The influence of climate on past, present, and future conservation translocations

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Declaration

No portion of the work referred to in this thesis has been submitted in support of an application for another degree or qualification of this or any other university or other institute of learning.

Abstract

A large proportion of conservation translocations fail to establish viable populations. Managers often attribute translocation failure to environmental conditions at recipient sites, however, no study has attempted to quantify the importance of environmental conditions, such as climate, in determining past translocation outcomes. In this thesis, I investigate the potential effects of recent and future climatic conditions on translocated populations of ectothermic vertebrate and invertebrate taxa across the globe. Using species distribution modelling techniques, I contrast predicted climate suitability between sites of successful and unsuccessful translocation programmes. I find that the probability of translocation success increases as predicted climate suitability increases. Furthermore, when contrasting the effect of climate suitability against five other variables often considered in the peer-reviewed literature as important to translocation outcome, climate suitability exerted the strongest effect and explained the most variation in translocation outcome. While these results highlight the potential of predicted climate suitability to inform translocation management, the rapidly changing climate means that matching species climatic preferences to existing conditions will be insufficient to secure the long-term viability of translocated populations. I demonstrate this by projecting species distribution models (SDMs) onto scenarios of future climate change for species that have been successfully established through translocation. SDMs project that at least 74% of recipient sites will decline in suitability in the future, and alarmingly, this percentage is based on an optimistic scenario of greenhouse-gas emissions for the near-future (2021-2040). The final data-chapter of this thesis applies the findings and methodologies of the preceding chapters to support conservation decision-making in an ongoing translocation programme in the North West of England, by using SDM outputs to facilitate the prioritisation of translocation efforts towards species with the greatest likelihood of establishing long-term populations under climate change. My findings call for greater integration of the spatiotemporal properties of climate into translocation management planning and suggest that SDMs offer an effective tool for achieving this.

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Contents

Chapter 1:

General Introduction

The recent assessment by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) presents a bleak outlook for global biodiversity, predicting that up to 1 million species are at risk of extinction, many within decades (Díaz et al. 2019). Across the globe, humans are the main evolutionary force driving increased extinction rates (Ceballos et al. 2017). Human activities implicated in the biodiversity crisis include over-exploitation (e.g. fishing, hunting, and poaching), habitat destruction, pollution, introduction of invasive species, and climate change (Díaz et al. 2019). In what is now frequently referred to as the 'Anthropocene' (Zalasiewicz et al. 2011; Waters et al. 2016), human action will be fundamental to halting and reversing further losses of biodiversity (Johnson et al. 2017).

Human actions can take multiple forms, such as the protection of land, management of habitats and threats (e.g. invasive species control), enacting and enforcing laws and policies, captive-breeding, gene-banking, ecosystem restoration and translocation (IUCN 2012). The majority of these actions rely on conservation *in-situ*, while *ex-situ* conservation has typically been considered as a back-up option, for when threats cannot be mitigated onsite (Canessa et al. 2014; Corlett 2016). However, there is growing recognition among conservationists that *ex-situ* approaches, such as the translocation of organisms to more suitable habitat, will be essential to securing viable metapopulations and reversing local extinctions in the future (Prober et al. 2019).

Conservation translocations

Conservation translocations are a popular and widely applied management tool that can aid species recovery and fulfil biodiversity or restoration objectives (Seddon et al. 2014; Hoffmann et al. 2015). Conservation translocations are defined as the deliberate human-mediated movement of organisms from one site for release into another, for the purposes of conservation (IUCN 2013). They can be categorised into four types: (i) reintroduction, introducing an organism within its indigenous range to a site where it became extinct, (ii) reinforcement, introduction within the indigenous range to an existing population of conspecifics, (iii) assisted colonisation, introduction beyond the indigenous range, and (iv) ecological replacement, introduction beyond the indigenous range to fulfil a missing ecosystem function.

As a conservation tool, reintroduction is perhaps the most well-known type of translocation, with a number of high-profile reintroductions of charismatic vertebrate species in the 1970s and 1980s raising awareness of the approach (e.g. Stanley Price 1989; Kleiman & Mallinson 1998; Cade & Burnham 2003). However, the available data from reintroductions undertaken during this period suggests that the majority of programmes failed to establish viable populations (Griffith et al. 1989; Wolf et al. 1996). The situation was exacerbated by a lack of monitoring in early reintroductions, so the causes of failure remained unknown (Seddon et al. 2007). These issues led to numerous calls in the literature for greater post-release monitoring of reintroduced populations (Armstrong & McLean 1995; Sarrazin & Barbault 1996; Hein 1997) and prompted formation of the World Conservation Union (IUCN) Reintroduction Specialist Group (RSG) in 1988 to provide guidance for reintroduction programmes. Since this time, through workshops and the publication of best-practice guidelines (IUCN 1998, 2013), there has been a considerable increase in monitoring and in the number of peer-reviewed publications in the conservation translocation literature (Seddon et al. 2007; Taylor et al. 2017). These advances have increased knowledge and furthered the field of conservation translocations, allowing progressively more challenging translocations to be attempted (e.g. Bouma et al. 2020).

Translocations as a conservation tool are now supported by several international and national governing bodies. In the European Union, there is a legal obligation for member states to consider the reintroduction of formally native species listed under Annex IV of the “Habitats Directive” (EC 1992). In Scotland, the devolved government has produced a framework on how to assess and plan conservation translocations (NSRF 2014) and England looks set to follow suit based on its recently published 25 Year Environment Plan (HM Government 2018). While in New Zealand, the Department of Conservation has provided a guide for community groups and other organisations to aid the planning and implementation processes of a conservation translocation (DOC 2012).

Despite advancements in the conservation translocation field, many translocation attempts still fail to establish viable populations, with estimated success rates varying from 20% to 60%, depending on the taxonomic group (Fischer & Lindenmayer 2000;

Germano & Bishop 2009; Godefroid et al. 2011; Dalrymple et al. 2012; Cochran-Biederman et al. 2015). Given the potential high costs (both financial and biological) associated with programme failure, research into the factors influencing translocation outcomes is critical to improving the prospects of future attempts (IUCN 2013). Species- and programme-specific factors such as the length of supplementary feeding (White et al. 2012), homing tendency (Germano & Bishop 2009), and behavioural variation (Bremner-Harrison et al. 2004; Sinn et al. 2014) have been shown to influence translocation outcomes. Additionally, several reviews across a range of taxonomic groups have identified broader correlates of translocation success, such as habitat quality at the recipient site, total number of released individuals, life stage of released individuals, and the choice of source population (wild or captive) (Griffith et al. 1989; Fischer & Lindenmayer 2000; Germano & Bishop 2009; Cochran-Biederman et al. 2015; Rummel et al. 2016). However, the relative importance of these factors varies between groups, most likely due to differing life-history traits (e.g. Ducatez & Shine 2019). Moreover, the importance of other potentially influential factors such as the climatic conditions of recipient sites, have not been broadly assessed in the peer-reviewed literature. Despite climate constituting a fundamental component of overall habitat suitability, past translocation attempts have often focused on the physical attributes of a potential recipient site to describe habitat suitability (e.g. Soorae 2008, 2010, 2011, 2013, 2016), or relied on the subjective intuition of involved parties (Osborne & Seddon 2012).

Ecological models

Outputs from ecological models, produced using the best available data and an understanding of ecological mechanisms, can increase objectivity in translocation decision-making. Hunter-Ayad et al. (2020) identify four key components of a translocation that can be informed by ecological modelling: habitat suitability (e.g. species distribution models, Maes et al. 2019), dispersal processes (e.g. least cost path models, Alexander et al. 2016), population dynamics (e.g. stochastic population models, Panfylova et al. 2016), and interspecies interactions (e.g. co-occurrence models, Lamothe et al. 2019). While models of each component can yield valuable practical insight, the first step should always be an assessment of habitat suitability. This is because if habitat at the recipient site does not meet the requirements for population persistence, the translocated population will not make it past the establishment phase (Armstrong & Seddon 2008).

Species distribution models

Estimating the habitat suitability of potential translocation recipient sites is possible with the use of species distribution models (also commonly referred to as habitat suitability models, ecological niche models, or bio-climate envelope models when climate variables are the main covariates). In their most widely used form, species distribution models (SDMs) identify correlations between multiple environmental descriptors (e.g. climate, altitude, landcover or soil type) and species occurrence records to produce spatially explicit predictions of habitat suitability (Guisan et al. 2017), although more mechanistic modelling approaches (Kearney & Porter 2009), and approaches involving expert opinion (Larson et al. 2004), also exist. Conceptually, correlative SDMs assume that a species is restricted to the portion of environmental space in which it is currently known to occur, often referred to as the 'realised niche' (sensu Hutchinson 1957).

Owing to the increased availability of biological and environmental data across a range of spatial and temporal scales (e.g. Fick & Hijmans 2017; Hengl et al. 2017; La Sorte & Somveille 2020), SDMs can now predict habitat suitability more reliably, and for more species, than ever before. This creates great potential for SDMs to support conservation decision-making (Guisan et al. 2013); output maps have effectively been applied to locate new populations of threatened species (e.g. Williams et al. 2009; McCune 2016), inform invasive species risk assessments, establish conservation priority areas, and identify translocation recipient sites (Guisan et al. 2013). The potential of SDMs for aiding recipient site selection is now widely acknowledged, having been the focus of multiple book chapters (Krause & Pennington 2012; Osborne & Seddon 2012), peer-reviewed papers (e.g. Hoegh-Guldberg et al. 2008; Chauvenet et al. 2013; Guisan et al. 2013), and a section in the IUCN's Guidelines for reintroductions and other conservation translocations (IUCN 2013).

At the macroecological scale ($\geq$ 1km), SDMs can identify areas with high habitat suitability for a translocation, while at finer spatial scales models can assess suitability within recipient areas to pinpoint the optimal release location, or to target active management efforts such as supplementary feeding. In recent years, translocation programmes involving insects (Maes et al. 2019), birds (Kalle et al. 2017), freshwater fish (Malone et al. 2018) and lichens (Brooker et al. 2018) have applied SDM techniques to estimate the suitability of candidate recipient sites. However, there are multiple potential pitfalls for the unwary user, which can impact model outputs and resulting management proposals (Guillera-Arroita et al. 2015; Araújo et al. 2019). For example, models constructed for species with small remaining distributions, as is frequently the case in conservation translocations, risk underestimating the range of potentially suitable environmental conditions (Franklin et al. 2009). Additionally, actual distributions may not be limited by environmental factors, but instead by dispersal barriers or biotic interactions, which can lead to misrepresentations of the species niche (Svenning & Sandel 2013). These factors, along with the challenge of making outputs interpretable for broad audiences, have inhibited the contribution of SDMs to management decision-making (Sofaer et al. 2019). However, thoughtful construction of SDMs with rigorous quality controls of input data and the production of model outputs that are tailored to the intended use can result in valuable predictions that can effectively support management decision-making (Araújo et al. 2019; Sofaer et al. 2019).

Projecting species distribution models

The impacts of climate change can be profound and, in recent years, have become increasingly observable (Scheffers et al. 2016). Many aspects of biodiversity are affected by climate change, including species distributions, phenology, population dynamics, community structure and ecosystem function (Díaz et al. 2019). In a global assessment of climate change impacts, local extinctions of natural populations were documented in 47% of 976 animal and plant species surveyed (Wiens 2016). The impacts of the changing climate are broad, reaching across biological kingdoms, latitudes, terrestrial biomes, and habitat types (Scheffers et al. 2016), and the rate of biodiversity loss as a result of this change is only forecast to accelerate (Urban 2015). If conservation is to be effective against this ubiquitous threat, management plans need to address the following question: What effect is climate change likely to have in the future?

SDMs offer an approach to forecast spatiotemporal changes in suitability under scenarios of future climate change (Araújo *et al.*, 2019; Foden *et al.*, 2019). Using a combination of general circulation models, which predict potential changes in atmospheric and oceanic processes, and greenhouse gas emission scenarios, which estimate alternative paths of societal development, SDM users can project their models to future time horizons. Future climatic variables from Intergovernmental Panel on Climate Change (IPCC) projections have been downscaled to more ecologically relevant resolutions and are openly available on databases such as WorldClim (Hijmans et al. 2005; Fick & Hijmans 2017) and CHELSA (Karger et al. 2017). By anticipating what is likely to happen in the future, projections from SDMs can help conservation managers to be more proactive in their decision-making, something which has been repeatedly called for in the peer-reviewed literature (Heller & Zavaleta 2009; Stein et al. 2013; Hagerman & Satterfield 2014; Prober et al. 2017).

In the context of conservation translocations, future projections can identify the location of climate refugia, which may be sites beyond the indigenous range (Chauvenet et al. 2013), or sites that are projected to remain stable within it (Osborne & Seddon 2012). While there has been significant scientific interest regarding the potential of SDMs to locate suitable areas beyond the indigenous range under climate change (e.g. Hoegh-Guldberg et al. 2008; Chauvenet et al. 2013; Lunt et al. 2013; Gallagher et al. 2015), practical examples of translocations being undertaken for climate change mitigation purposes are limited (Butt et al. 2020). There are even fewer examples of translocation programmes utilising future projection outputs to locate climatically stable areas within the indigenous range (i.e. for a reintroduction) (but see Maes et al. 2019). This is surprising given the widespread and well-publicised impacts of climate change, many of which could affect populations of translocated species that are often already of high conservation concern (Seddon et al. 2014).

Thesis structure and overview

Given the limited success rate of conservation translocations, it is critical that factors influencing outcomes are identified and their impact quantified. With translocations increasingly being undertaken, valuable opportunities to build on results from past attempts are arising. Quantitative global reviews, which are often taxonomically specific, have provided important information on how managers can optimise their translocation strategies. However, recommendations for optimisation vary between taxonomic groups, and some groups such as insects are yet to be the focus of a global review. Moreover, key factors that could potentially affect the outcome of conservation translocations have not been investigated, such as the climatic conditions of recipient sites. Two leading researchers in the fields of species distribution modelling and conservation translocations flagged poor recipient site selection as a major impediment to translocation success, noting that past attempts have often relied on previous occupancy and the intuition of involved parties to assess and select sites (Osborne & Seddon 2012). To date, no empirical association between climatic conditions at recipient sites and translocation outcome has been made, but if such an association is detectable using SDM techniques, these same techniques can help to better-inform recipient site selection in future translocation programmes. In addition, this association would allow managers to more confidently project SDM outputs onto scenarios of future climate change, to determine if and when recipient site conditions will become increasingly or decreasingly aligned with the preferences of focal species.

The goal of this thesis is to broaden our understanding of the factors that influence conservation translocations, so that future efforts can utilise this information to improve their probability of success. This thesis is structured as four research chapters, each written as stand-alone papers. The content of each chapter is briefly outlined below.

Chapter two investigates the factors that explain the successes and failures of terrestrial insect translocations globally. While peer-reviewed articles on correlates of translocation success have been published for most major classes of animal taxa, I identified a clear gap in the literature for terrestrial insect species.

Chapter three follows on from the results of Chapter two by focussing on the importance of climate as a determinant of translocation success for ectothermic taxa, including terrestrial insects, amphibians, and reptiles. I compare climate suitability predictions between sites of successful and failed translocation programmes and then quantify the importance of climate suitability relative to five other variables commonly reported in the literature.

Chapter four investigates the potential future impacts of climate change at recipient sites where translocations have been successful, according to the definition adopted in Chapter three. I assess the resilience of these sites to projected climate change relative to the rest of each species regional and global ranges. I then identify spatial attributes of recipient sites that are associated with higher levels of climate stability.

Chapter five utilises the methods applied and developed throughout the thesis to support management decisions for a series of planned conservation translocations in the North West of England. Working with partners from NGOs, private organisations and academic institutions, the candidacy of thirteen plant and invertebrate species earmarked for reintroduction is assessed. This work focuses on the macroecological suitability of the potential recipient sites for each species, and how this may change under projected climate change.

Chapter six synthesises the findings of the previous four research chapters, discusses the limitations of my work, and considers future avenues of research arising from this thesis.

In combination, this work will improve the outcomes of future conservation translocations and provide threatened species with a better chance of survival in this rapidly changing world. Besides the ecological value of these species, it is expensive to collect or rear individuals for translocation and to maintain source populations that are healthy enough to sustain harvest. Identifying factors that can help to improve the effectiveness of translocations will minimise the loss of ecologically, financially and genetically valuable individuals in future programmes.

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Chapter 2:

Identifying factors associated with the success and failure of terrestrial insect translocations

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Abstract

Translocation is increasingly used as a management strategy to mitigate the effects of human activity on biodiversity. Based on the current literature, we summarised trends in terrestrial insect translocations and identified factors associated with success and failure. As the authors' definitions of success and failure varied according to the individual sets of goals and objectives in each project, we adopted a standardised species-specific definition of success. We applied generalised linear models and information-theoretic model selection to identify the most important factors associated with translocation success. We found literature documenting the translocation of 74 terrestrial insect species to 134 release sites. Of the translocations motivated by conservation, 52% were considered successful, 31% were considered to have failed and 17% were undetermined. Our results indicate that the number of individuals released at a translocation site was the most important factor associated with translocation success, despite this being a relatively infrequent perceived cause of failure as reported by authors. Factors relating to weather and climate and habitat quality were the most commonly perceived causes of translocation failure by authors. Consideration of these factors by managers during the planning process may increase the chance of success in future translocation attempts of terrestrial insects.

Introduction

Translocation represents a valuable tool for wildlife conservation (Fischer and Lindenmayer, 2000; Germano and Bishop, 2009). There has been substantial growth in translocation practice during the past three decades (Seddon et al., 2007; Taylor et al., 2017), resulting in a taxonomically diverse assemblage of translocation case studies. In response to the growing use of translocation as a management tool, the International Union for the Conservation of Nature (IUCN) published a set of broad guidelines in 2013 for conservation-based translocations (IUCN, 2013). These guidelines offer a detailed framework for all phases of a translocation, generalised for all organisms and have likely contributed to the successful recovery of threatened species. In addition to the IUCN guidelines, there have been a number of global reviews, covering amphibians and reptiles (e.g. Dodd and Seigel, 1991; Germano and Bishop, 2009), birds and mammals (Griffith et al., 1989; Wolf et al., 1996), plants (Dalrymple et al., 2012), freshwater fish (Cochran-

Biederman et al., 2015) and freshwater macroinvertebrates (Jourdan et al., 2018). The majority of these reviews also aim to improve the success rate of translocations for their focal taxa, by identifying specific factors associated with success. Terrestrial insects represent one of the major taxonomic classes that is yet to be the focus of a global review. Terrestrial insects are defined as insect species with lifecycles that are partly or fully dependent on habitats existing in the terrestrial environment.

The Class Insecta has the highest abundance, biomass and diversity in the animal kingdom (Wilson, 1987; Kim, 1993). Insects occupy almost every type of terrestrial habitat and they provide numerous ecosystem services (Losey and Vaughan, 2006). The value of their ecosystem services has been conservatively estimated at US$57 billion per year in the United States alone (Losey and Vaughan, 2006). Despite their enormous contribution, insects are often neglected in conservation strategies, which typically focus on more iconic vertebrate species (Seddon et al., 2005). The lack of attention given to insects is reflected by the paucity of policies that protect them, for example, legislation in Europe protects only 0.12% of the region’s insect species (Leandro et al., 2017). This figure is concerning, particularly given recent research revealing a dramatic global decline in insect populations that could lead to the extinction of over 40% of the world’s insect species during the next few decades (Sánchez-Bayo and Wyckhuys, 2019). The growing recognition of the global decline in insect populations (e.g. Hallmann et al., 2017; Vogel 2017; Taylor et al., 2018) is likely to increase the demand for methods and approaches, such as translocation, to restore lost species and functions.

Despite having not featured as frequently in translocation projects as vertebrate groups such as birds and mammals (Seddon et al., 2005), the life-history attributes of insects would suggest they are potentially ideal candidates for translocation. The small body size and short generation time of insects makes them comparatively low cost and quick to propagate in preparation for a translocation (Balmford et al., 1996). They also require smaller habitat patches to support viable populations compared to most vertebrate species (e.g. Baur et al., 2017), meaning pre- and post-release habitat management costs are more economical. Indeed, many managers already recognise the candidacy of insects for translocation, which has led to the instigation of insect translocation projects for a variety of motivations including conservation (e.g. Baur et al., 2017), mitigation (e.g.

Simon et al., 2016), research (e.g. Forsman et al., 2012) and biological control (e.g. Kapranas et al., 2014).

In this paper, we begin by exploring the global trends in terrestrial insect translocations. This includes regional trends, taxonomic trends and their respective biases. We will then focus more specifically on conservation translocations with the objective of identifying the general mechanisms that explain past successes and failures. Knowledge of such mechanisms has the potential to inform future management decisions, and encourage further investigation into how these and other factors influence translocation outcome for terrestrial insects.

