Iberian diving beetles. *Diversity and Distributions*, *17*(1), 163–171. https://doi.org/10.1111/j.1472-4642.2010.00716.x

Seddon, P. J., Armstrong, D. P., & Maloney, R. F. (2007). Developing the science of reintroduction biology. *Conservation Biology*, *21*(2), 303–312. https://doi.org/10.1111/j.1523-1739.2006.00627.x

Slatyer, R. A., Hirst, M., & Sexton, J. P. (2013). Niche breadth predicts geographical range size: A general ecological pattern. *Ecology Letters*, *16*(8), 1104–1114. https://doi.org/10.1111/ele.12140

Stadtmann, S., & Seddon, P. J. (2018). Release site selection: Reintroductions and the habitat concept. *Oryx*, *54*(5), 687–695. https://doi.org/10.1017/S0030605318001199

Stephens, P. A., Mason, L. R., Green, R. E., Gregory, R. D., Sauer, J. R., Alison, J., Aunins, A., Brotons, L., Butchart, S. H., Campedelli, T. & Chodkiewicz, T. (2016). Consistent response of bird populations to climate change on two continents. *Science*, *352*(6281), 84–87. https://doi.org/10.1126/science.aac4858

Suggitt, A. J., Wilson, R. J., Isaac, N. J., Beale, C. M., Auffret, A. G., August, T., Bennie, J. J., Crick, H. Q. P., Duffield, S., Fox, R., Hopkins, J. J., Macgregor, N. A., Morecroft, M. D., Walker, K. J., & Maclean, I. M. (2018). Extinction risk from climate change is reduced by microclimatic buffering. *Nature Climate Change*, *8*(8), 713–717. https://doi.org/10.1038/s41558-018-0231-9

Taylor, G., Canessa, S., Clarke, R. H., Ingwersen, D., Armstrong, D. P., Seddon, P. J., & Ewen, J. G. (2017). Is reintroduction biology an effective applied science? *Trends in Ecology and Evolution*, *32*(11), 873–880. https://doi.org/10.1016/j.tree.2017.08.002

Thomas, J. A., Simcox, D. J., & Clarke, R. T. (2009). Successful conservation of a threatened Maculinea butterfly. *Science*, *325*(5936), 80–83. https://doi.org/10.1126/science.1175726

Thompson, J., Charpentier, A., Bouguet, G., Charmasson, F., Roset, S., Buatois, B., Vernet, P., & Gouyon, P. H. (2013). Evolution of a genetic polymorphism with climate change in a Mediterranean landscape. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(8), 2893–2897. https://doi.org/10.1073/pnas.1215833110

Thuiller, W., Georges, D., Engler, R., & Breiner, F. (2016). biomod2: Ensemble platform for species distribution modeling. R package version 3.3-7.

Titeux, N., Maes, D., Van Daele, T., Onkelinx, T., Heikkinen, R. K., Romo, H., García-Barros, E., Munguira, M. L., Thuiller, W., van Swaay, C. A. M., Schweiger, O., Settele, J., Harpke, A., Wiemers, M., Brotons, L., & Luoto, M. (2017). The need for large-scale distribution data to estimate regional changes in species richness under future climate change. *Diversity and Distributions*, *23*(12), 1393–1407. https://doi.org/10.1111/ddi.12634

Title, P. O., & Bemmels, J. B. (2018). ENVIREM: An expanded set of bioclimatic and topographic variables increases flexibility and improves performance of ecological niche modeling. *Ecography*, *41*(2), 291–307. https://doi.org/10.1111/ecog.02880

Topić, J., & Stančić, Z. (2006). Extinction of fen and bog plants and their habitats in Croatia. *Biodiversity and Conservation*, *15*(11), 3371–3381. https://doi.org/10.1007/s10531-005-4874-2

Trabucco, A., & Zomer, R. (2009). Global aridity index (global-aridity) and global potential evapo-transpiration (global-PET) geospatial database. CGIAR Consortium for Spatial Information.

Urban, M. (2015). Accelerating extinction risk from climate change. *Science*, *348*(6234), 571–573. https://doi.org/10.1126/science.aaa4984

Valiente-Banuet, A., Aizen, M. A., Alcántara, J. M., Arroyo, J., Cocucci, A., Galetti, M., García, M. B., García, D., Gómez, J. M., Jordano, P., Medel, R., Navarro, L., Obeso, J. R., Oviedo, R., Ramírez, N., Rey, P. J., Traveset, A., Verdú, M., & Zamora, R. (2015). Beyond species loss: The extinction of ecological interactions in a changing world. *Functional Ecology*, *29*(3), 299–307. https://doi.org/10.1111/1365-2435.12356

VanDerWal, J., Shoo, L. P., Graham, C., & Williams, S. E. (2009). Selecting pseudo-absence data for presence-only distribution modeling: How far should you stray from what you know? *Ecological Modelling*, *220*(4), 589–594. https://doi.org/10.1016/j.ecolmodel.2008.11.010

Virkkala, R., & Rajasärkkä, A. (2011). Climate change affects populations of northern birds in boreal protected areas. *Biology Letters*, *7*(3), 395–398. https://doi.org/10.1098/rsbl.2010.1052

Wiens, J. J. (2016). Climate-related local extinctions are already widespread among plant and animal species. *PLoS Biology*, *14*(12), 1–18. https://doi.org/10.1371/journal.pbio.2001104

Willi, Y., & Hoffmann, A. A. (2009). Demographic factors and genetic variation influence population persistence under environmental change. *Journal of Evolutionary Biology*, *22*(1), 124–133. https://doi.org/10.1111/j.1420-9101.2008.01631.x

Young, C. H., & Jarvis, P. J. (2001). Measuring urban habitat fragmentation: An example from the Black Country, UK. *Landscape Ecology*, *16*(7), 643–658. https://doi.org/10.1023/A:1013108005347

Zhang, K., Yao, L., Meng, J., & Tao, J. (2018). Maxent modeling for predicting the potential geographical distribution of two peony species under climate change. *Science of the Total Environment*, *634*(9), 1326–1334. https://doi.org/10.1016/j.scitotenv.2018.04.112

SUPPORTING INFORMATION

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

How to cite this article: Bellis, J., Longden, M., Styles, J., Dalrymple, S. Using macroecological species distribution models to estimate changes in the suitability of sites for threatened species reintroduction. *Ecol Solut Evidence*. 2021;*2*:e12050. https://doi.org/10.1002/2688-8319.12050