Methodology

Data Collection

We performed a literature search to find examples of terrestrial insect translocations from across the globe. We used the search engines 'Thomson Reuters Web of Science' and 'Directory of Open Access Journals', and the 'Conservation Evidence Individual Studies repository' to retrieve relevant papers published at the earliest possible date up until 08/10/2018 (for further detail on the search methodology and search terms used on each platform, see Appendix 2.1). Once we had performed the search, we imported all of the resulting papers into EndNote referencing software and manually screened each record to verify its relevance to insect translocation. Articles were not included in the study if they were irrelevant to insect translocation based on their title and abstract or upon further scrutiny of the paper. We also screened the bibliographies of each relevant publication identified during our search to find additional studies of relevance. Using the methods outlined above, we found two national cross-taxonomic translocation reviews, one for the United Kingdom (Carter et al., 2017) and one for New Zealand (Sherley et al., 2010), which led to the addition of eighteen translocation projects that were not found individually through our search methodology. In every case, this was because these translocations were restricted to the grey literature or unpublished reports and accounts.

Once our literature search was complete, we categorised each translocation project based on its primary motivation. We identified five types of translocation motive from the dataset: conservation, mitigation, research, functional restoration and biological control. We could often infer the motivation of the translocation based on the article's stated aims or objectives and these were recorded accordingly. However, this was not possible for every article, in which case authors were contacted to corroborate. We categorised translocations as research-motivated if they aimed to further the field of conservation translocations through the release of insects in more experimental circumstances. For example, Willis et al. (2009) translocated two common butterfly species ~35 and ~65 km beyond their current ranges in the United Kingdom to test the use of species distribution models for identifying potential assisted colonisation release sites. In this study, the aim was to test the principle of the approach, rather than to establish populations of the two species for conservation purposes. We made the decision to remove biological control-related articles from the dataset, as this is an extensive discipline with core objectives that diverge significantly from the ones typical of the other motives. As one of the primary goals of our study is to identify the key determinants of success in insect translocations, we split the dataset based on motivation. Every translocation, irrespective of motivation (except biological control), was used to identify general trends in insect translocations, such as regional and taxonomic biases, i.e. descriptive statistics. However, in order to identify the key determinants of success using statistical analyses, we incorporated only translocations where the primary motivation was conservation. This decision was made because conservation translocations principally aim to establish a viable population (IUCN, 2013), whereas translocations motivated by other factors often do not (e.g. Willis et al., 2009; Pratt and Emmel, 2010; Forsman et al., 2012).

Data Extraction and Refinement

For every translocation, we collected data on the Order of species translocated, continent and country of translocation, type of translocation, motivation of translocation and year of release. For conservation translocations, we also collected data on most recent year of monitoring, population status at most recent year of monitoring, origin of source population, number of release years, life stage of released individuals, total number of each life stage released across all years, distance between release site and source population (if translocation was from wild to wild) and perceived cause of project failure (if applicable). We identified this set of variables based on their potential importance for terrestrial insect translocations and their inclusion and relative importance in previous translocation reviews (e.g. Germano and Bishop, 2009; Rummel et al., 2016). The one exception being distance between release site and source population, which to our knowledge has not been considered in previous reviews, but is potentially important given the general assumption that populations that are physically closer to the release site will be better adapted to the environmental conditions present (e.g. IUCN, 2013). If the source individuals originated from both wild and captive-bred populations (*n*=4), we treated the source population as 'captive-bred'. Translocations that used headstarted individuals (*n*=2) were also grouped with 'captive-bred', as they had spent at least part of their lifecycle in captive conditions. In order to maximise the amount of data available for statistical analyses, we grouped translocation projects that released larvae, pupae or nymphs into one variable state labelled 'immatures'. Variable states with a small sample size (<4) were not included in the statistical analyses (e.g. release of 'colonies', *n*=2). In cases where we could not obtain all the required information by examining relevant articles we contacted authors directly to acquire missing information.

Defining Translocation Success

The authors' definitions of success varied according to the individual set of goals or objectives in each study. There is still no general and broadly accepted definition of translocation success (Robert et al., 2015), therefore, in order to conduct a more objective analysis, we adopted a species-specific approach to defining translocation success. We considered a translocation successful if it met two criteria: i) the time elapsed between the most recent release and most recent post-release monitoring exceeded the lifecycle duration of the species and ii) the most recent monitoring results indicated population persistence at the release site. If a translocation did not meet these criteria, we did not necessarily consider the translocation to be unsuccessful, as a failure to meet this definition was often due to a lack of post-release monitoring; in this case the outcome was classified as undetermined. If the length of the lifecycle of a species was unknown, then we placed a minimum threshold of five years between date of latest release and date of latest monitoring. This covers most insects except in exceptional cases e.g. cicadas and certain wood boring beetles, such as Cerambycidae and Buprestidae.

Statistical Analyses

We used a generalised linear model (GLM) with a logit link and binomial random component that can be used with mixed data categories to identify variables associated with successful translocations (see Table 2.1 for list of predictor variables). The binary response variable was success or failure. We refer to this statistical approach herein as logistic regression. As our statistical analyses were of a more exploratory than confirmatory nature, we included all single-variable models and models with two-way interactions that represent potentially meaningful ecological relationships between variables and are not in breach of the assumptions of logistic regression analysis.

Table 2.1. Predictor variables used in generalised linear models to identify factors relating to terrestrial insect translocation success.

Variable abbreviation	**Variable description (states)**
LifeHistory	Life History (Hemimetabolous or Holometabolous)
LifeStageRel	Life stage released (Adults, Immatures, Eggs or Mixed)
NRelYears	Total number of release years
NumRel	Total number of individuals released
Origin	Origin of source population (Wild or Captive-bred)

We used the information-theoretic approach to compare the different models by methods based on the Kullback-Leibler distance (Burnham and Anderson, 2003). Models were ranked using Akaike's information criterion corrected for small sample size (AICc). This method encourages parsimony by applying a penalty for the number of parameters in a model (Burnham and Anderson, 2003). AICc differences ($\triangle_i$) representing the distance between the selected (best) model and *i*th model were also calculated. AICc differences were then used to estimate Akaike weights (w_i), indicating the probability that a particular model performed best for the sampling situation under consideration. All analyses were performed in R (Version 3.5.1) using the AICcmodavg package (Mazerolle and Mazerolle, 2017).

Values for the distance between source population and release site variable (SourceRelDist) could only be calculated for translocation projects that sourced wild individuals. As this caused SourceRelDist to be correlated with Origin, a separate analysis was conducted to test for differences in translocation outcome based on SourceRelDist. Shapiro-Wilk normality tests suggested that neither the original nor the log-transformed data followed a normal distribution. Therefore, the non-parametric Mann-Whitney U test (Mann and Whitney, 1947) was adopted to compare the distributions of success and failure.

Results

We found literature documenting the translocation of 74 terrestrial insect species to 134 release sites. A total of seven different taxonomic orders received translocations (Figure 2.1). Lepidoptera was the most frequently translocated Order with 52 translocations (39%) involving this group, while Orthoptera was second with 39 translocations (29%) (see the Appendix 2.2 for a list of species translocated). Translocations of insect species were most commonly conducted on the European continent (*n*=74), with Oceania (*n*=35) and North America (*n*=19) carrying out the second and third most translocations respectively (Figure 2.2). There were a very limited number of terrestrial insect translocations in Africa, Asia and South America.

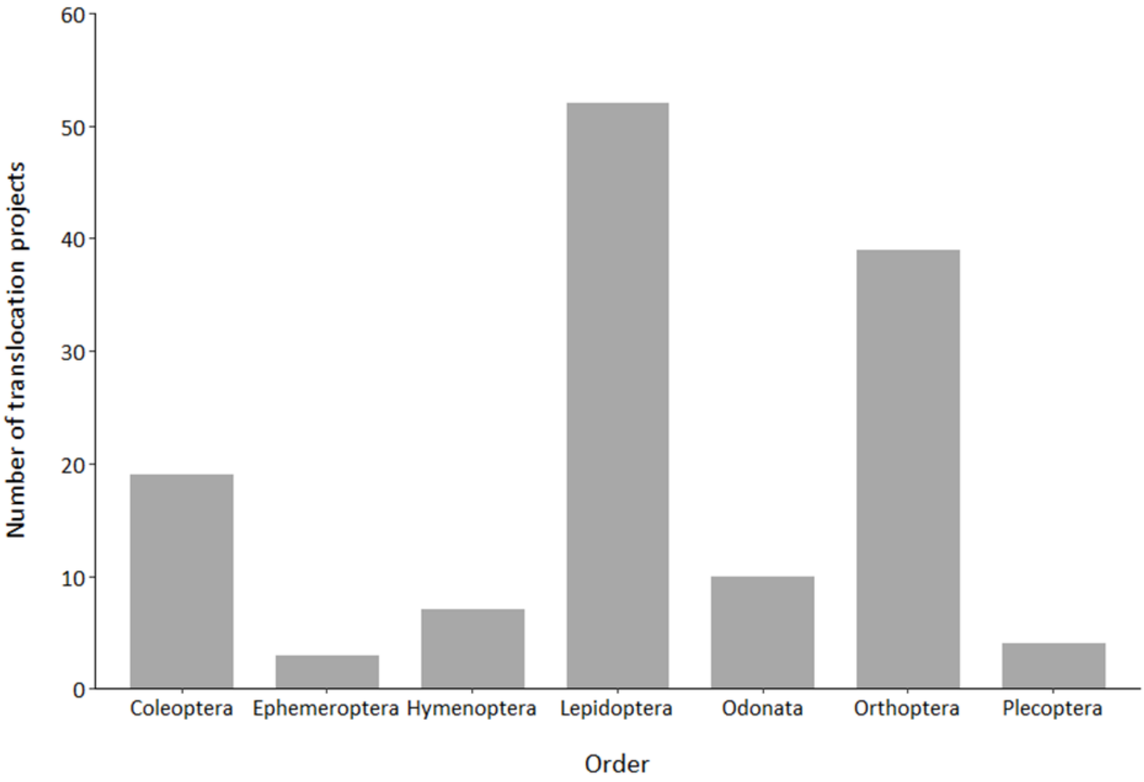

Figure 2.1. Number of terrestrial insect translocations reviewed for each insect Order (*n*=134).

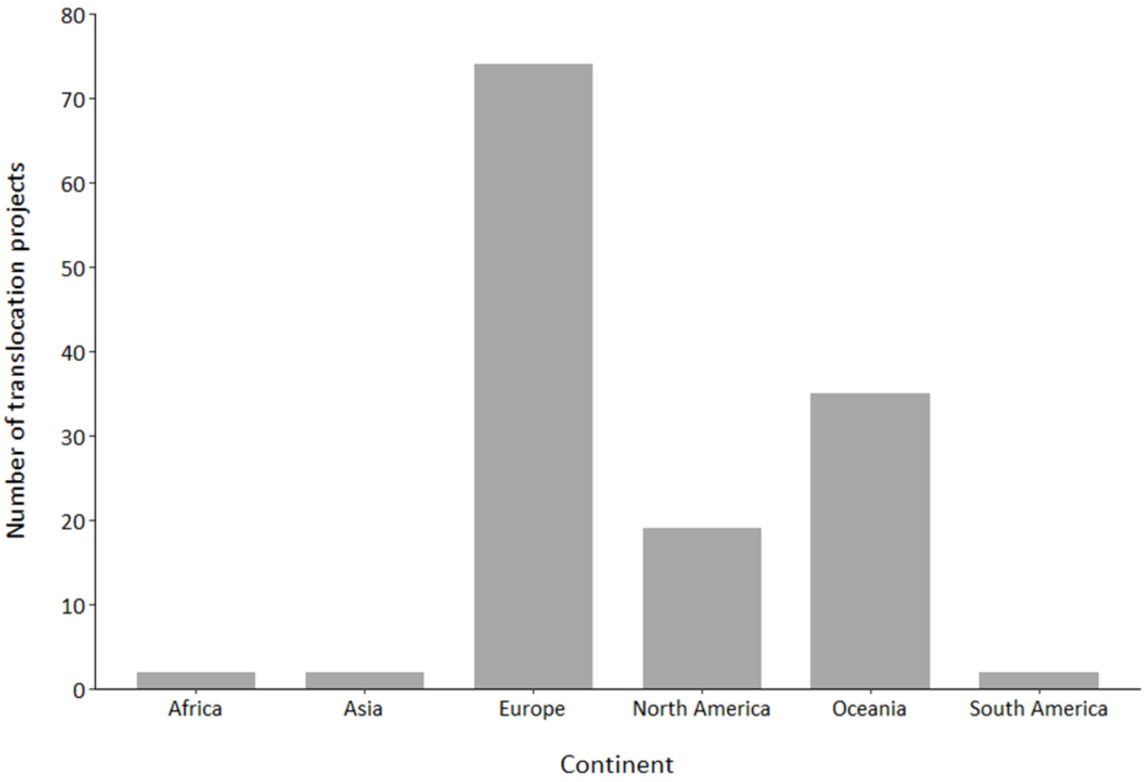

Figure 2.2. Number of terrestrial insect translocations reviewed by continent (*n*=134).

There were some notable regional biases in the orders targeted for translocation projects (Appendix 2.2). For example, Orthoptera, the second most frequently translocated order globally, were not the subjects of any translocation projects in North America, but comprised the majority of projects in Oceania (71%). In Europe and North America, the taxonomic bias was skewed more towards Lepidoptera species, with 54% and 58% of translocation projects comprising this group, respectively. Just one project focused on the translocation of a Lepidoptera species in Oceania.

Conservation was the most commonly identified motivation behind terrestrial insect translocation projects, with a total of 107 translocations being conducted for this purpose. Research was a relatively frequent motivation (n=20), whereas translocations for mitigation (n=4) or functional restoration (n=3) were uncommon.

Based on our success criteria, 56 conservation translocation projects were successful (52%), 33 failed (31%) and 18 were undetermined (17%). Based on a subset of these translocations that were eligible for statistical analysis, the information-theoretic model selection resulted in the highest ranked logistic regression model consisting of the number of individuals released (NumRel) as a single predictor variable (Table 2.2). The second and third highest ranked models also featured the NumRel variable, with Origin and LifeHistory as additive terms, respectively. When Origin and LifeHistory were taken individually the models had considerably less support, suggesting that NumRel was more influential than these two variables. A proportion of support was given to every model considered in the analysis, with the three highest performing models accounting for 40% of the Akaike weights, which we acknowledge as being relatively low. However, the consistent presence of NumRel amongst the top performing models suggests that this variable was the most important determinant of success for terrestrial insect translocations.

Table 2.2. Information-theoretic model selection results for models relating predictor variables with the probability of successful translocation of terrestrial insect species. Number of estimable parameters (k), the second order Akaike Information Criterion (AICc), the Akaike differences ($\triangle \boldsymbol{i}$) and the Akaike weights (w_i) are presented.

Model description	**K**	**AICc**	$\triangle_i$	$\mathbf{w}_i$
NumRel	2	104.27	0	0.19
NumRel + Origin	3	104.96	0.69	0.13
NumRel + LifeHistory	3	105.87	1.6	0.08
Origin	2	106.38	2.12	0.06
LifeHistory	2	106.40	2.14	0.06
NumRel + NRelYears	3	106.42	2.15	0.06
NRelYears	2	106.78	2.52	0.05
LifeStageRel	4	106.86	2.59	0.05
NumRel * Origin	4	106.97	2.71	0.05
NumRel * LifeHistory	4	108.09	3.82	0.03
NumRel * NRelYears	4	108.15	3.88	0.03
Origin + LifeHistory	3	108.16	3.89	0.03
NRelYears + Origin	3	108.34	4.07	0.02
NRelYears + LifeHistory	3	108.43	4.16	0.02
LifeStageRel * LifeHistory	8	108.46	4.2	0.02
LifeStageRel + LifeHistory	5	108.46	4.2	0.02
NRelYears + LifeStageRel	5	109.14	4.87	0.02
Origin + LifeStageRel	5	109.14	4.87	0.02
Origin * LifeHistory	4	109.33	5.06	0.01
NRelYears * Origin	4	109.75	5.49	0.01
NRelYears * LifeHistory	4	110.41	6.14	0.01
NRelYears * LifeStageRel	7	110.99	6.73	0.01
Origin * LifeStageRel	8	111.02	6.76	0.01

Successful translocation projects released more individuals than failed projects - successful projects released a mean average of 2030 ± 706 individuals, while failed projects released a mean average of 667 ± 166 individuals. Most terrestrial insect translocation projects sourced their stock from wild populations, with 66% of translocation projects opting to release wild-caught individuals. Success rate was 67% when using wild stock, which was marginally higher than the 59% success rate achieved by translocation projects that used captive-bred stock. The average distance between source population and release site was 110.9 ± 28.9 km. However, there was no statistically significant difference in the distance separating source population and release site between successful and failed translocation projects (*p*=0.714).

Habitat quality, as well as weather and climate, were the most frequently cited causes of translocation failure according to those involved with terrestrial insect translocation projects (Figure 2.3). Of the 33 insect translocations that resulted in failure, over a third were believed to have failed due to poor habitat quality or the effects of weather and climate at the release site. After these two factors, the main reported causes of translocation failure were predation pressure and pollution. Factors relating to the technique of a translocation were rarely considered as potential causes of failure. Similarly, an insufficient number of individuals released was rarely considered as a potential cause of failure (*n*=2), despite successful translocation projects releasing an average of around three times as many individuals compared to those that failed.

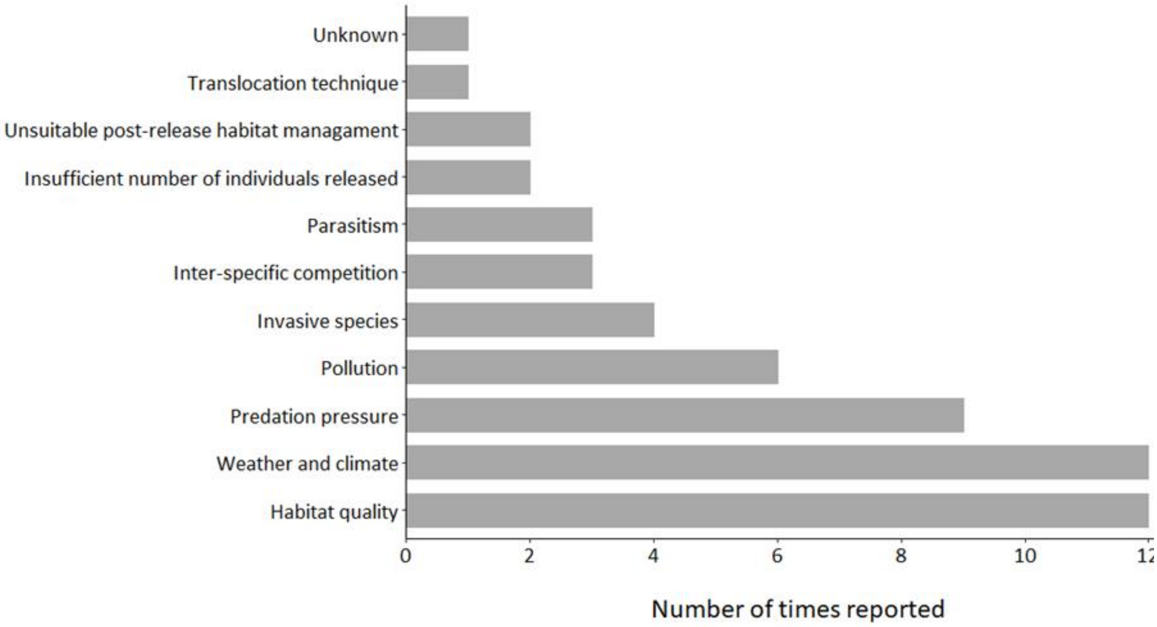

Figure 2.3. Factors reported as influencing the failure of terrestrial insect translocations (*n*=33). Several influential factors may have been reported for a single translocation project.

Discussion

The state of terrestrial insect translocations

The terrestrial insect translocation literature is regionally and taxonomically diverse, and contains a wealth of case studies possessing the potential to inform future translocation management decisions. Of the translocation projects summarised here, around half were defined as successful. This figure is slightly higher than the success rates reported for other animal groups (e.g. Griffith et al., 1989; Germano and Bishop, 2009), suggesting that insects respond comparatively well to translocation. Although more translocations were defined as successful (52%), the proportion of undetermined (17%) and failed translocations (31%) suggests that there is room for improvement in terms of planning and conducting terrestrial insect translocations, as well as post-release monitoring and the reporting of results.

Unlike for other animal taxa (Fischer and Lindenmayer, 2000; Seddon et al., 2014), the majority of insect translocation projects originated from Europe, rather than Oceania or North America. This places Europe as a global leader in insect translocations, a position that has generally been filled by Oceania with respect to vertebrate translocations due to the large number of translocations that have been undertaken there (Fischer and Lindenmayer, 2000; Seddon et al., 2014). It is possible that some regional biases were introduced to the dataset through our decision to include national translocation reviews (e.g. Sherley et al., 2010; Carter et al., 2017). However, the omission of these reviews would have had little effect on the regional trends that were detected via our search methodology (Figure 2.1 and Figure 2.2) and their inclusion provided valuable additional case studies for analysis.

Taxonomic biases in reintroduction projects have been noted in the past towards different vertebrate groups (Seddon et al., 2005), and our findings indicate similar biases in insect translocations. These biases may be partly explained by the composition of regional and national conservation lists of species-of-concern (e.g. Walsh et al., 2013). In the United States, Lepidoptera, Coleoptera and Odonata dominate conservation priorities, representing a combined total of 89% of insect species listed, a proportion far greater than the relative species diversity in these orders (Bossart and Carlton 2002). In the present study, Lepidoptera formed the majority of insect translocations in the United States (58%), despite this group accounting for just 12.6% of insect species in the country (Bossart and Carlton, 2002). Conversely, we did not find any translocation projects targeting Diptera or Hemiptera species in the United States (or globally), despite these two orders accounting for a combined total of 34.1% of the named insect species in the country. Bossart and Carlton (2002) suggest that these taxonomic biases are likely as a result of both the iconic appeal of taxa such as Lepidoptera, and the availability of taxonomic specialists. These factors appear to be driving insect translocations globally, and they threaten the viability of countless other species by potentially misdirecting conservation priorities and limited resources towards species perceived as iconic or interesting (e.g. Sitas et al., 2009; Di Marco et al., 2017).

There are many motivations behind animal translocations (Seddon et al., 2012) with conservation the most frequently identified motivation in the present study due to our search focus. However, translocations motivated by biological control, which were beyond the scope of this study, are frequently conducted with insects as the control agent species. Biological control has been used extensively around the world: 6,158 documented insect introductions were conducted prior to 2010 for this purpose (Cock et al., 2016), of which 32.6% resulted in the establishment of the control agent species. This level of establishment is high given that such a large proportion of biological control releases are far outside the species indigenous range (e.g. Dahlsten et al., 1998; Chauzat et al., 2002; Quacchia et al., 2007). Although the field of biological control is ecologically, economically and socially divergent from that of conservation translocations, there remains scope for practical skill exchange. Biological control programmes often involve highly skilled entomologists that use increasingly sophisticated technologies and protocols to maximise the population viability and chances of establishment for their captive-bred stock (e.g. Duan et al., 2013; van Lenteren et al., 2018). Conservation translocation programmes with a captive-breeding component, which remain less common than wild to wild translocations for insects, can incorporate many of the pathogen screening, animal husbandry and genetic management procedures used in successful biological control programmes to develop their own existing and future programmes.

Characteristics of translocation success

Ratios of translocation success based on academic literature reviews should be approached with a degree of caution, due to the decreased likelihood of authors publishing failed translocations. Successful translocation projects are more likely to be published than failures because authors do not wish to portray themselves or other involved parties unfavourably and publication bias favours articles with positive outcomes (Forstmeier et al., 2017). A review of amphibian and reptile translocation projects in New Zealand found that the published success rate was considerably higher than the rate of success found across all translocations, and successful translocations were more likely to be published than those that failed (Miller et al., 2014). Based on these findings, the proportion of failures found during our research may not be representative of all failed terrestrial insect translocations, but instead represent the available literature.

The definition of translocation success adopted for this research is similar to that for reviews of other animal taxa (e.g. Germano and Bishop, 2009; White et al., 2012; Cochran-Biederman et al., 2015). This definition ensures that the focal species has completed all phases of its lifecycle at the release site, which is widely regarded as a fundamental indicator of translocation success (McCoy et al., 2014; Robert et al., 2015). The potential drawback of defining success in this way is that it may allow for more translocations that only achieved short-term success to be defined as successful (e.g. translocated population still present after one lifecycle duration of a univoltine species). However, the conservation translocations analysed during this study generally established long-term populations, with 80% reporting the persistence of the translocated population for >5 years after the most recent release and 46% for >10 years (see Appendix 2.2).

Our results indicate that terrestrial insect translocation success is influenced most by the number of individuals released – translocations are more likely to be successful when releasing more individuals. Our findings are unsurprising – with a greater number of founder individuals, a translocated population is less vulnerable to the effects of demographic stochasticity, loss of genetic diversity by drift, and inbreeding depression, which are more prevalent in smaller populations. Therefore, we suggest that managers should aim to maximise the number of individuals released. Population models can be a useful tool for predicting the optimal number of individuals for release (e.g. Wagner et al., 2005; Unger et al., 2013; Heikkinen et al., 2015), but their outputs are less valuable for species with inadequate population and life-history data. The optimal number of individuals for release will vary depending on their life stage due to fluctuating mortality rates between adult, juvenile and egg phases (Price et al., 2011). With a large enough sample size, we would have split the number of individuals released variable based on the life stage released variable and compared differences in translocation outcome for each life stage category, but this was impractical with the number of cases that were available.

Reviews of vertebrate translocations suggest that wild source populations are generally associated with greater translocation success than captive-bred source populations (e.g. Griffith et al., 1989; Rummel et al., 2016), and concerns have been raised over the behavioural, morphological, demographic and genetic changes resulting from captive-breeding programmes (Lewis and Thomas, 2001; Williams and Hoffman, 2009). Our results suggest that insect translocations are also more successful when individuals are sourced from wild populations, though the magnitude of this difference is marginal (<10%), and is much less than that found for vertebrate taxa (e.g. 37% for birds and mammals, Griffith et al., 1989). It may not always be feasible to acquire large numbers of wild individuals for translocation as remaining wild populations may have declined in abundance and extent-of-occurrence to the point where they are too fragile to withstand the loss of a sufficiently large number of source individuals (Dimond and Armstrong, 2007). Under these circumstances, captive-breeding programmes provide a possible alternative for the acquisition of large numbers of individuals whilst minimising loss of viability of wild populations.

Insects are particularly suitable for captive-breeding due to their life-history attributes, such as small body size and rapid reproductive potential, meaning that viable populations can be managed more cost-effectively than most vertebrate species (Balmford et al., 1996). In North America, zoological institutions are increasingly involved in captive-breeding programmes aiming to release animals into the wild (Brichieri-Colombi et al., 2018). A specially designated breeding facility at Roger Williams Park Zoo has been responsible for the propagation and release of over 2,800 Critically Endangered American Burying Beetle (*Nicrophorus americanus* Olivier, 1790) to Nantucket Island, Massachusetts (Mckenna-Foster *et al.,* 2016). In addition to their contribution of valuable source stock, involving zoos in translocation projects has the additional benefits of promoting the conservation of the focal species, raising public awareness, educating the public and raising extra funds (Miller et al., 2004).

The IUCN Guidelines for Reintroductions and Other Conservation Translocations (2013) recommend the selection of source populations that are physically closer to release sites, however, we found no statistical difference in the outcome of terrestrial insect translocations based on the distance between source population and release site. The international translocations of three butterfly species in Europe achieved long-term success (≥10 years) when sourcing individuals from populations more than 1,000 km away (Wynhoff 1998; Wynhoff et al., 2008; Thomas et al., 2009). Due to the perceived increase in risk (e.g. Scottish Natural Heritage, 2014), long-distance translocations are likely to be approached with extra caution, meaning more time and attention is paid to researching the ecological requirements of the focal species and optimising and maintaining release site habitat suitability; as was the case with the three long-distance European butterfly translocations.

Examining translocation failure

The effects of weather and climate were one of the most frequently reported causes of translocation failure. Insect life-cycles and abundance are influenced strongly by temperature (Danks, 1987) and precipitation (Roy et al., 2008; Liberal et al., 2011). Mismatches in climate conditions between source populations and release sites, and extreme weather (e.g. drought or high rainfall) can be detrimental to translocated insect populations (e.g. Dempster and Hall, 1980; Daniels, 2009) and difficult to avoid or manage. However, there are preventative steps prior to translocation that can be taken. For example, estimating the climate suitability of potential release sites under current and future environmental conditions can minimise the risk of selecting sub-optimal release sites or sites that will become unsuitable under future climate change (Guisan et al., 2013). This is possible with the use of species distribution models (SDMs), which in their most widely used form, correlatively identify suitable environmental conditions for a species based on the conditions present at sites supporting extant populations.

The use of SDMs during the translocation planning process is highly advised when contemplating the movement of a species beyond its indigenous range (i.e. assisted colonisation) (Chauvenet et al., 2013). However, SDMs are also useful for reintroduction planning (see Osborne and Seddon, 2012 for potential applications and issues of using SDMs for reintroductions), especially if the focal species became extinct at the proposed reintroduction site some time ago. It is risky to use historic site occupancy as a prerequisite for site suitability; climate change during the intervening period between the initial extinction and time of release could have rendered the site unsuitable. For example, the Apollo Butterfly (*Parnassius apollo* Linnaeus, 1758) went extinct in southern Finland in the 1950s and reintroductions were attempted to a number of islands between 2009 and 2011 (Fred and Brommer, 2015; J. Brommer pers. comm.). The reintroduction failed, and the authors hypothesise that climatic factors, such as unfavourable winter conditions and the timing of spring, may have played a role in the failure of the species to persist on the islands.

To our knowledge, no attempt has been made within the peer-reviewed literature to assess the extent to which climate conditions at release sites may have influenced the outcome of past translocation attempts. The frequent attribution of translocation failure to unsuitable weather and climate conditions by those involved with insect translocations suggests there is a necessity to investigate this factor further. A statistical modelling approach similar to the one applied in Csergő et al., (2017), in which predicted climate suitability values generated from SDMs were related to the demographic performance of plant populations, could be applied to detect potential correlations between release site climate suitability and the outcome of insect translocations.

The quality of release site habitat has been identified as an important factor for translocation success in previous animal translocation reviews (e.g. Dodd and Seigel, 1991; White et al., 2012). We were unable to assess habitat quality for the projects that we reviewed, but habitat quality was one of the most frequently reported causes of translocation failure by authors. The importance of habitat quality for population viability has repeatedly been shown across a diverse range of insect taxa (Baur et al., 2002; Franzén and Nilsson, 2010; Pasinelli et al., 2013) and consequently, defining the crucial habitat requirements prior to reintroduction is required. Habitat descriptions for the focal species at sites supporting healthy populations, preferably including the candidate source population(s), should be conducted to ensure the proposed translocation site is suitable prior to release (IUCN, 2013). Furthermore, assurances of long-term active management should be obtained prior to translocation to safeguard habitat quality under future pressures. Changes to land tenure and discontinuation of habitat management activities have been responsible for the failure of insect translocations in the past (e.g. *Deinacrida mahoenui* Gibbs, 1999 C. Watts pers. comm; *Cicindela dorsalis* Say, 1817 M. Brust pers. comm.).

Based on our method of data collection, we were unable to obtain data on the habitat quality of release sites for insects. This type of data would be obtainable through the circulation of a survey to translocation practitioners, as demonstrated in a review of mammal and bird translocations in which respondents ranked habitat quality as “excellent”, “good” or “fair or poor” (Griffith et al., 1989). However, it can be particularly challenging to gauge habitat quality for insects, as highlighted in Williams et al., (2014), in which conservation professionals often ranked habitat quality for carabid beetles as both “good” and “bad” in areas where there was maximal diversity. The subjectivity of habitat quality assessment suggests that, although this variable is of importance, the method by which this data is collected requires careful consideration of how to maximise objectivity.

Recommendations for improving standardisation and dissemination

Many of the translocations reviewed during this research were poorly documented either methodologically and/or in terms of long-term results. This presents a challenge to managers who wish to learn from the successful and the unsuccessful aspects of previous translocations in order to make evidence-based decisions regarding their own projects. For vertebrates, there is a growing body of literature encouraging the standardisation of documenting and monitoring the methods and outcomes associated with translocations (e.g. Fischer and Lindenmayer, 2000; Sutherland et al*.,* 2010; Ewen et al., 2012). Recently, similar standardisation-based recommendations have also been published for lepidopteran translocations (Daniels et al., 2018). Complementary to improved standardisation, we also advise the dissemination of information, ideally through a centralised international database that facilitates the dispersion of information to an audience beyond academic circles (e.g. TRANSLOC, a translocation database for the Western Palearctic region, link: http://translocations.in2p3.fr/). In comparison to translocation reviews of other taxonomic groups (e.g. Griffith et al., 1989; Cochran-Biederman et al., 2015) the body of literature surrounding terrestrial insect translocations is limited; thus it is all the more important that platforms exist on which successful and unsuccessful projects can be shared and accessed effectively.

Author contributions statement

J.B., S.D., D.B. and C.W. 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.

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Chapter 3:

Climate suitability as a predictor of conservation translocation failure

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Abstract

The continuing decline and loss of biodiversity has caused an increase in the use of interventionist conservation tools such as translocation. However, many translocation attempts fail to establish viable populations, with poor release site selection often flagged as an inhibitor of success. We used species distribution models (SDMs) to predict the climate suitability of 102 release sites for amphibians, reptiles, and terrestrial insects and compared suitability predictions between successful and failed attempts. We then quantified the importance of climate suitability relative to 5 other variables frequently considered in the literature as important determinants of translocation success: number of release years, number of individuals released, life stage released, origin of the source population, and position of the release site relative to the species' range. Probability of translocation success increased as predicted climate suitability increased and this effect was the strongest among the variables we considered, accounting for 48.3% of the variation in translocation outcome. These findings should encourage greater consideration of climate suitability when selecting release sites for conservation translocations and we advocate the use of SDMs as an effective way to do this.

Introduction

Threatened species management is increasingly involving more interventionist forms of conservation to secure viable metapopulations and reverse local extinctions (Hobbs et al. 2011). Conservation translocation, defined as the intentional human-mediated movement of organisms from one location to another for conservation purposes (IUCN 2013), represents one such approach. In recent decades, there has been a global proliferation in the number of translocation-related studies (Seddon et al. 2007; Taylor et al. 2017). However, many translocations fail to establish viable populations (Fischer & Lindenmayer 2000; Cochran-Biederman et al. 2015). Attempts to improve translocation practice have identified a number of influential factors, such as origin of the source population (Cayuela et al. 2019), length of supplementary feeding (White et al. 2012), life stage of individuals released (Muths et al. 2014), and overall habitat suitability of the release site (Cochran-Biederman et al. 2015). Climate constitutes a fundamental component of overall habitat suitability but has received little attention in the literature; very few translocation projects explicitly cite the use of techniques to estimate climate suitability (but see Brooker et al. 2018). Instead, past attempts have often relied on previous occupancy and the intuition of involved parties to select release sites (Osborne & Seddon 2012).

Poor release site selection has been flagged as an impediment to translocation success (Osborne & Seddon 2012). To mitigate the risk of poor release site selection, the updated 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) represent the most widely advocated approach for dealing with the challenge of selecting climatically suitable release sites (Osborne & Seddon, 2012; IUCN, 2013) (but see White et al. 2015). An SDM identifies statistical relationships between species occurrence and environmental descriptors. However, SDMs have weaknesses, such as the potential for disequilibrium between range and niche due to dispersal limitations and biotic interactions (Svenning & Sandel 2013). Furthermore, examples of translocation projects explicitly outlining the use of SDMs to guide management decisions are scarce (Guisan et al. 2013) (but see Brooker et al. [2018] and Maes et al. [2019]).

Ectothermic species are particularly sensitive to climate (Angilletta et al. 2004). Temperature regulates the metabolism and physiology of ectotherms, which in turn affects the demographic performance of ectothermic populations through controls on their development, growth, reproduction, overwinter survival, and behaviour. Precipitation also affects many of these parameters (Saenz et al. 2006), not as directly as temperature, but in some cases with equal or increased severity (Ficetola & Maiorano 2016). The metabolic and physiological controls imposed by temperature and precipitation on ectotherms mean that the performance of translocated populations is strongly influenced by exposure to climatic conditions present at release sites. Therefore, it is unsurprising that for a number of failed translocation projects involving ectotherms, the authors proposed that unfavourable temperature and precipitation regimes impeded population establishment (e.g. Dempster & Hall 1980; Kuussaari et al. 2015).

We analysed data extracted from the literature on the outcomes of amphibian, reptile, and terrestrial insect translocations from a range of biogeographical regions. We constructed global SDMs for each species to compare the predicted climate suitability between sites of successful and failed translocation projects and then quantified the importance of climate suitability as a predictor of translocation success relative to five other variables commonly reported in the literature. These include how many individuals were released (Germano & Bishop 2009; Bellis et al. 2019), duration of releases (Griffith et al. 1989), life stage of individuals released (Muths et al. 2014; Cayuela et al. 2019), whether the source population was captive bred or wild caught (Rummel et al. 2016), and the position of the release site relative to the species' range (Griffith et al. 1989). We hypothesized a priori that translocations have a higher probability of success at sites with higher predicted climate suitability (Lee-Yaw et al. 2016). Ours is the first global comparative analysis of the importance of climate suitability in determining translocation outcome and the usefulness of SDMs as a conservation tool for aiding the selection of release sites.

Methodology

Literature search

We applied a range of approaches to find translocation case studies useful for quantifying the relative importance of climate suitability as a predictor of translocation success. Because translocation reviews have already been published for herpetofauna (Dodd & Seigel 1991; Germano & Bishop 2009) and terrestrial insects (Bellis et al. 2019), we began by capitalizing on the case studies in these reviews. The herpetofauna reviews covered literature only up until 2006; thus, for relevant literature published after 2006 (until 2018) we performed our own search on the Web of Science. We used the following advanced search criteria: TS=((*reintro** OR *re-intro** OR *translocat** OR *conservation translocat** OR *reinforce** OR *re-inforce** OR *reenforce** OR *re-enforce** OR *assisted migration* OR *assisted colonisation* OR *assisted colonization* OR *conservation introduction* OR *ecological replacement* OR *augment** OR *restor** OR *restock** OR *re-stock** OR *reseed** OR *re-seed** OR *managed relocation*) AND (*amphibian* OR *reptile*)). The search retrieved 1,419 results. We then imported all of the resulting papers into EndNote referencing software and manually screened each record to verify its relevance to amphibian and reptile translocation (see Appendix 3.1 for full inclusion criteria). We screened the reference sections of each relevant paper to find additional studies of relevance. We also included translocation projects that were found via personal communication with authors. For terrestrial insects, as well as using the case studies found in Bellis et al. (2019), which covered the published literature up until the time of the current study, we also included translocation projects found through personal communication with authors. For every conservation translocation, we collected data on five predictor variables in addition to climate suitability (Table 3.1).

Defining translocation success

There is no broadly accepted definition of translocation success (Robert et al. 2015), and this was reflected in the variability of definitions adopted in the translocation projects that we found. For the purposes of this study, we adopted our own definition, but note that alternative metrics such as a translocated population's finite rate of increase (growth rate predicted when the sex and age distribution stabilises) have been used (Armstrong & Reynolds 2012). We defined translocations as successful if they met the following three criteria: ≥10 years had elapsed between the time of most recent release and most recent monitoring; the period between the most recent release and most recent monitoring exceeded the generation time of the species; and the results of the most recent monitoring indicated individuals were still present. We applied a 10-year minimum threshold to reduce the potential for abnormally favourable conditions following release to have temporarily benefitted the translocated species. Enforcing the second criterion led to the omission of seven translocations, all of which involved turtle or tortoise species with generation times >15 years. A translocation project was only considered to have failed if monitoring indicated that the species was no longer present at the site. Translocation projects that could not be categorized as a success or failure were not considered for analysis. In total, 102 translocation projects covering 50 different species were eligible for statistical analysis (full eligibility criteria in Appendix 3.1).

Species distribution models

We downloaded species occurrence data from the Global Biodiversity Information Facility (GBIF). Because occurrences were very limited for endemic New Zealand species, we supplemented the GBIF data with records from the New Zealand Department of

Conservation. For all species, we considered their global range to model the full extent of their climatic niche (Barbet-Massin et al. 2010; Raes 2012). For quality control, we checked each species' occurrence data set and reduced spatial bias caused by unequal sampling (Appendix 3.2). We downloaded current climate data from the WorldClim Database (Fick & Hijmans 2017) at a 30 arc-second resolution (approximately 1 km) for eight standard bioclimate predictors known or presumed to be important in structuring the distributions of ectotherms (Wiens et al. 2006; Kozak & Wiens 2007; Clusella-Trullas et al. 2011) that describe annual averages, seasonality, and highest and lowest monthly values of temperature and precipitation. Based on Barbet-Massin et al. (2012), pseudo-absences were sampled at random from the background extent for each species and weighted to reach an equal prevalence with presence records (details in Appendix 3.2).

We used an ensemble of species distribution model algorithms to minimise the uncertainty associated with single modelling techniques (Buisson et al. 2010). Our ensemble consisted of random forests (RF), generalized boosted models (GBM), and MaxEnt and was implemented in the biomod2 package (version 3.3-7) (Thuiller et al. 2016) in R version 3.5.1 (R Core Team 2018). We evaluated model performance with the receiver operating characteristic to determine an area under the curve (AUC) (Appendix 3.3). To make SDM predictions comparable across species, we standardized the predicted climate suitability values to range from 0 to 1 with the following formula: (x - min) / (max - min). Using the standardized outputs, we extracted the climate suitability values for the 1 x 1 km grid cell or cells corresponding to the location of each translocated population (Appendix 3.3).

Statistical analyses

We fitted a binomial multivariate generalized linear model with mixed effects (GLMM) to test how translocation outcome (binary success or failure) depends on climate suitability and five other predictor variables commonly considered in comparative analyses of translocation outcomes (Table 3.1; Appendix 3.4). These five variables were treated as fixed effects in the GLMM. Because the three continuous variables (climate suitability, number of release years, and number of individuals released) were on very different scales, we standardized them for easier interpretation of model outputs. To account for evolutionary differences between the three taxonomic groups when submitted to a translocation, we included taxonomic Class as a random effect in the model. We tested for multicollinearity among the predictor variables with the variance inflation factor (VIF), implemented in R with the package car (version 3.0-2) (Fox et al. 2019). Each predictor variable had a VIF of <2, indicating minimal correlation between the predictors (Quinn & Keough 2002). The global model, including all five predictor variables and Class, was implemented in R with the package lme4 (version 1.1-19) (Bates et al. 2019).

Table 3.1. Predictor variables used in generalized linear model with mixed effects to identify factors relating to translocation success.

Variable abbreviation	Variable description (levels)
ClimSuit	predicted climate suitability of release site
NRelYears	total number of release years
NumRel	total number of individuals released
LifeStageRel	life stage released (adults, immatures, or mixed)
Origin	origin of source population (wild or captive bred)
Position	position of release site relative to the species' range (core or edge)

Hierarchical partitioning (Chevan & Sutherland 1991) was employed to identify the predictor variables that best accounted for variation in translocation outcome. This method calculates goodness-of-fit measures for the entire hierarchy of regression models based on all two-way combinations of predictor variables to obtain the average independent contribution of each predictor to translocation outcome. Statistical significance of the independent contribution of each predictor variable was determined using a randomisation approach with 1000 iterations and a significance level of 0.05 (Mac Nally 2002). Hierarchical partitioning and associated randomisation tests were executed in R with the package hier.part (version 1.0-4) (Walsh & Mac Nally 2013).

Results

The definition of *translocation success* we adopted resulted in the categorisation of 61 successful translocations and 41 failures. The majority of translocation projects were carried out on the European (61%) and North American continents (35%). A limited number of projects originated in Oceania (3%), and 1 project was from Asia.

The SDMs of the final species set were generally of high quality (AUC: mean [SE] = 0.935 [0.003]), indicating good predictive power. There was a positive relationship between the SDM-based predicted climate suitability and the probability of conservation translocation success (Figure 3.1; Table 3.2). The average climate suitability was higher at sites where conservation translocations were successful (mean ± S.E. = 0.576 ± 0.030) than at sites where translocations failed (0.365 [0.037]). This was consistent across amphibians (successful = 0.741 ± 0.048; failed = 0.433 ± 0.092), reptiles (successful = 0.538 ± 0.048; failed = 0.356 ± 0.123), and terrestrial insects (successful = 0.533 ± 0.045; failed = 0.329 ± 0.034).

When comparing the variation in translocation outcome explained by each of the variables, climate suitability came out on top (48.3%) (Figure 3.2). Life stage released and number of release years accounted for the second (21.3%) and third (15.3%) most variation, respectively (Figure 3.2). The independent effect of each of these three variables was significant ($p< 0.05$), but this was not the case for origin, number of individuals released, or position of the release site. For the variable life stage released, releasing a mixture of life stages proved the most successful approach among the three categories considered (Table 3.2; Table A3.4.1). When considering the number of years to release individuals at a site, the probability of success increased with the number of release years (Table 3.2; Table A3.4.1).

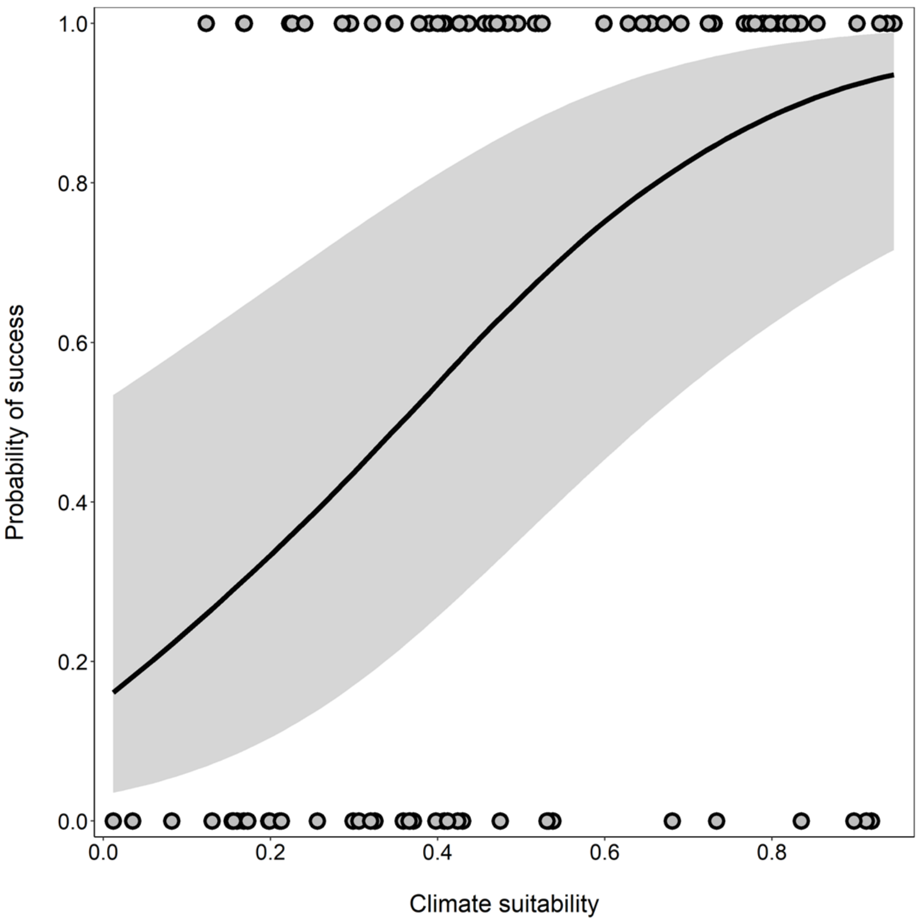

Figure 3.1. Effect of predicted climate suitability on model-based probabilities of translocation success for amphibians, reptiles, and terrestrial insects (shading, 95% CIs).

Table 3.2. Generalised linear mixed model results used to assess the effect of each parameter on translocation outcome for amphibians, reptiles, and terrestrial insects. Abbreviations are described in Table 3.1.

Parameter[a]	*β* [b]	SE
Intercept	1.008	0.852
ClimSuit	1.161 **	0.337
NRelYears	0.764 *	0.419
NumRel	-0.083	0.383
LifeStageRel (immature)[c]	-0.892	0.719
LifeStageRel (mixed)[d]	-0.267	0.876
Origin (captive)[e]	-0.940	0.631

Position(edge)[f]	0.827	0.585

[a] Abbreviations are described in Table 3.1.

[b] Significance: *, 0.1; **, 0.001.

[c] Immature versus adult.

[d] Mixed versus adult.

[e] Captive bred versus wild caught.

[f] Edge versus core.

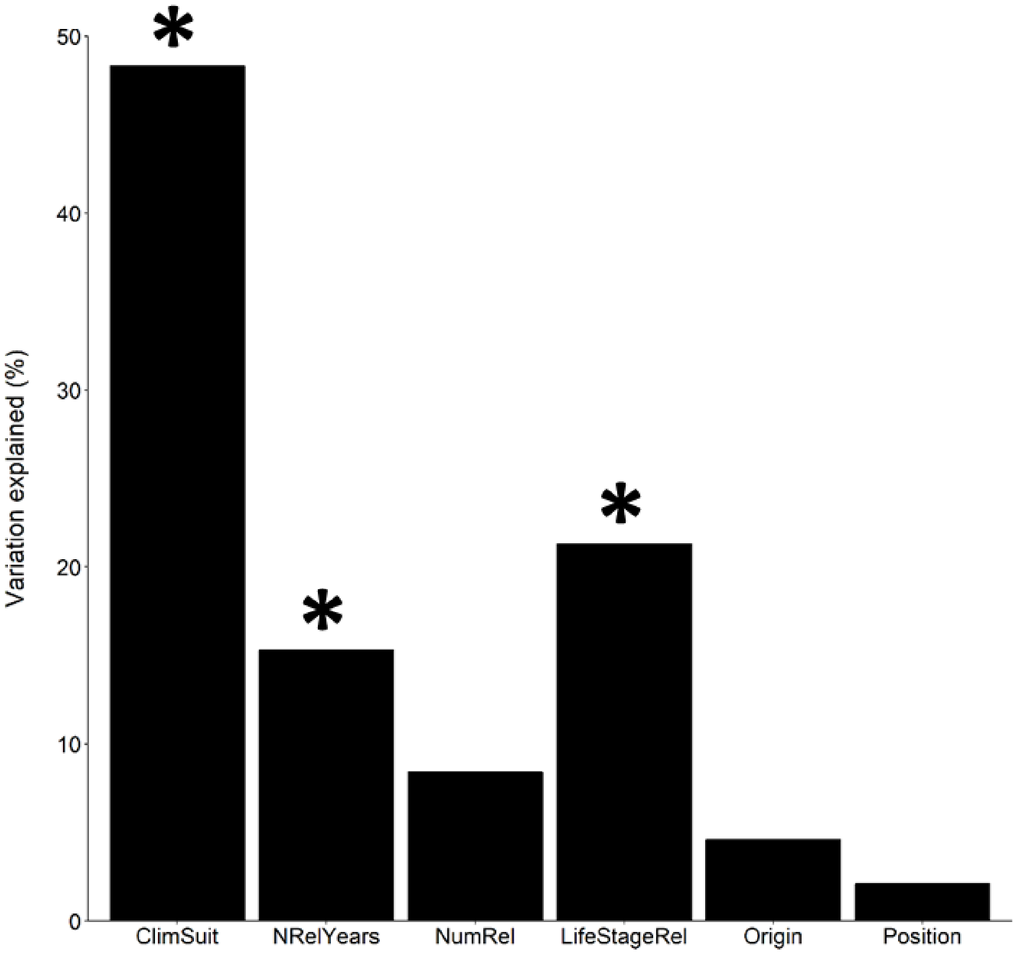

Figure 3.2. Percent independent contribution of each predictor variable derived by hierarchical partitioning to translocation outcome for amphibians, reptiles, and terrestrial insects (*, predictor variables with significant (*p*< 0.05) independent contributions to translocation outcome). Variable abbreviations are described in Table 3.1.

Discussion

Climate suitability predicted from SDMs was higher at sites of successful translocation. When comparing the strength of this effect against five other variables commonly considered in comparative analyses of translocation outcomes, climate suitability explained the most variation in translocation outcome. Using real-life case studies with known outcomes, our findings provide the first evidence-based support for the use of SDMs to select suitable release sites (as recommended in Osborne & Seddon [2012] and IUCN [2013]). These findings both highlight the importance of climate as a key influencer of translocation outcome, as well as validating the usefulness of SDMs as a tool to aid release site selection.

Climate-driven translocation failure

Explicit consideration of release site climate suitability is rarely reported in the translocation literature (but see Brooker et al. 2018), but our results indicate it is important to the outcome of conservation translocations. This supports the findings of a recent review of terrestrial insect translocations, where weather and climate-related factors were the most frequently reported causes of failure (Bellis et al. 2019). We suspect that most managers do not explicitly consider the climate suitability of release sites because the majority of translocation projects involve the release of organisms into their indigenous range (definition as per IUCN [2013]), (97% of our sample were reintroductions). The failure to assess climate suitability may be excusable given the constraints facing conservation workers on the ground; however, the frequent concordance between predicted climate suitability and translocation outcome we found shows that climate warrants consideration.

Climate change offers one potential explanation for why areas within the indigenous range fail to support the establishment of translocated populations; areas that once met the climatic niche requirements of species may no longer be able to support viable populations (Wiens 2016). Some reintroductions in our sample took place many decades after the species' initial extirpation (e.g. Knisley et al. 2006; Fred & Brommer 2015), potentially allowing for considerable climate alteration at their release sites. The longer the time between initial extirpation and the planned release, the less likely the site will have retained its climatic suitability (Dalrymple & Broome 2010) and the greater the need to apply tools such as SDMs to assess the current suitability (Osborne & Seddon 2012).

An interactive effect of climate with other limiting factors not considered in our analyses offers another potential cause of climate-driven translocation failure. A substantial proportion of the release sites in our sample received climate suitability predictions of 0.3 - 0.5 (Figure 3.1), and there was a relatively even mixture of successes (*n* = 16) and failures (*n* = 14) within this range. When examining the authors' perceived causes of failure, suboptimal climate conditions in addition to other factors, such as predation, competition, and disease, were frequently reported to have constrained population establishment (e.g. Harvey et al. 2014; Fred & Brommer 2015; Kuussaari et al. 2015). Behavioural alterations in response to sub-optimal climates (e.g. altered activity patterns) may diminish the effectiveness of an organism's antipredator strategy (Mori & Burghardt 2004) or its ability to forage (Traniello et al. 1984), thus reducing its fitness. This suggests that sites with low to intermediate climate suitability (0.3 – 0.5) may require more detailed assessments of other potentially limiting factors (e.g. density of predators) before they are designated for translocation.

There were some instances of inconcordance between SDM predictions and translocation outcome in our sample (Figure 3.1). Local-scale processes (e.g. habitat type, biotic interactions, and environmental disturbances) in addition to the global macroclimate influence the overall habitat suitability of individual sites (Louthan et al. 2015). If local interactions dominate species distributions in suitable climates then the population dynamics of translocated populations may be decoupled from macroclimatic suitability. For example, in areas of high predicted climate suitability, populations may perform poorly due to intense competition or in response to a temporary period of unfavourable weather (Fancourt et al. 2015; Louthan et al. 2015). The same counterintuitive trend may be observed in areas of low predicted climate suitability, where populations may perform well through confinement to suitable microclimates (Dullinger et al. 2012; Dahlberg et al. 2014). However, local-scale processes may also be influenced by the global macroclimate (Louthan et al. 2015), and our results suggest that generalisations about habitat suitability can be made with global SDMs.

Using SDMs for release site selection

Several authors have examined potential links between climate suitability estimated from SDMs and measures of demographic performance (Thuiller et al. 2014; Lee-Yaw et al. 2016; Csergő et al. 2017). Lee-Yaw et al. (2016) used SDMs and transplant experiments to uncover the positive relationship between predicted climate suitability and the short-term individual fitness of plant and invertebrate species. The frequent concordance between climate suitability and the translocation outcome of the three ectothermic groups we considered provides fresh support for the use of SDMs to infer measures of demographic performance.

Our results indicated that the decision to select release sites based on SDM predictions of climate suitability influences translocation outcome more than other decisions frequently identified as important in the literature, such as how many individuals should be released (Germano & Bishop 2009; Bellis et al. 2019), duration of releases (Griffith et al. 1989), life stage of individuals released (Muths et al. 2014; Cayuela et al. 2019), whether to source from captive-bred or wild-caught stock (Rummel et al. 2016), or position of the release site relative to the species' range (Griffith et al. 1989). There are many examples of translocation projects devoting resources to the construction of population models for making recommendations on the optimum number of animals to be released (e.g. Wagner et al. 2005; Tocher et al. 2006; Unger et al. 2013; Heikkinen et al. 2015). In contrast, none of the translocation projects included in our analyses cited the use of SDMs for making recommendations as to the optimum site for release.

Guisan et al. (2013) noted the limited uptake of SDMs to guide conservation decisions. Based on personal experiences with managers involved in translocation projects, we believe the lack of uptake may partly be resulting from a general assumption that parameterising and running SDMs requires advanced statistical and coding expertise. Although we chose an ensemble modelling approach that requires the use of coding software, one of the individual modelling techniques that contributed to our ensemble, MaxEnt, can be run through a standalone software package with a graphical user interface (Phillips et al. 2006). MaxEnt represents one of the most popular SDM techniques and can achieve high levels of predictive performance (Elith & Graham 2009; Merow et al. 2013). Our model evaluation results support this (AUC mean ± S.E. = 0.849 ± 0.007), as do the climate suitability predictions, which also indicated an overall contrast between successful (0.579 ± 0.033) and failed (0.398 ± 0.040) translocations. Moreover, these outputs were generated with MaxEnt's default configurations (see Merow et al. [2013] for potential shortfalls of retaining the default configurations). These results should encourage wider uptake of SDMs by the translocation community, irrespective of statistical and coding expertise.

Limitations

Although there was frequent concordance between predicted climate suitability and translocation failure, failures were not always equally represented in the data set. Specifically, due to a skewed success:failure ratio (26:5) of reptile translocations, our findings potentially carry less relevance for this group. The paucity of failed reptile translocations is not necessarily indicative of a high success rate, but instead may be explained by the greater likelihood of reporting a successful project (see Miller et al. [2014] for a review of publication rates according to translocation outcome). The large number of successful reptile translocations also provides an explanation for the unexpected negative effect of number of individuals released on translocation outcome (Table 3.2), which contrasts with findings from previous reviews of insect and herpetofauna translocations (Germano & Bishop 2009; Bellis et al. 2019). In our data set, reptile translocations contributed the greatest number of successes but on average released far fewer individuals than projects involving amphibians or insects. This outcome likely results from the fewer offspring produced per annum by reptiles than most amphibian and insect species, which constrains the number of individuals available for release. Because our sample was of an insufficient size to split by taxonomic class, the variable number of individuals released may have been less informative than in previous reviews.

Using correlative SDMs fitted with macroclimatic data to estimate the suitability of potential release sites may be hindered by their known weaknesses. A source of uncertainty may arise from not incorporating physiologically meaningful climate variables for all species or meaningful interactions between variables (Mod et al. 2016). The AUC represents one of the most widely used evaluation metrics for SDMs, but it has been criticised for its ability to assess the biological significance of models based on the set of predictor variables used (Fourcade et al. 2018). We applied a standardised approach to predict the suitability of translocation release sites by selecting eight climate variables known or presumed to be important in structuring the distributions of ectotherms (Wiens et al. 2006; Kozak & Wiens 2007; Clusella-Trullas et al. 2011), thereby conferring biological realism to the models. However, when planning for a translocation, it is advisable to adopt a more detailed species-specific variable-selection protocol based on the known ecophysiology of the species of interest (Austin & Van Niel 2011).

Correlative macroclimatic SDMs may also be less informative for species with few occurrence records, such as rare or data-deficient species. For rare species, the geographical range limit may be controlled by other factors, such as dispersal capacity and biotic interactions (Svenning & Sandel 2013), whereas data deficiency is often an artefact of reporting mechanisms and therefore strongly dependent on the location of the species (e.g. species in the tropics [Feeley & Silman 2011]). We excluded species with under 30 spatially distinct occurrences because SDM accuracy tends to decline severely beyond this threshold (Wisz et al. 2008). However, rare species are often the focus of translocation projects, and for managers considering the movement of these species, alternative SDM methods, such as the calibration of an ensemble of bivariate models (Breiner et al. 2015) or the construction of more complex mechanistic models (Kearney & Porter 2009), could be explored.

The effects of management decisions in conservation translocations are inherently uncertain and the fundamental step of selecting the release site is no exception (Osborne & Seddon 2012). By conducting the first global comparative analysis on the importance of climate suitability in determining translocation outcome, we provide evidence to suggest that climatic SDMs can help reduce uncertainty in translocation projects by locating release sites with a higher probability of success. Furthermore, climate suitability explains more variation in translocation outcome than five other management-related variables that have received more attention in the literature. These findings should encourage wider adoption of SDMs by the translocation community because they represent a useful predictive tool capable of reducing uncertainty in the planning and implementation of future translocation projects.

Author contributions statement

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

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Chapter 4:

Climate change threatens the viability of populations at sites of successful translocation

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Abstract

The dynamic nature of climate change diminishes the effectiveness of fixed system approaches to nature conservation. Areas that were once suitable for species will no longer be suitable, and areas that are suitable now, will be unsuitable in the future. Despite increasing global awareness of the threats posed by climate change, it remains poorly accounted for in conservation programmes, such as translocation. To uncover what lies ahead for populations that have been successfully established through translocation efforts, we apply an ensemble of species distribution models (SDMs) to forecast changes in macroclimatic suitability across 66 recipient sites involving 39 species of amphibian, reptile, and terrestrial insect. We consider optimistic (SSP126) and pessimistic (SSP370) scenarios of climate change spanning three time horizons from 2021-2040 up to 2061-2080. Our models predicted that translocated populations are most frequently located in areas with very high current (1960-2010) macroclimatic suitability (0.75 – 1; 39% of populations). However, >74.3% of recipient sites are forecast to decline in suitability in the future, regardless of the SSP scenario or time horizon. By the end of the modelling period, the lowest suitability bracket (0 – 0.25) is predicted to switch from representing the least- to the most- recipient sites under both SSP126 (35%) and SSP370 (39%). When contrasting predictions of recipient site suitability change with species regional (national or provincial level) and global averages, we found that sites more frequently outperformed global averages but underperformed against regional averages, suggesting that translocation programmes could benefit from using SDMs to pinpoint areas with more stable suitability in target regions. Our results call for greater consideration of climate change during recipient site selection, as this should help to avert the need for costly interventions in the future.

Introduction

Climate change affects many aspects of biodiversity, including species distributions, phenology, population dynamics, community structure and ecosystem function (Díaz et al. 2019). Local extinctions caused by climate change are becoming widespread, with one recent study finding that 47% of species from a global sample of animals and plants have already experienced losses (Wiens 2016). These impacts have occurred as the average global temperature has increased by less than 1°C, yet without major reductions in greenhouse gas emissions, a rise of 2°C or more is increasingly probable. Consequently, many more declines and extinctions are likely (Urban 2015), leading to a deterioration in ecosystem health and functioning (Pecl et al. 2017).

In the past, conservation has predominantly relied on a fixed-system approach, whereby protected areas are managed to maintain their species assemblages (Hannah 2008). When species have been lost from protected areas, or reached critically low numbers, reintroductions and reinforcements have been used in attempts to restore viable populations (Seddon 2010). However, the dynamic nature of climate change diminishes the effectiveness of the fixed-system approach (Prober et al. 2019), as areas that were once suitable for a species will no longer be suitable, and areas that are suitable now, will be unsuitable in the future. Climate change leaves populations with three possible responses: migrate, adapt, or face extinction (Davis et al. 2005). To effectively prevent species from local extirpation, conservation programmes will need to anticipate future conditions (Thomas 2011).

Conservation translocation, which is an umbrella term covering reintroduction, reinforcement, assisted colonisation, and ecological replacement (IUCN 2013), is the intentional movement of organisms for conservation purposes. As with the conservation sector more widely, there is increasing recognition that translocation programmes should be more forward-looking in their approach (e.g. Hoegh-Guldberg et al. 2008; Thomas 2011; Butt et al. 2020). When selecting a site for release, the Guidelines for Reintroductions and Other Conservation Translocations (IUCN 2013) recommend that the climate requirements of the focal species be “matched to current and/or future climate at the destination site”. Despite extensive calls for increased consideration of climate change in translocation management plans, evidence of translocation programmes proactively taking decisions based on potential climate change impacts is scarce (Butt et al. 2020). To illustrate this point, we combined translocation reports from the IUCN SSC Conservation Translocation Specialist Group database (Soorae et al. 2008, 2010, 2011, 2013, 2016, 2018) with translocations found during a literature search described in Bellis et al. (2020) to estimate how often climate change is factored into decisions related to recipient site selection (methods detailed in Appendix 4.1). Of the 369 translocation articles examined, <2% explicitly mentioned that climate change had been a consideration during the recipient site selection process. While it is important to recognise that papers and reports do not always provide detailed accounts of translocation planning and implementation processes, this figure is still alarmingly low.

Currently, species distribution models (SDMs) represent the most widely proposed approach for assessing climate change impacts at prospective recipient sites (Krause & Pennington 2012; Osborne & Seddon 2012; Chauvenet et al. 2013; IUCN 2013). Outputs from SDMs can indicate if a species' physiological preferences or limits will become decreasingly or increasingly aligned with changing environmental conditions at recipient sites. Although the potential of SDMs for this purpose has received notable attention in the context of assisted colonisation (e.g. Hoegh-Guldberg et al. 2008; Chauvenet et al. 2013; Butt et al. 2020), there has been minimal focus on reintroductions, which account for the majority of conservation translocations (e.g. Brichieri-Colombi & Moehrenschlager 2016; Bellis et al. 2019). Given that assisted colonisation involves the movement of species beyond their indigenous range and is often motivated by ongoing and future threats (Chauvenet et al. 2013), the need to confirm that a recipient site will retain its suitability under climate change is self-evident. It is perhaps less obvious in the context of reintroductions, as they are motivated by the recreation of historical conditions (but see Maes et al. 2019). Additionally, the well-known limitations of SDMs such as the potential for disequilibrium between geographic range and niche (Galante et al. 2018) and the inherent uncertainties of future climate projections (Kujala et al. 2013), may deter conservationists from integrating them into their reintroduction programmes. However, when validated using previous translocation attempts, under both experimental and applied conservation conditions, SDMs have been shown to perform well in predicting translocation outcome (Bellis et al. 2020) and individual survival (Lee-Yaw et al. 2016). Furthermore, SDMs have successfully predicted changes in abundance and distribution when validated using species observed responses to recent climatic changes (Green et al. 2008; Gregory et al. 2009; Stephens et al. 2016).

In this study, we use an ensemble of SDMs (Araújo & New 2007) to estimate changes in the macroclimatic suitability of sites where amphibian, reptile and terrestrial insect populations have been successfully established through translocation. These translocated populations have persisted for more than 10 years and have progressed through multiple generations at their sites of release, demonstrating the alignment between recent environmental conditions and their physiological preferences (Bellis et al. 2020). However, with so few translocation programmes (<2%) appearing to explicitly factor climate change into recipient site selection processes (Appendix 4.1), there is a risk that sites were chosen in areas where physiological tolerances may be breached in the future (e.g. Soroye et al. 2020). Broadly, research indicates that populations are more likely to be buffered from climate change if they are located closer to the poles and/or at higher altitudes relative to the wider species range (Somero 2011). Theoretically, these populations are temporally further from reaching the species thermal maximum, however, this pattern does not always hold (Clusella-Trullas & Chown 2014) and the potential usefulness of spatial attributes, such as latitude and altitude, for inferring the climate change resilience of recipient sites is yet to be explored. Here, we focus on three questions about climate change in the context of translocation. (1) What proportion of translocated populations are threatened by projected climate change in the short (2021-2040), medium (2041-2060) and long-term (2061-2080)? (2) Are predicted changes in recipient site suitability concordant with changes forecast across species' regional and global ranges? (3) Which measurable spatial attributes of recipient sites most influence climate change exposure predicted by SDMs?

Methodology

Our dataset comprises a subset of the amphibian, reptile and terrestrial insect conservation translocations that were defined as 'successful' in a study by Bellis et al. (2020). This study found that conservation translocations had a higher probability of success in areas where SDMs predicted higher macroclimatic suitability. Given this association between recent macroclimatic conditions and translocation outcome, the present study assumes that projections of future climate suitability will indicate how climate change may impact the survival of translocated populations in the future.

The definition of success adopted in Bellis et al. (2020) was based on three criteria: i) $\geq$10 years had elapsed between the time of most recent release and most recent monitoring, ii) the period between the most recent release and most recent monitoring exceeded the generation time of the species, and iii) the results of the most recent monitoring indicated individuals were still present. This is a generalised definition of translocation success that was selected according to the availability of usable information in the literature. Owing to the rapid increases in available occurrence data since the downloads were conducted for Bellis et al. (2020) in 2018, two additional species (involved in two translocation programmes) were eligible for inclusion in the present study. In total, our subset of conservation translocations included 66 recipient sites involving 39 species, including 9 amphibians (to 14 sites), 12 reptiles (to 26 sites), and 18 insects (to 26 sites).

Our sample predominantly consisted of temperately distributed species, mostly centred in the Palearctic (*n* = 19) and Nearctic (*n* = 13) biogeographical realms (Table 4.1). Typically, species had large range sizes (e.g. 1,000,000 – 5,000,000 km^2; *n* = 24) and were distributed over wide latitudinal extents (e.g. 20 – 30°, *n* = 19).

Table 4.1. Spatial summary of species translocated.

Parameter	**Number of species**
Biogeographical realm	
Australasia	4
Holarctic	2
Palearctic	19
Nearctic	13
Neo-tropical	1
Range size (km^2)	
< 100,000	4
100,000 – 1,000,000	5
1,000,000 – 5,000,000	24
> 5,000,000	6
Latitudinal extent (Decimal Degrees)	
< 10°	4
10 – 20°	11
20 – 30°	19

> 30°	5

Species distribution models

To ensure that our work is transparent and reproducible, we include an Overview, Data, Model, Assessment, and Prediction protocol (ODMAP; Zurell et al. 2020) in Appendix 4.3. This metadata summary provides a detailed key to the steps of our SDM-based analyses.

Species data

We compiled a database of occurrences for each species using records from the Global Biodiversity Information Facility (GBIF) and relevant articles in the academic and grey literature (see Table A4.2.1). As the number of occurrences were very limited for species endemic to New Zealand, we supplemented species' occurrence databases with records from the New Zealand Department of Conservation.

Although SDMs constructed with occurrences from freely available data repositories have demonstrated comparable accuracy to those constructed with field-sampled data (Jackson et al. 2015), there are a number of potential limitations associated with sourcing records in this way (e.g. coordinate imprecision, spatial biases and inclusion of historical records) (Beck et al. 2014). Therefore, we cleaned and prepared each species' occurrence dataset by excluding unreliable records where possible. We maximised occurrence precision by retaining only records reported to at least two digits (precision of ca. 1 km) and deleting redistributed records, duplicated records and those explicitly collected prior to 1960. We consulted expert-drawn range maps and distribution descriptions where possible to remove records outside of the indigenous range (Table A4.2.1).

In order to reduce the effects of spatial bias caused by unequal sampling (Boria et al. 2014; Radosavljevic & Anderson 2014), we subsampled the cleaned occurrence datasets by randomly selecting records that were at least 20 km apart, using the *rangeBuilder* package (v1.5) (Rabosky et al. 2016) in R (v3.5.1) (R Core Team 2018). This approach has demonstrated improved SDM predictions through reductions in sampling bias, spatial autocorrelation and overfitting (Galante et al. 2018). All presence locations excluded during spatial thinning were then subsampled again (following the same approach) and used for independent model evaluation (Maiorano et al. 2019). We also removed translocation site locations from species occurrence datasets to avoid biasing SDM predictions. As the accuracy of SDMs can be poor if there are too few occurrence records, we excluded species with fewer than 30 presence records post cleaning (Wisz et al. 2008). To include a species from the tropics, *Eumaeus atala*, which fell below the minimum occurrence threshold after 20 km thinning, we adjusted the thinning resolution to the resolution of our climate variables (~ 4km).

Climate data

We downloaded climate data from the WorldClim Database (v2.1) at a resolution of 2.5 arc-minutes (~ 4km at the equator), which represented the finest resolution available for the newest future projections at the time of download. WorldClim v2.1 provides current global climate data averaged for the period 1960-2010 (Fick & Hijmans 2017). We selected nine bioclimatic variables known or presumed to be important in structuring the distributions of ectotherms (Wiens et al. 2006; Kozak & Wiens 2007; Clusella-Trullas et al. 2011) and that had been selected *a priori* in previous SDM studies on the same taxonomic groups (Carvalho et al. 2010; Ihlow et al. 2012; Cabrelli et al. 2014). These variables describe annual averages of temperature and precipitation (BIO1 and BIO12), seasonality (BIO4 and BIO15), and highest and lowest monthly values of temperature (BIO5 and BIO6) and precipitation (BIO13 and BIO14). We also generated growing degree days (GDD) (sum of all monthly temperatures greater than 5°C, Prentice et al. 1992) using the *envirem* package (v2.0) (Title & Bemmels 2018) in R, as this variable is considered to be one of the best standard climate predictors for temperate species (Foden et al. 2019), which represented 97% of our sample. For the tropical species (*Eumaeus atala*) we selected an alternative set of predictors, with the addition of isothermality (BIO3) and precipitation of the wettest and driest quarters (BIO16 and BIO17) and the removal of GDD, BIO13 and BIO14 (Nix 1986; Foden et al. 2019).

To avoid issues arising from multicollinearity between the predictors, we removed variables that were highly inter-correlated according to the results of a variance inflation factor (VIF) test. Variables with a VIF of >10 (Dormann et al*.,* 2013; Guisan et al*.,* 2017) were removed from the set of predictors used to run each SDM with the R package *usdm* (v. 1.1-18) (Naimi 2015).

For future climate change projections, we selected general circulation models (GCMs) from the sixth phase of the Coupled Model Intercomparison Project (CMIP6) averaged across three time horizons: 2021-2040, 2041-2060 and 2061-2080. As no GCM perfectly reproduces all the features of the global climate system, we selected five models originating from five different institutions: CanESM5, CNRM-CM6-1, IPSL-CM6A-LR, MIROC6 and MRI-ESM2-0.

To simulate alternative future scenarios of societal development, shared socioeconomic pathways (SSPs) have been adopted for CMIP6. SSPs describe plausible alternative changes in aspects of society such as demographic, economic, technological, social, governance and environmental factors (O'Neill et al. 2017). For each GCM, we selected two SSPs, one best-case scenario (SSP126) in which there is rapid sustainable development and a lessening of global inequalities, and a worst-case scenario (SSP370), where there is slow technological change, a rapidly growing population with unmitigated emissions and high levels of inequality. For each time horizon and SSP scenario, we averaged the predictions across the individual GCMs to produce an ensemble and calculated the degree of agreement using the coefficient of variation.

To assess the degree of model extrapolation under current conditions and each set of projected climate conditions (Barbosa et al. 2009), we computed a multivariate environmental similarity surface (MESS) analysis (Elith et al. 2010). To compute the MESS we used the *dismo* package (v1.1-4) (Hijmans et al. 2017) in R. MESS values of < 0 indicate that at least one predictor variable has values outside of the range of climates used to construct the models. Following on from previous studies (Iannella et al. 2017; Di Febbraro et al. 2019), we considered MESS values of < -20 to present extrapolation problems. As some sites spread across multiple grid cells, we focused on the cell with the minimum MESS value (i.e. the most dissimilar) when assessing potential extrapolation issues.

Modelling and evaluation

When transferring SDM predictions under scenarios of climate change, an ensemble forecasting approach (Araújo & New 2007) is frequently advocated to account for algorithmic uncertainty (Araújo et al. 2019; Thuiller et al. 2019). Therefore, we adopted an ensemble modelling approach with 5 algorithms implemented in the package *biomod2* (v. 3.3-7) in R: Generalised Additive Model (GAM), Multivariate Adaptive Regression Splines (MARS), Generalised Boosted Model (GBM), Random Forest (RF) and Maxent (Thuiller et al. 2016). The default *biomod2* configurations were adopted for each algorithm (Appendix 4.3).

As we were reliant on presence-only data, we generated pseudo-absences (PAs) for each SDM. We began by extending expert-drawn range maps (e.g. IUCN and GARD), or cleaned occurrences if these were not available, using a 2 degree buffer (ca. 200km), in order to define the area from which to select PAs from. We randomly selected PAs from unoccupied cells within the newly extended polygons according to the number of presences after spatial thinning *N* (if *N* ≤ 1000 then 1000 PAs were selected, otherwise 10,000 PAs were selected) (Barbet-Massin et al. 2012; Bellard et al. 2016).
If expert-drawn range maps were unavailable for a species, we used the α-hull method to estimate species ranges in accordance with each cleaned occurrence dataset. We established an alpha value based on the smallest value (according to incremental adjustments of 0.1) that provided a single hull encompassing all species occurrence records but without any holes (Capinha & Pateiro-López 2014; Meyer et al. 2017). For species with disjunct distributions, multiple hulls were tolerated based on the same principle described for species with more continuous distributions. The α-hull approach is less prone to biases that may result from the spatial arrangement of habitat than the more conventional convex hull (Burgman & Fox 2003).

The chosen PA selection method was intended to avoid the selection of PAs within the same cell of a presence point and the selection of PAs too far from presence localities. Restricting the selection of PAs too tightly within the region covered by presences increases the probability of producing low performing SDMs (VanDerWal et al. 2009), while drawing PAs from too broad of an area increases the probability of PAs falling in regions with climatic conditions markedly different to those of presence localities, potentially leading to oversimplified and artificially accurate SDMs (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 standardised the predicted climate suitability values to range between 0 and 1 with the following formula: (x – min)/(max – min).

To evaluate model discrimination accuracy (i.e., the ability of the model to correctly predict events within the area being modelled (Araújo et al. 2019), we calculated the area under the curve (AUC) and the true skill statistic (TSS). We used a cross-validation procedure with five repetitions (70% of records selected for model calibration and 30% set aside for model testing). Models with an AUC score of >0.70 were considered to have good model performance (Swets 1998) and were retained in the final ensemble. In order to gain more insight on the calibration accuracy of our SDMs (Warren et al. 2020), we evaluated the final ensemble model with the continuous Boyce index (CBI) (Boyce et al. 2002; Hirzel et al. 2006) using the *ecospat* package (v3.0) (Di Cola et al. 2017) in R. The CBI ranges between +1 and -1, with positive values indicating a positive correlation between model outputs and the true probability of presence, and negative values indicating a negative correlation. To calculate the CBI, we used a set of independent records that had been removed from each species occurrence dataset during spatial thinning (Maiorano et al. 2019).

Quantifying suitability change

Suitability change was quantified by calculating the difference between the current and future predicted suitability at each recipient site. Future suitability was averaged across the five GCMs for each time period/SSP combination (n = 6) and the total number of recipient sites with negative suitability changes was calculated. To account for the varying magnitude of suitability declines across recipient localities, we categorised losses into “decline” (<0.25), “medium decline” (0.25 – 0.5), and “large decline” (>0.5) (e.g. Zamora-Gutierrez et al. 2018).

To establish whether site-level changes in suitability are concordant with trends at wider spatial scales, we compared recipient site suitability change with regional and global averages. Regional and global suitability change was calculated by extracting predicted suitability values at cleaned occurrence locations (limited to one value per 2.5 arc-minute grid cell) and calculating the median average across suitability predictions. Globally, conservation management plans are often set within geopolitical boundaries by national governments or NGOs (Halpern et al. 2006; Moilanen et al. 2009; Jantke & Schneider 2010). To reflect this, we defined regional as any occurrence points that fell within the national borders where the translocation took place. However, in some larger countries, such as the United States and Canada, translocations are often motivated by state-level conservation objectives (Brichieri-Colombi & Moehrenschlager 2016). Therefore, for translocations in these countries, we extracted suitability values from occurrences located within the relevant state boundaries. The same approach was applied for translocations in Australia. In New Zealand, we defined regional points as any occurrences in the county where the translocation was undertaken, due to our sample consisting solely of nationally endemic species. When visually and statistically comparing suitability change across spatial scales, we omitted translocations with too few regional occurrences from which a useful data distribution ($\leq$5) could be produced (resulting in $n = 55$). To statistically compare site-scale suitability change with regional and global predictions, we computed multiple paired Wilcoxon Signed-Rank tests (significance set at $p < 0.05$).

Spatial attributes of recipient sites

We identified two spatial attributes of recipient sites that could potentially be associated with climate change exposure: Latitude relative to latitudinal mean of distribution (LatDiff) and altitude relative to altitudinal mean of distribution (AltDiff). Research suggests that populations at the equatorial edge of species distributions are performing worse than populations elsewhere under climate change, due to these populations being pushed beyond their thermal tolerance (Reich et al. 2015; Lesica & Crone 2017). Accordingly, we hypothesised that there would be a positive relationship between LatDiff and the favourability of predicted recipient site suitability change. We calculated LatDiff for each translocation by calculating the difference between the mean latitude of the species spatially thinned occurrence dataset and the latitude of the recipient site. For translocations in the southern hemisphere (*n* = 4), positive values of LatDiff were changed to negative and vice versa, to allow comparison with translocations in the northern hemisphere.

During warm postglacial periods, higher elevation areas have acted as places of refuge for some species as conditions in the lowlands changed (e.g. Martinet et al. 2018). As our sample did not consist of any alpine specialists, which are highly vulnerable to climate change, we hypothesised that there would be a positive relationship between AltDiff and the favourability of predicted suitability change at recipient sites. We calculated AltDiff for each translocation by calculating the difference between the altitudinal mean of the species distribution and the altitude of the recipient site.

Statistical analyses

To understand how the spatial attributes of recipient sites related to predicted suitability change, we computed a linear mixed model (LMM) for each future climate change projection using the *lme4* package (v 1.1-19) in R (Bates et al. 2015). The response variable was the change in suitability between current and projected future conditions. LatDiff and AltDiff were fixed effects, and species was set as a random effect. We tested for multicollinearity amongst the spatial attributes using the variance inflation factor (VIF), implemented in R with the package *car* (v. 3.0-2) (Fox et al. 2019a). Each spatial attribute had a VIF of <2, indicating minimal correlation between them (Quinn & Keough 2002). Before analysis, the two independent variables were standardised to subsequently produce beta estimates of regression coefficients (β), whereby each cell was subtracted from the variable mean and then divided by its SD, allowing comparisons of the standardised regression coefficients, SE and 95% confidence intervals of the independent variables (Schielzeth 2010). We only considered independent variables to have significant effects if confidence intervals did not overlap zero (McDonald et al. 2006). In the AltDiff dataset, we detected a single outlier (recipient site of *Pelobates syriacus*) that when included in the LMMs, resulted in a significant association with the response variable. However, when this record was omitted from the LMMs, no significant association was detected, thus, we excluded this record from our statistical analyses. Similarly, the recipient site of *Ceruchus chrysomelinus* represented a clear outlier in the LatDiff dataset, thus this record was also omitted from our statistical analyses. As our sample consisted of just a single species from the tropics and the SDM input data for this species was handled differently to the rest of the sample (e.g. different predictors and coarser thinning), we tested the sensitivity of our LMM outputs to the inclusion of this species (see outputs without *E. atala* in Table A4.8.1).

Results

Model evaluation

The SDMs of the final species set (*n* = 39) generally had high discrimination metric values (AUC: mean [minimum – maximum] = 0.910 [0.810 – 0.978]; TSS: 0.664 [0.480 – 0.903]) (Table A4.2.1), indicating good discrimination capacity. Similarly, evaluations of calibration accuracy indicated that models performed well on average (CBI: 0.960 [0.515 – 0.999]).

Model extrapolation

Based on our MESS analyses, we found that 85% of the recipient sites had no extrapolation issues under the current conditions or future projections. Of the sites where extrapolation was detected, the effects were deemed negligible (i.e. > -20) for 10%. In all these cases, the extrapolation was limited to the most extreme and distant climate change projection: SSP370 for the period 2061-2080 (Table A4.4.1). The remaining 5% of translocations covered three recipient sites involving two species, *Boloria eunomia* and *Eumaeus atala.* Extrapolation issues (i.e. < - 20) were detected under one climate change projection, the CanESM5 GCM based on SSP370 for the period 2061-2080 (Table A4.4.1).

Predicted suitability and projected changes

Our SDMs predicted that translocated populations were most frequently located at sites with very high macroclimatic suitability (0.75 – 1; *n* = 26) (Figure 4.1). However, when projecting our models onto scenarios of future climate change, there was a shift towards less suitable climates, and this was consistent under both SSP scenarios and all time periods. In fact, by 2061-2080 more translocated populations will be situated in the lowest suitability classification (0 – 0.25) than in any other classification, with an estimated 23 sites under SSP126 and 26 under SSP370 falling within this bracket.

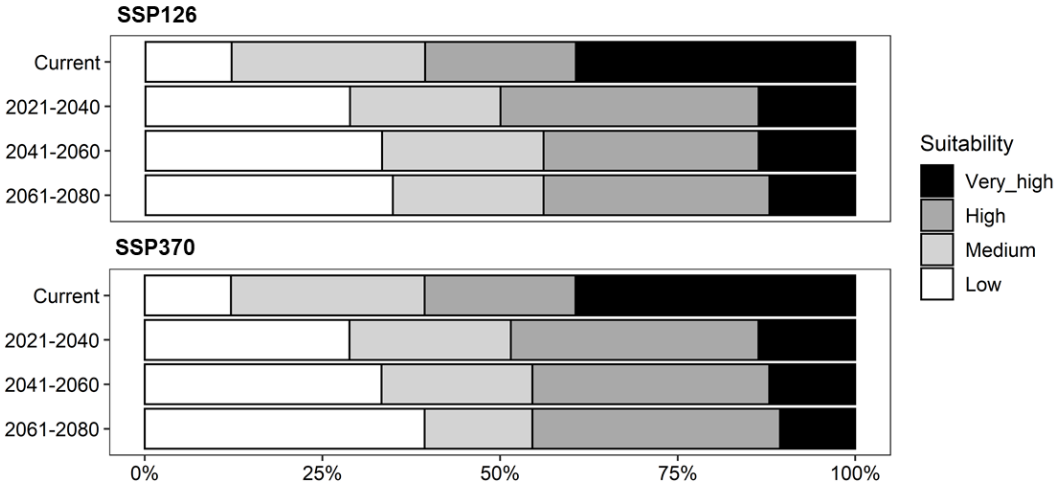

Figure 4.1. Predicted standardised suitability of translocation recipient sites (*n* = 66) under current macroclimatic conditions and future projected conditions for 2021-2040, 2041-2060 and 2061-2080. Future projections have been averaged across 5 GCMs for each SSP scenario. Suitability categorisations are as follows: Low = 0 – 0.25, Medium = 0.25 – 0.50, High = 0.50 – 0.75 and Very high = 0.75 – 1.

Suitability at recipient sites is predicted to decline for most species regardless of SSP scenario or time horizon (Table 4.2). By the middle of the century, SDM outputs indicate a deterioration in the macroclimatic suitability of recipient sites for 75.7% of the sample under both SSP scenarios. The magnitude of suitability change was highly variable across sites (Figure 4.2; Table 4.2), with most declining sites falling into the smallest percentage change category (0 – 0.25). However, there was a notable increase in the percentage of sites forecast to undergo a medium decline in both 2041-2060 and 2061-2080 under the SSP370 scenario, where this was the most represented category.

Table 4.2. Percentage of recipient sites predicted to decline in suitability across six climate change projections. Results are compared across three suitability

change categorisations (decline = <0.25, medium decline = 0.25 – 0.5, and large decline = >0.5). Future projections have been averaged across 5 GCMs for each SSP/time period combination.

Scenario	Decline	Medium decline	Large decline	Total
2021-2040				
SSP126	45.5	22.7	6.1	74.3
SSP370	47.0	24.2	4.5	75.7
2041-2060				
SSP126	39.4	33.3	3.0	75.7
SSP370	34.8	34.8	6.1	75.7
2061-2080				
SSP126	44.0	27.3	3.0	74.3
SSP370	33.3	37.9	7.6	78.8

Of the five different GCMs included in our analyses, CanESM5 was the most pessimistic, consistently predicting suitability declines at more recipient sites than any other GCM. By the middle of the century, projections based on CanESM5 forecast that 84.8% of recipient sites will decrease in suitability under SSP370 (Table A4.5.1). The CanESM5 model also forecasted the greatest declines in magnitude, particularly under the SSP370 scenario, whereby 10.6% of recipient sites are predicted to undergo a large decline in suitability (>0.5) by 2061-2080. In contrast, the CNRM-CM6-1 model often predicted the smallest proportion of recipient site declines (<70% under all but one projection), reaching a >20% difference with the CanESM5 model under SSP370 for 2041-2060.

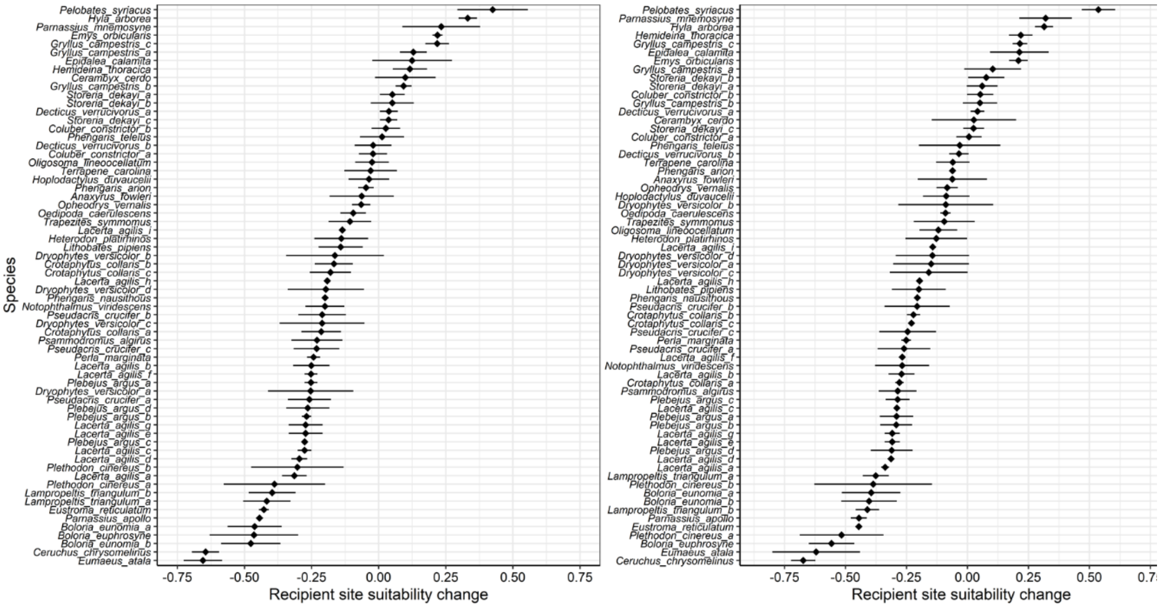

Figure 4.2. Mean (SD) predicted changes in standardised suitability at 66 translocation recipient sites between current conditions and those projected for mid-century (2041-2060), according to two different climate change scenarios: SSP126 (left) and SSP370 (right). Future projections have been averaged across 5 GCMs for each SSP scenario. Outputs for 2021-40 and 2061-2080 are presented in Figure A4.6.1.

Comparing suitability change across spatial scales

Suitability is forecast to decline across most species' global ranges in the future (Figure 4.3; Table A4.7.1). The magnitude of predicted suitability change at the recipient site scale was, on average, less severe than changes forecast across the rest of the species range (Table A4.7.1), with 65– 70% of recipient sites faring better than the global median, depending on the time horizon and SSP scenario. Differences between predicted suitability change at the recipient site and global scale were statistically significant under all climate change projections, according to Wilcoxon signed-rank tests ($p < 0.01$, $n = 6$).

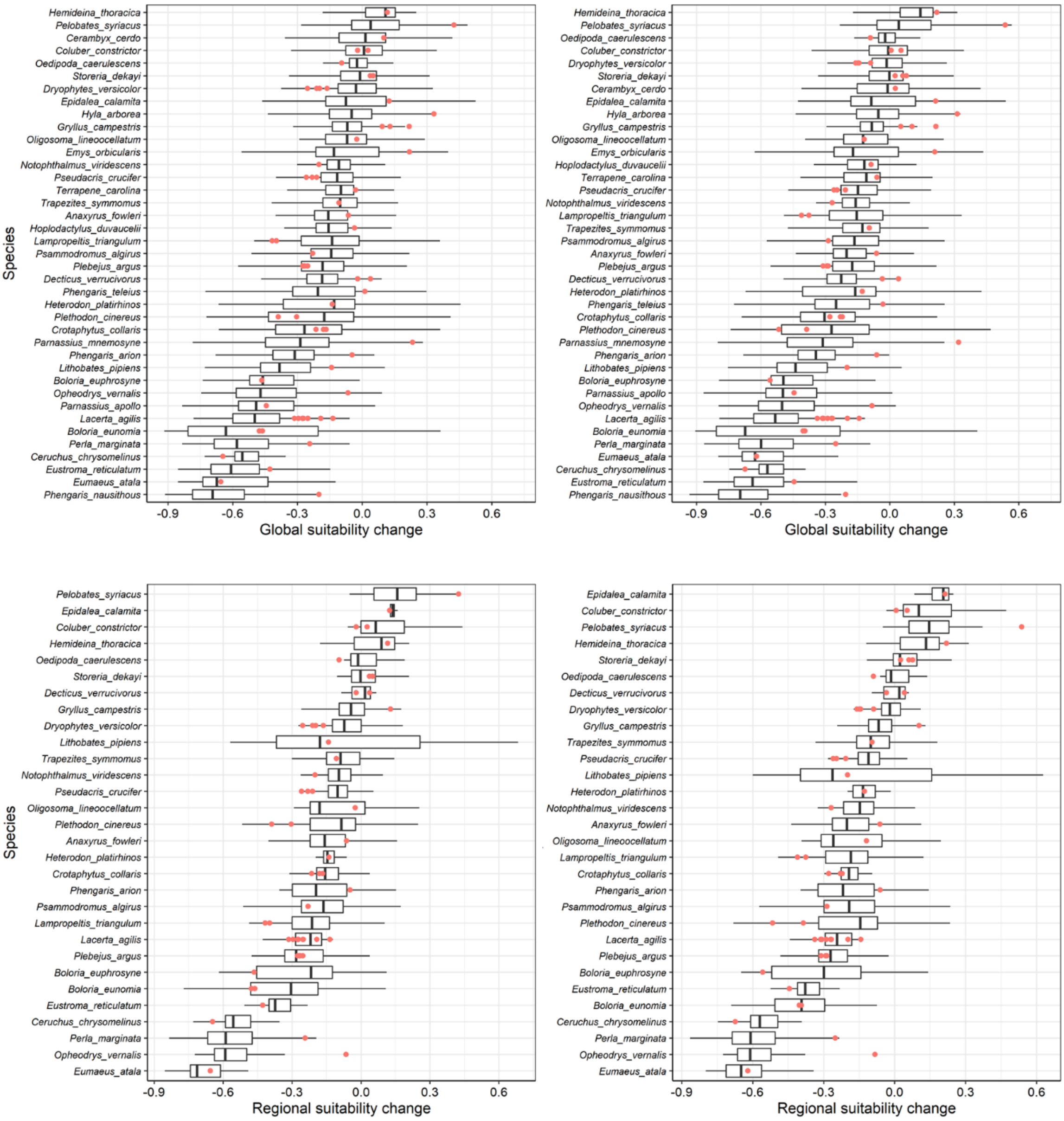

Figure 4.3. Average predicted change in suitability across species global (top) and regional (bottom) ranges by 2041-2060, according to two different climate change scenarios: SSP126 (left) and SSP370 (right). Red dots represent predicted suitability change for translocated populations. Future projections have been averaged across 5 GCMs for each SSP scenario. Outputs for 2021-40 and 2061-2080 are presented in Figure A4.7.1-2.

Despite the favourability of recipient sites relative to global averages, when repeating the same comparison at the regional scale, the reverse was observed, with far fewer recipient sites faring better than the regional average (34.5 – 41.8% depending on the climate projection; Figure 4.3, Table A4.7.2). The difference in predicted suitability change between the two scales was statistically significant under scenario SSP126 for 2041-2060 (*p* = 0.03), SSP370 for 2021-2040 (*p* = 0.05), and SSP370 for 2041-2060 (*p* = 0.04).

Spatial attributes of recipient sites

The effect of latitudinal difference between recipient site and distribution centre (LatDiff) on suitability change was consistently stronger than the effect of altitudinal difference between recipient site and distributional average (AltDiff) (Table 4.3). The effect of LatDiff was statistically significant across every projection. A large proportion of recipient sites were located close to the centre of species' distributions, where they were generally forecast to decline in suitability, though the magnitude of predicted decline varied markedly (Figure 4.4). In contrast, recipient sites located closer to the poleward range margin were associated with more favourable predicted suitability change at recipient sites (e.g. Figure 4.4). The effect of AltDiff was considerably weaker and not statistically significant (Table 4.3).

Table 4.3. Beta coefficients (β), standard error and 95% confidence intervals of the spatial attributes influencing predicted changes in macroclimatic suitability at recipient sites. Bold 95% CI (i.e. non-overlapping CI) indicates statistical significance (i.e. non-overlapping CI).

Spatial attribute	**β**	**β SE**	**95% CI**	
2021-2040 – SSP126				
(Intercept)	0.09	0.15	-0.21	0.39
Altitudinal difference	-0.01	0.13	-0.26	0.24
Latitudinal difference	0.51	0.14	**0.24**	**0.78**
2021-2040 – SSP370				
(Intercept)	0.08	0.15	-0.21	0.38
Altitudinal difference	-0.01	0.13	-0.26	0.24
Latitudinal difference	0.54	0.14	**0.27**	**0.81**
2041-2060 – SSP126				
(Intercept)	0.06	0.15	-0.24	0.36
Altitudinal difference	-0.09	0.13	-0.34	0.16
Latitudinal difference	0.51	0.14	**0.24**	**0.79**

2041-2060 – SSP370				
(Intercept)	0.05	0.16	-0.26	0.36
Altitudinal difference	-0.09	0.13	-0.35	0.17
Latitudinal difference	0.50	0.14	**0.22**	**0.78**
2061-2080 – SSP126				
(Intercept)	0.05	0.16	-0.26	0.36
Altitudinal difference	-0.09	0.13	-0.34	0.17
Latitudinal difference	0.50	0.14	**0.22**	**0.78**
2061-2080 – SSP370				
(Intercept)	0.03	0.16	-0.29	0.36
Altitudinal difference	-0.14	0.14	-0.41	0.13
Latitudinal difference	0.42	0.15	**0.13**	**0.71**

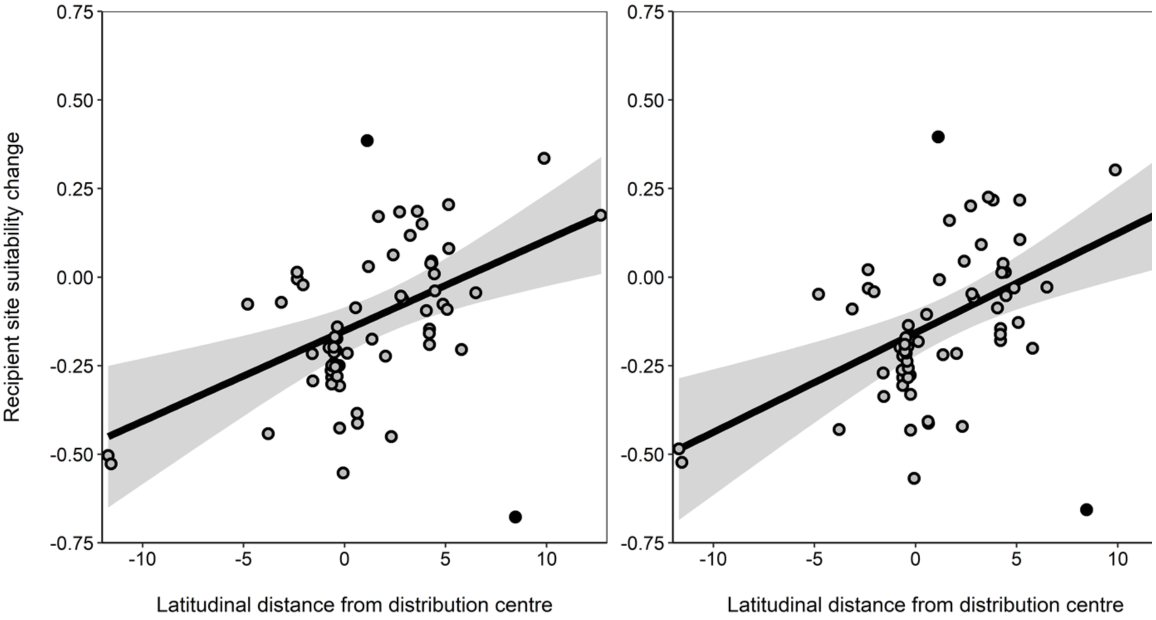

Figure 4.4. Effect of distance from latitudinal centre (decimal degrees) on predicted changes in macroclimatic suitability at recipient sites, according to SSP126 (left) and SSP370 (right) for the period 2041-2060. Effect plots for other time horizons are presented in Figure A4.8.1. The two black dots (upper = *Pelobates syriacus*; lower = *Ceruchus chrysomelinus*) represent outliers that were omitted from the LMM.

Discussion

While our sample of 66 recipient sites have supported the successful establishment of translocated populations, more than two-thirds are forecast to decline in suitability under climate change, regardless of the scenario or time horizon. In the recent past, favourable macroclimatic conditions have likely facilitated the successful establishment of many of these translocated populations – the largest proportion of recipient sites are in areas of high suitability under current climates (0.75 – 1). However, our SDMs predict a marked shift in suitability at many sites, causing the lowest suitability category (0 – 0.25) to change from the least- to the most-represented by the middle of the century onwards. Based on recent research, this is concerning as low suitability estimated from macroecological SDMs is associated with populations that have lower abundance (Braz et al. 2020), reduced individual survival (Lee-Yaw et al. 2016), and a heightened probability of extinction (Bellis et al. 2020).

Similarities in the direction and magnitude of suitability change between the two SSP scenarios (Table 4.2; Figure 4.2) suggests that global climate mitigation efforts will not be enough to prevent medium (-0.25) and large (-0.50) suitability declines for around a third of translocated populations. Whether declines of this magnitude will lead to population extirpation will depend on multiple factors, such as the availability of microhabitats (De Frenne et al. 2019), the adaptability of the species (Fox et al. 2019b), and the level from which suitability has declined. The latter point is critical because a future decline in climate suitability does not mean that the projected climate suitability is intolerable, for example, if a suitability decline of 0.3 is predicted to occur, but from a baseline of 0.8, then the site may still meet the macroclimatic requirements of the focal species.

The latitude of recipient sites relative to the latitudinal mean of distribution (LatDiff) proved to be a useful indicator of SDM-based climate change vulnerability (Table 4.3), with sites closer to the poleward range margin receiving more favourable suitability change predictions. This finding is in concordance with several other studies that have predicted greater vulnerability from climate change for populations located closer to equatorial range margins (e.g. Araújo et al. 2006; Cheaib et al. 2012; Bell et al. 2014). Moreover, intraspecific comparisons of demographic performance have revealed reductions in survival and higher rates of extinction in southerly distributed populations of northern hemisphere species (Reading 2007; Nicastro et al. 2013; Lesica & Crone 2017). In the mid-century SSP370 scenario, all but one recipient site located in the equatorial half of species' distributions were predicted to decline in suitability. Given the risk of suitability decline, translocation programmes aiming to secure long-term population viability would be sensible to avoid the selection of recipient sites at latitudes closer to the equator than the species' mean latitude, unless outputs from spatiotemporal models suggest otherwise.

The altitude of recipient sites relative to the wider species range had little effect on predicted suitability change when modelled using LMMs (Table 4.3). However, there was a lack of higher altitude translocations in our sample, with just one release, of *Pelobates syriacus,* above 1000 m. As this record represented an extreme outlier, it was removed from the LMMs. But it is notable that the recipient site of this species, located in the Geghama Mountains of Armenia, consistently ranked as the best performing site in our sample, gaining >0.5 in suitability under some projections (e.g. Figure 4.2). Climate changes rapidly with rising altitude; a simple altitude-for-latitude model estimates that a fall in temperature of 1°C that occurs with an increase of 167 m altitude is equivalent to a 145 km change in latitude (Jump et al. 2009). During warm postglacial periods in Europe, some species contracted their ranges and took refuge in southerly mountainous areas, where temperatures were cooler and competition was lower (e.g. Martinet et al. 2018). Mountains may represent an opportunity for conservation managers to translocate species shorter geographical distances, which was shown to better preserve post-release survival in birds (Skikne et al. 2020), while gaining the level of climate stability equivalent to a translocation of hundreds of kilometres in latitude.

Our sample was biased towards species with large range sizes distributed across the temperate region (Table 4.1). After the data cleaning and thinning stage, just a single species with a tropical distribution (Atala Butterfly *Eumaeus atala*) was eligible for inclusion in our SDM analyses. Although rates of projected warming are lower in the tropics (IPCC 2014), ectotherms of tropical regions have more narrow thermal thresholds and are particularly susceptible to temperature increases (Sunday et al. 2011; Shah et al. 2017). The closer association between climate and the physiology of tropical ectotherms means that changes in climatic conditions at recipient sites may present more of a threat.

Although just a single example, it is noteworthy that the recipient site, as well as the regional and global range of *E. atala,* was forecast to undergo some of the largest suitability decreases observed in our sample (Appendix 4.6). Notwithstanding the poor representation of tropical species in our study, physiological research suggests that translocation programmes involving tropical ectotherms would be well-advised to integrate methods for identifying climatically stable recipient sites into future management plans; an endeavour that should be aided by the rapid increases in biodiversity data (Feeley 2015; La Sorte & Somveille 2020) and the development of SDM techniques for small sample sizes (Breiner et al. 2015).

Recipient sites generally fared better under projected climate change than sites across species global ranges, but worse than sites across species regional ranges. While it is encouraging that translocations were less frequently undertaken into parts of species ranges that are most at risk from climate change (Table A4.7.1), the poor performance of recipient sites relative to regional trends indicates there is room for improvement. This finding supports our interpretation of the result from the keyword search presented in Appendix 4.1 – climate change is rarely factored into decisions regarding recipient site selection. Consequently, organisms are being released into sites with more severe suitability reductions than the projected regional average. Although macroclimatic conditions represent a single tier of overall habitat suitability (Johnson 1980; Stadtmann & Seddon 2018), ongoing and future conservation translocation programmes could benefit from the use of SDMs to pinpoint those areas in the target region (or beyond) where conditions most favourably align with the goals of the programme.

Correlative SDMs, such as the ones used in the present study, are a pragmatic tool for predicting the nature, magnitude, and rate of extrinsic climatic change likely to be experienced by a translocated population (i.e. climate change exposure). But if SDMs predict a decline in macroclimatic suitability to low levels (e.g. 0 – 0.25, Figure 4.1), an obvious question for managers is: What action should be taken to best serve the conservation of the species? This question has been approached from numerous angles in the peer-reviewed literature (e.g. Hoegh-Guldberg et al. 2008; Aitken & Whitlock 2013; Gilbert et al. 2020), resulting in a broad range of suggestions for conservation managers that depend on factors such as the genetic diversity of the population, the conservation status of the species, and the available resources at the manager's disposal. While low macroclimatic suitability can be associated with higher vulnerability (Lee-Yaw et al. 2016; Bellis et al. 2020; Braz et al. 2020), intrinsic factors such as the sensitivity and adaptive capacity of the focal taxa may increase or decrease the overall vulnerability of the translocated population. These intrinsic factors can be identified and quantified using trait-based approaches, and then combined with SDM predictions to produce a climate change vulnerability assessment (CCVA) (e.g. Garcia et al. 2014). CCVAs can identify the attributes that could make a translocated population vulnerable to climate change and thus potential conservation actions—adaptation measures—that can be proactively taken to reduce vulnerability. For example, species are likely to be especially sensitive to climate change if they are highly dependent on beneficial interspecific interactions with another species, such as butterflies and their hostplants, or if they have specialised microhabitat requirements across multiple life stages, such as water-dependent larval amphibians (Foden et al. 2013, 2019). Moreover, translocated populations may be limited in their capacity to adapt to changing recipient site conditions if there is little potential for phenotypic plasticity, or if genetic diversity and gene flow are low (Foden et al. 2013, 2019).

Many species in our sample are distributed across wide latitudinal gradients and this increased the insight obtainable from the LatDiff spatial attribute. The diversity of LatDiff across recipient sites demonstrates the macroclimatic stability and gains that can be obtained through longer distance poleward translocations (Figure 4.4). However, it is common for translocation attempts to focus on species that have small ranges. Thus, the distances required to translocate them into areas of stable suitability (e.g. Figure 4.4), could equate to translocations beyond their indigenous range, i.e. an assisted colonisation (IUCN 2013). Although the concept of introducing species to new areas has sparked criticism due to the potential for unintended consequences (e.g. Mueller & Hellmann 2008; Ricciardi & Simberloff 2009), there is increasing recognition that this may be the only option for safeguarding some species (Prober et al. 2019). Conservation researchers have already created decision frameworks (Richardson et al. 2009; Rout et al. 2013), designed strategies for selecting candidate species (Gallagher et al. 2015), and provided recommendations on the best time to conduct assisted colonisation (McDonald-Madden et al. 2011). However, to date there has been a significant reluctance to use assisted colonisation as a management tool under climate change (Butt et al. 2020). Our results indicate that the business-as-usual approach to conservation translocations will lead to more populations that are threatened, unnecessarily, by deteriorating environmental conditions. Therefore, a forward-looking approach to recipient site selection is needed so that translocated populations are strategically placed in areas with future viability. While the risk associated with assisted colonisation may be deemed too great in some contexts, selecting recipient sites that are oriented towards the poles and further from source populations will be inevitable if translocations are to keep pace with climate change.

Conclusions

Calls for a more proactive approach to conservation management (Drechsler et al. 2011; Sterrett et al. 2019) resonate with the key findings of this study. The lack of explicit anticipation of climate change in translocation papers and reports, coupled with the predictions of widespread deterioration at recipient sites, will likely lead to future management interventions that are reactive in nature. While some species may be able to adapt in-situ to changing climatic conditions, translocations usually involve threatened taxa with small populations, properties that are not typically associated with a capacity to adapt (Foden et al. 2013, 2019). Thus, managers may be forced to undertake more translocations to keep pace with the shifting climate. Given that translocation attempts can be costly, time-consuming (Jones & Kress 2012) and sometimes contentious (Serfass et al. 2014), proactively identifying sites that are forecast to retain their suitability under climate change could improve the long-term effectiveness of translocations and minimise the need for additional costly interventions in the future.

Author contributions statement

J.B., S.D., and D.B. conceived the ideas and designed the work. J.B. collected and analysed the data. J.B. led the writing of the manuscript. J.B., S.D., D.B., and J.M. contributed to the final draft and approved the final version for thesis submission.

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Chapter 5:

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

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Abstract

Species reintroductions often aim to establish populations of threatened taxa over the long-term. However, climate change may jeopardise 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. 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. 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. The findings presented here made a valuable contribution to the reintroduction planning process, by facilitating the prioritisation of reintroduction efforts towards species with a greater likelihood of establishing long-term populations at the prospective recipient sites.

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 recolonise restoration sites through natural dispersal mechanisms, others will struggle due to an increasingly fragmented landscape (McGuire et al., 2016). To aid the colonisation process, reintroductions and other conservation translocations are increasingly utilised (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 (Fischer & Lindenmayer, 2000; Dalrymple et al., 2012).

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 specialised 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 (Topić & Stančić, 2006; Hughes et al., 2008). 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 thirteen 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 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 U.K. and Ireland.

Methodology

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 5.1). 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 organisations 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 5.1). 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*).

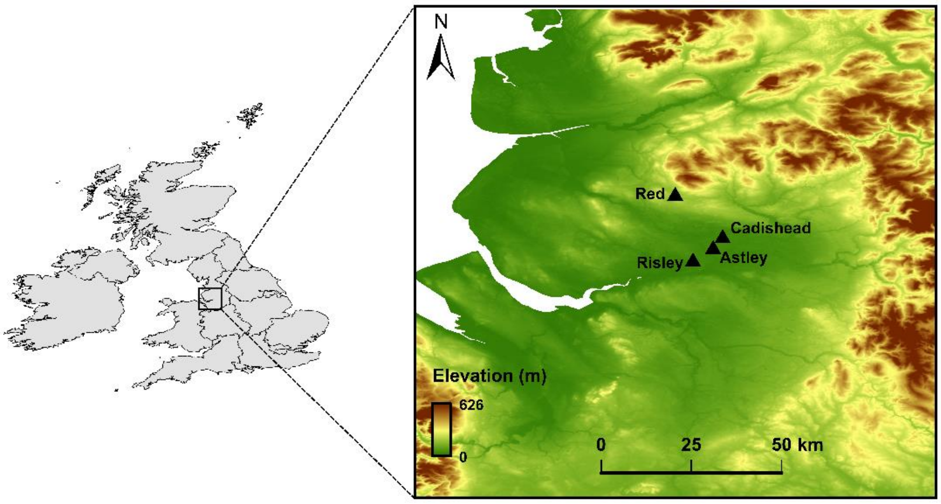

Figure 5.1. Map of the study area and the locations of the four raised bog restoration sites in North West England.

Table 5.1. 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

Species distribution models

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 maximise spatial and temporal reliability in preparation for modelling (further details are given in Appendix 5.1).

We considered a combination of nine climatic variables and soil pH as macroecological predictors in our SDMs, based on their eco-physiological 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 (GDD) (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 (SMD) (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 ten predictors, we removed variables that presented a variance inflation factor (VIF) of >10 (Dormann et al*.,* 2013; Guisan et al*.,* 2017) using the R package *usdm* (v. 1.1-18) (Naimi, 2015) (Appendix 5.1).

To estimate future suitability, we used three general circulation models (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 5.1).

Modelling approach

We used an ensemble of SDM algorithms to minimise the uncertainty associated with single modelling techniques (Buisson et al., 2010). Our ensemble consisted of Generalised Additive Model (GAM), Multivariate Adaptive Regression Splines (MARS), Generalised

Boosted Model (GBM), 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 (Chefaoui & Lobo, 2008; VanDerWal et al., 2009; Barbet-Massin et al., 2012). 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 standardised the predicted climate suitability values to range between 0 and 1 with the following formula: (x – min)/(max – min) (Appendix 5.1).

To categorise 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 maximised the TSS score. We chose this method because it demonstrated improved reliability over other commonly applied approaches when only presence data was available (Liu et al*.,* 2013).

Data analyses

To estimate the future suitability of the recipient sites (and across the whole of the U.K. and Ireland), we averaged the SDM projections for the three GCMs to produce a consensus prediction of suitability. For the purposes of this manuscript, 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 A5.2.3) 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 U.K. and Ireland ranges of our focal species (Ohlemüller et al., 2006), we calculated three types of suitability change based on the binary output maps:

i) *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.

ii) *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.

iii) *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, i.e. 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 U.K. and Ireland.

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). 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 A5.2.2). Proportions of the U.K. 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 5.2). 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, 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 5.2).

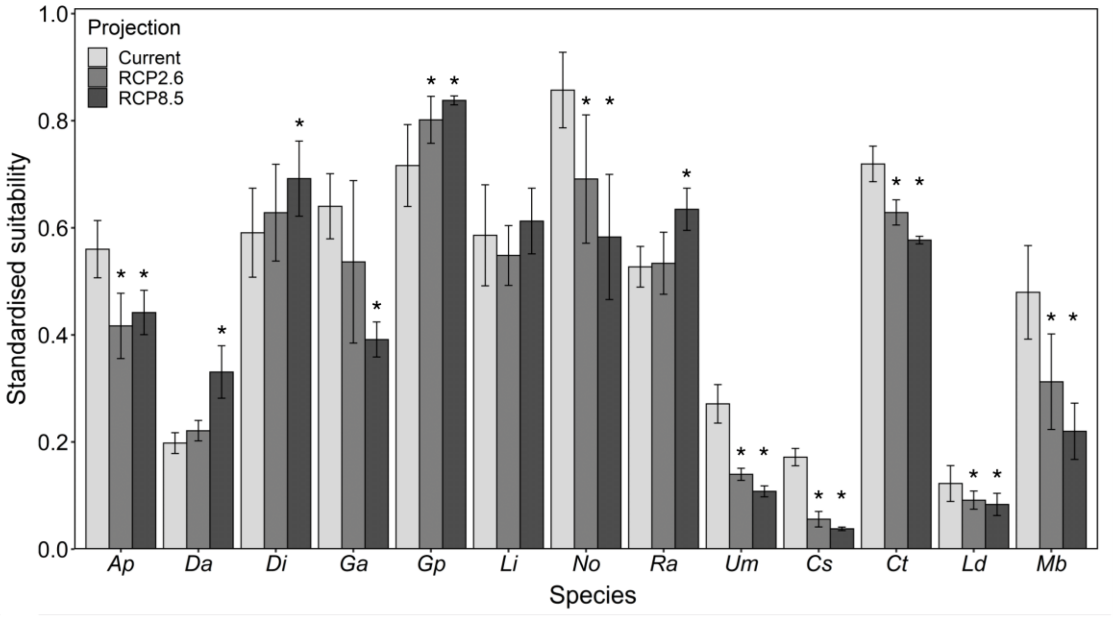

Figure 5.2. Mean (SD) predicted environmental suitability of potential recipient sites for nine plant and four invertebrate species. SD represents the variation in predicted suitability between the four sites. * indicates statistically significant differences between current and future climate suitability according to a Wilcoxon Signed-Rank test (significance set to $p < 0.05$). Abbreviations are: *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.*

Under current conditions, at least one of the sites was categorised as suitable for nine species (Table A5.2.3). 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 A5.2.3). According to the RCP2.6 scenario, all sites were categorised 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 A5.2.3), 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 A5.2.4). 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 U.K. 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 5.3) and *M. brachyptera* (Figure A5.2.1), 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 5.3). 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 5.3) and is actually forecast to experience a large increase in climatically suitable area (> 120%) across the U.K. and Ireland by 2041-2060 (Figure 5.4).

Climate change presented a greater risk to species with more northerly distributions (Figure 5.3), 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 5.3). However, *M. brachyptera* was an outlier to this trend, with a large proportion of its current U.K. range threatened by climate change despite having a relatively low mean latitudinal centre.

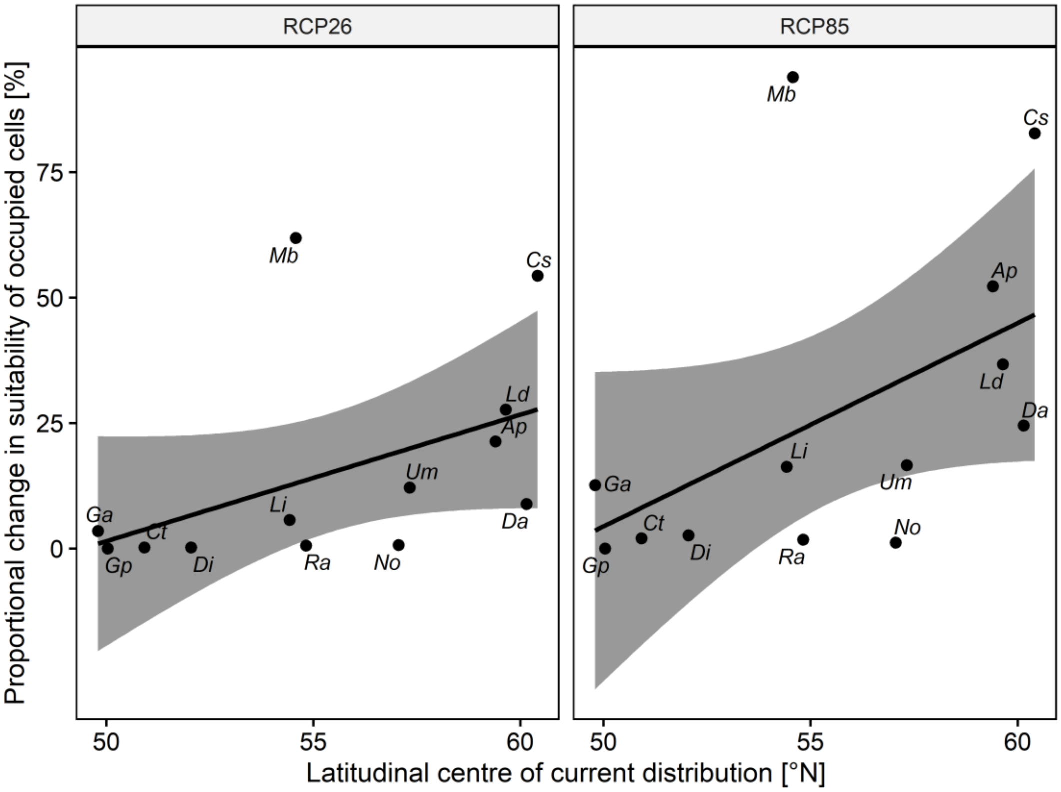

Figure 5.3. Association between mean latitude of global distribution and proportion of threatened occupied area in the U.K. and Ireland. Left panel is based on RCP2.6 and right panel RCP8.5. The shaded areas represent 95% confidence intervals. Abbreviations are: *Ap* = *Andromeda polifolia*; *Cs* = *Carsia 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.*

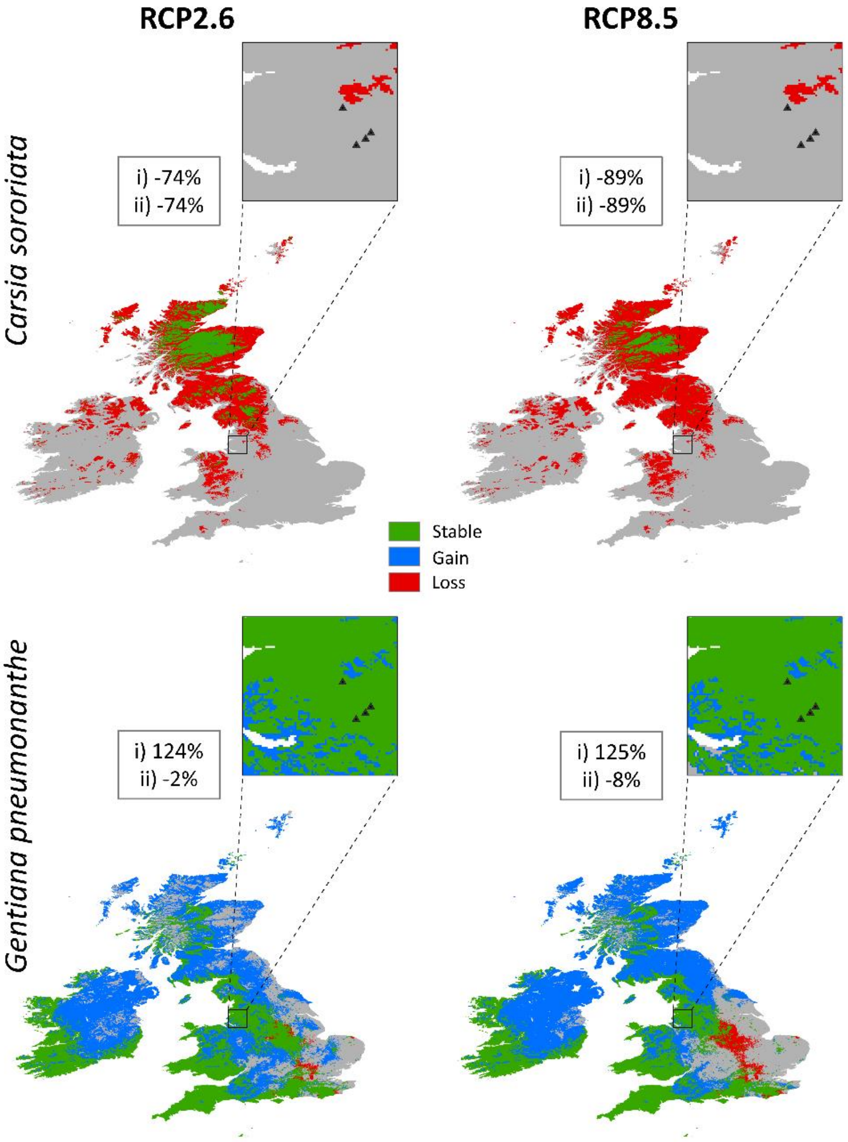

Figure 5.4. Predicted changes in suitable area across the U.K. and Ireland for *Carsia sororiata* and *Gentiana pneumonanthe* by 2041-2060 under RCP2.6 and RCP8.5. The proportional change in overall suitability (i) and the proportional change in currently suitable cells (ii), which are described in more detail in the methods section, are also presented. Species presented here represent the extremes of negative and positive projections. Suitability change maps for other species are available in Figure A5.2.1.

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 U.K. 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, i.e. 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 is favourable under current conditions (above binary threshold) but is forecast to decline significantly by 2041-2060 at three of the potential recipient sites (Table A5.2.3; Figure 5.2). 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 categorise the candidacy of species for reintroduction and to estimate future distributional changes. While binary predictions are frequently used for biogeographical and conservation applications (Dyderski et al., 2018; Maiorano et al., 2019; Cerasoli et al., 2020), research has shown that discretising 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.

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 5.3). However, *M. brachyptera* was an outlier to this trend, with >80% of currently occupied cells in the U.K. 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. Firstly, *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 U.K. distribution of *M. brachyptera* having the largest proportion of non-analogue future climates; Table A5.2.2). Secondly, 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 A5.2.1). Although previous modelling studies have also found temperature seasonality to be an important variable in the structuring of species' distributions (e.g. Barbet-Massin and Jetz, 2014; Zhang et al., 2018; Cerasoli et al., 2020), 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 pseudo-absence (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) (e.g. Csergő et al., 2017; Bellis et al., 2020). 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 colonise newly emerging suitable climates (e.g. Figure 5.3; Figure A5.2.1). 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 U.K. has become highly fragmented by human infrastructure (Young & Jarvis, 2001; Hooftman & Bullock, 2012), reducing the connectivity of remnant patches of suitable habitat and limiting the ability of species to colonise 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.

Conservation/management implications

The potential of SDMs to inform reintroduction decision-making has been widely discussed (Krause & Pennington, 2012; Osborne & Seddon, 2012; IUCN, 2013). 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 5.1), 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 prioritise 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 A5.2.3), 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 – 50 m ASL) (see Figure 5.1). 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 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 U.K., 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.

Author contributions statement

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.

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Chapter 6:

General Discussion

Overview

With conservation translocations increasingly being used to halt and reverse the effects of human activities on species and ecosystems, the conservation community has a responsibility to take whatever steps possible to improve the outcomes of existing and future translocation programmes.

This thesis investigates the potential effects of recent and future macroclimates on populations that have resulted from a conservation translocation. Based on these real-life case studies, which involved ectothermic vertebrate and invertebrate taxa, a case is made for increased consideration of macroclimate during translocation planning and implementation. The species distribution modelling techniques used to estimate existing and future climate suitability are then applied to support conservation decision-making in an ongoing translocation programme in the North West of England.

Synthesis of results

Translocations have made a significant contribution to the conservation status of many species (Seddon et al. 2014). Nevertheless, numerous translocation attempts fail to establish populations. Programme failure, while undoubtedly useful as a learning exercise, equates to loss of life, loss of financial resources and loss of time, each of which is becoming increasingly scarce in conservation. Consequently, there has been wide recognition that analyses targeted at identifying causes of translocation outcomes are essential to improving success rates in the future (Ewen & Armstrong 2007; Sutherland et al. 2010; Armstrong & Reynolds 2012). Reviewing the causes of translocation outcomes has been an active area of research during the past three decades, with numerous articles published in highly respected journals (e.g. Griffith et al. 1989; Wolf et al. 1996; Fischer & Lindenmayer 2000; Seddon et al. 2007; White et al. 2012; Cochran-Biederman et al. 2015). However, the focus of these reviews has been taxonomically biased, with multiple articles focusing on large vertebrate taxa, such as mammals and birds, while other major taxonomic groups, such as insects (but see review of freshwater invertebrate translocations published recently; (Jourdan et al. 2019), are yet to be the focus of a global review. While this emphasis on large vertebrate taxa partly reflects the number of translocations being conducted (Seddon et al. 2005; Bajomi et al. 2010), and biases in conservation more widely (e.g. Leandro et al. 2017), the significant body of literature on insect translocations presented in *Chapter 2* of this thesis indicates that the situation is changing. This is a timely development because recent studies have documented alarming declines in insect numbers (Hallmann et al. 2017; Vogel 2017; Lister & Garcia 2018), suggesting that there will be a greater demand for conservation techniques such as translocation.

One of the main findings of *Chapter 2* was that increasing the number of individuals released (NumRel) was a key determinant of success in terrestrial insect translocations. While this result is concordant with reviews of other small-bodied taxa with relatively short lifecycles (e.g. amphibians; Germano & Bishop 2009), an examination of the authors perceived causes of failure in unsuccessful insect translocations revealed that the release of insufficient numbers was rarely suggested as a possible cause of failure (*n* = 2; 6% of cases). Based on the somewhat low support given to the top performing models in *Chapter 2*, which consistently included NumRel, it seemed plausible that other factors were having more influence over the outcome of insect translocations. The weather and climate conditions of recipient sites could be one such factor, as this represented the joint most frequently reported cause of failure by authors (Figure 2.3). The results presented in *Chapter 3* strongly supported the perceptions of the authors involved in the terrestrial insect translocations, as climate was identified as the most important factor influencing translocation outcome, relative to the other factors analysed in *Chapter 2*.

Past translocation reviews have tended to focus on simple demographic metrics such as short-term survival rates and evidence of reproduction when defining success. Sarrazin (2007) proposed to split the dynamics of successful translocations into three main phases, namely, establishment, population growth, and regulation, and to focus on the regulation phase to assess the ultimate success of a translocation. While it is difficult to dispute that evidence of population regulation represents the ultimate indicator of success, publications and reports on translocations are rarely produced long enough after the translocation to confirm that a population has reached the regulation phase (but see (Dolný et al. 2018). Therefore, if reviews are to categorise translocation outcomes into success and failure and have sufficient sample sizes to conduct meaningful quantitative analyses, then a more pragmatic definition of success is required. In a review of freshwater fish translocations, Cochran-Biederman et al. (2015) reported the outcome of translocations according to the authors own definitions of success, but found that the author's perceptions of success were highly variable and dependent on the individual goals and objectives of the translocation programme. This variability presents an obstacle to the comparability of translocation outcomes between programmes.

In *Chapter 2*, a standardised definition of translocation success was adopted based on the specific life-history of the focal species. By ensuring that a species had persisted at a recipient site for longer than its lifecycle, it can be reasonably inferred that the site provides the necessary resources for each lifecycle phase. However, what this definition did not fully account for was the potential for abnormally favourable biotic or abiotic conditions following release, which could result in premature declaration of success. For example, an attempted reintroduction of the Eastern Baton Blue Butterfly *Pseudophilotes vicrama* in southern Finland appeared to be highly successful in the years immediately following release (Marttila et al. 1997), but then heavy rainfall during the flight period led to the subsequent decline and extirpation of the population (K. Saarinen pers. comm.). To reduce the risk of prematurely declaring a translocation successful, I chose to extend the criteria of success for *Chapter 3*, by requiring a translocated population to have persisted for ≥10 years after the most recent release. Given that there is no universally accepted definition of translocation success (Robert et al. 2015) and previous reviews have opted for less robust short-term indicators such as survival and reproduction, the adoption of this definition in future translocation reviews could enhance comparability and provide a more rigorous indication of factors effecting long-term translocation success.

While translocation reviews have contributed to our collective knowledge on factors such as release techniques, less tractable but potentially critical aspects of the translocation process have remained uncertain (Armstrong & Seddon 2008; Taylor et al. 2017). Although the quantitative analyses of *Chapter 2* were focused on aspects of translocation protocols that are typically considered in reviews, this was supplemented with qualitative data based on expert-knowledge (perceived causes of translocation failure). This qualitative data provided a foundation for the formulation of the main hypothesis in *Chapter 3*; that the climatic suitability of recipient sites, measurable using SDMs, is associated with the outcome of translocations. Outputs from statistical analyses supported this hypothesis – probability of translocation success increased as predicted climate suitability increased. Moreover, climate suitability explained more variation in translocation outcome than five other variables identified as important in previous studies.

Given the direct influence of ambient temperature on the physiology of ectotherms (Angilletta 2009), the association between climate suitability and translocation outcome detected in *Chapter 3* is unsurprising. However, the fact that this association was successfully modelled by SDMs fitted with macroclimatic variables is important, because this can encourage future translocation programmes to adopt a more objective approach to recipient site selection (Osborne & Seddon 2012). In the past, lack of SDM uptake in conservation programmes (Guisan et al. 2013) is likely to have partly stemmed from the assumption that parameterising and running SDMs requires advanced statistical and coding expertise. However, global macroecological data and species occurrence data are freely available from multiple online platforms (e.g. WorldClim, CHELSA, and GBIF), and MaxEnt (Phillips et al. 2006), a high performing presence-only SDM algorithm, can be run through a standalone software package with a graphical user interface. The accessibility of these components, coupled with my empirical evidence that SDMs can provide useful insight on recipient site suitability, should lead to greater integration of SDMs into translocation management plans.

While this thesis has demonstrated the value of SDMs to support conservation decisions, it is important to emphasise the need to follow best-practice principles. If SDMs are to offer tangible value to decision making processes, they need to be constructed in a thoughtful and reproducible manner (Araújo et al. 2019), regardless of a user's experience and individual time pressures. Decisions about data preparation, selection of predictor variables, choice of algorithm, model fitting and evaluation can all impact SDM predictions, which in turn, can affect the resulting management proposals (Muscatello et al. 2020). Poorly constructed and interpreted models that are not fit for the targeted decision-context can lead to erroneous conservation actions (Guillera-Arroita et al. 2015). To avoid this, model production decisions should be clearly reported and justified, which could be achieved by following a standardised protocol, such as the recently published ODMAP protocol in Zurell et al. (2020). The ODMAP protocol represents a quick guide and generic workflow for SDM-based research and introduces a structured format for documenting and communicating models, ensuring transparency and reproducibility, as well as facilitating peer-review and expert evaluation of model quality.

After establishing that macroclimatic suitability, measurable using SDMs, was strongly associated with the outcomes of previous translocation attempts, the next step was to find out whether translocated populations would be threatened by future changes in macroclimatic conditions. This was the focus of *Chapter 4*, which used a keyword search and SDM projections to expose the lack of climate change preparation in previous and ongoing translocation programmes. The keyword search revealed that climate change-related terms were mentioned in less than 2% of 338 translocation papers and reports in relation to recipient site selection processes, while the SDMs estimated that at least 74% of recipient sites will decline in suitability in the future, regardless of the climate change scenario or time horizon. Although there was significant variation in the magnitude of predicted suitability declines between recipient sites, more than a third of sites were predicted to reach low suitability (0 – 0.25) by the middle of the century. This is concerning given that low suitability estimated from SDMs is associated with populations that have lower abundance (Braz et al. 2020), reduced individual survival (Lee-Yaw et al. 2016), and a heightened probability of extinction (*Chapter 3*).

Managers tasked with conserving the translocated populations forecast to experience large suitability reductions in *Chapter 4* have both *in-situ* and *ex-situ* management options available (Heller & Zavaleta 2009). To be effective, *in-situ* measures will require close monitoring of population trends and the minimisation of potential climate change impacts and other stressors on population viability (e.g. invasive species). For forest-dwelling species, restoration and greening efforts could function as proactive management to mitigate local-scale warming (De Frenne et al. 2019), while species with semiaquatic lifecycles (e.g. larval amphibians and dragonflies) could benefit from restoration of marginal and riparian vegetation to provide cool, moist conditions and lower pond or stream temperatures (Shoo et al. 2011). For particularly sensitive species, managers may also need to consider rescue measures, such as adding irrigation systems to secure populations against draught (Mathwin et al. 2020).

If *in-situ* management is predicted to be insufficient, an alternative strategy could be to translocate the species again. In an analysis of bird translocations, Skikne et al. (2020) proposes sequential, shorter distance translocations in response to climate change, as longer distance translocations reduced annual survival. However, when I compared the distances between successful and unsuccessful translocations of terrestrial insects in *Chapter 2*, no significant difference was detected (p = 0.714). Unfortunately, the number of translocations for which geographical distance was obtainable was too limited to quantify variable importance relative to other explanatory factors. Nevertheless, provided the necessary steps are taken to rigorously assess the biotic and abiotic conditions of a site (Gallagher et al. 2015), strategically conducted long-distance translocations oriented towards the poles can offer greater security against climate change (climate projections currently available up until the end of the century). Furthermore, a single long-distance translocation is likely to be a more cost-effective strategy than several short-distance translocations (e.g. Martínez-Abraín et al. 2011). Trials of long-distance translocations are already being undertaken in North America, with experimental plantings of Whitebark Pine *Pinus albicaulis* finding that the species could establish at sites identified as suitable by SDMs that were hundreds of kilometres north of the current range limit (McLane & Aitken 2012).

An alternative but highly contentious option for managers would be to deprioritise populations deemed unviable under climate change (Cornwall 2018), such as those at the trailing-edge of a species range. Gilbert et al. (2020) term this approach ‘trailing-edge triage’; as climate envelopes shift beyond these populations, trailing-edge triage allocates resources within the species range toward populations likely to remain viable under future climate change and away from those at the trailing-edge, where efforts are least likely to be effective. The findings of *Chapter 4*, in which translocated populations at latitudes closer to the trailing edge were generally projected to experience larger reductions in suitability (Figure 4.4), support the idea that these populations are more vulnerable to climate change and thus there is a greater risk of squandering conservation resources by prioritising them. However, one could argue that trailing-edge populations are still important to the conservation of a species because these populations often exhibit high degrees of local adaptation and contain unique genotypes that may be necessary to species’ persistence under future climates (Hampe & Petit 2005; Rehm et al.

2015). Specific adaptive traits from these populations can be identified and introduced into populations located closer to the poles, to mitigate maladaptation under future climates (Aitken & Whitlock 2013; Macdonald et al. 2017).

The final data chapter of the thesis (*Chapter 5*) aimed to integrate the methods and findings of the preceding chapters into on-ground conservation practice. To do this, SDMs were computed for 13 species earmarked for reintroduction at a series of raised bog sites undergoing restoration in North West England. The SDM outputs indicated that nine species represented viable candidates for reintroduction based on current climatic conditions. However, when accounting for projected changes in climate by 2041-2060, the number of candidates was reduced to seven species, according to the highest greenhouse gas concentration scenario (RCP8.5). These findings made an important contribution to the reintroduction planning process, by facilitating the prioritisation of reintroduction efforts towards species with a greater likelihood of establishing long-term populations at the recipient sites.

The context in which the restoration project required species-level recipient site suitability assessments is unique amongst existing SDM-based studies in the peer-reviewed reintroduction literature, due to the key question under investigation: which species from this list of candidates can be reintroduced into macroecological conditions that are suitable now *and* in the future? This question sets the research apart for two reasons, firstly, most previous studies citing the use of SDMs to aid recipient site selection did so for a single species (e.g. Kalle et al. 2017; Brooker et al. 2018; Maes et al. 2019), and secondly, just a single other study has used SDMs to forecast the future suitability of potential recipient sites in a reintroduction programme (Maes et al. 2019). Unlike most reintroduction programmes where the focal species dictates the location of the recipient site, in this case, the recipient site dictated the choice of focal species. Typically, this type of situation will arise when plans to reintroduce threatened species are embedded within wider restoration efforts to restore functional integrity and biological diversity (e.g. Zamboni et al. 2017).

Despite a lack of representation in the peer-reviewed literature, the need to assess the long-term suitability of a recipient site (or multiple sites) for a suite of species is likely already a common problem in conservation, and one which will become increasingly common in the future (Braidwood et al. 2018). Global ecological restoration efforts have been ramped up in recent years (McDonald et al. 2016), with continued increases likely as the United Nations has labelled the 2020s as the “Decade Of Ecosystem Restoration” (United Nations 2020, https://www.decadeonrestoration.org/). At the same time, there are mounting calls for increased integration of climate change into restoration and reintroduction management plans (IUCN 2013; McDonald et al. 2016). Accordingly, the work presented in *Chapter 5*, which has been accepted for publication in the open-access journal Ecological Solutions and Evidence, is uniquely placed to demonstrate, as a proof of concept, the use of SDMs for prioritising reintroduction efforts towards species with macroecologically favourable suitability predictions.

Bridging the gap between SDMs and practice

To achieve the aims of Chapters 3-5, I applied species distribution modelling techniques, which represent one of the most common classes of biodiversity modelling (Araújo et al. 2019). Although thousands of studies in the peer-reviewed literature cite the use of SDMs (Araújo et al. 2019), evidence of SDMs supporting decision-making in on-ground conservation situations is scarce (Guisan et al. 2013). The work presented in *Chapter 5*, where SDMs were constructed specifically to support decisions relating to the reintroduction of threatened plant and insect species, is a rare example of SDMs being applied in conservation practice (Guisan et al. 2013). The work involved in this chapter was the most rewarding of the whole PhD project, as the SDM outputs made a direct contribution to on-ground conservation efforts. However, the process of disseminating the SDM outputs posed multiple challenges.

The stakeholders involved in the restoration project, consisting of representatives from NGOs and government agencies, were generally unfamiliar with SDMs. As these individuals operate under time- and resource-limited conditions, they had restricted capacity to explore the vast field of SDMs. Moreover, much of the peer-reviewed literature on SDMs requires costly subscriptions that many practitioners do not have access to (Sunderland et al. 2009; Fuller et al. 2014) and this was the case for those involved in the restoration project. Nonetheless, within the project team there was a wealth of knowledge and experience in habitat management, restoration, and the ecology of the reintroduction candidate species, and I was able to utilise this information for model development (e.g. selection of eco-physiologically relevant predictor variables for each species' distribution model). Previous studies have suggested that if ecological models are to be used effectively in conservation decision-making, the process used to build the models must be credible, transparent, and reproducible (Guisan et al. 2013; Morisette et al. 2017; Villero et al. 2017). Furthermore, support for the interpretation of model outputs should be accessible to people that lack technical expertise in SDMs for those products to bear on important decisions (Sofaer et al. 2019).

In recognition of this, I produced a report of the species distribution modelling work tailored to the expertise of key stakeholders. I worked closely on this report with two of the project leaders, the Lancashire Peatland Initiative Project officer, Mike Longden, and the head of the North West Rare Plants Initiative, Joshua Styles. The final report consisted of three main sections: i) a 'background' section, which described the data and methods used to run the SDMs, ii) a results section, summarising model accuracy, broad trends in outputs and species-specific profiles based on the SDM outputs, and iii) a variation section, displaying the uncertainty in the suitability predictions. Each species-specific profile contained a table of the predicted suitability under current and future conditions, an SDM output map (as in Figure 5.4), and my own interpretation of the SDM outputs based on predicted suitability, suitability change and the associated SDM and GCM uncertainty. The uncertainty was measured and visualised according to the coefficient of variation and its inclusion in the report was key to maximising effective and transparent communication with the stakeholders (Sinclair et al. 2010).

Future directions

The need for centralised databases

Back in *Chapter 2* of this thesis, I suggested that a database of insect translocations would represent a valuable resource for informing future translocation programmes. This point remains pertinent, though I would like to expand on it by highlighting the potential opportunities for advances in practice and research arising from translocation databases, which are relevant to any taxonomic group. The Avian Reintroduction and Translocation Database (ARTD) (Lincoln Park Zoo 2014) represents the most comprehensive and well-known translocation database, containing information on the release events of 202 bird species to 764 recipient sites, standardised for comparability. This information has contributed to multiple peer-reviewed papers aimed at advancing knowledge and informing future management tactics in translocation, such as the recent study by Ducatez & Shine (2019), which used the ARTD to examine the effects of life history traits on survival and breeding success, finding that bird species with fast life histories have higher post-release mortality rates but are more likely to breed successfully than species with slow life histories. Additionally, Skikne et al. (2020) used predictors of past annual survival rates from programmes in the ARTD to inform the feasibility of future efforts under climate change, finding that longer distance translocations may be less feasible than shorter distance translocations in response to the changing climate. Unfortunately, the opportunities to analyse and learn from the contents of a global translocation database currently only exist for birds (though TRANSLOC [http://translocations.in2p3.fr/index.php] is currently in development for animal, plant, and fungi translocations in the Western Palearctic region). However, reviews (Dodd & Seigel 1991; Griffiths & Pavajeau 2008; Germano & Bishop 2009) and my own first-hand experience during data collection show that there are many hundreds of translocation programmes involving amphibians, reptiles and terrestrial insects, that if combined into a centralised database (or multiple databases), would allow managers to efficiently access information.

This review-based approach to management decision-making has been termed Evidence-Based Conservation (EBC) (Sutherland et al. 2004). EBC involves the collection of evidence concerning the outcomes of conservation management actions, the standardisation of such evidence, and the dissemination of this information (Gillson et al. 2019). The aim of EBC is to better predict the effects of different management actions, thereby allowing conservation problems to be addressed more effectively and efficiently. In the context of conservation translocations, guidance for standardising the documentation of methods and outcomes has been provided for vertebrate and invertebrate taxa (Sutherland et al. 2010; Daniels et al. 2018), and many programmes have published their management strategies in the open-access EBC journal Conservation Evidence (e.g. Hooson & Haw 2008; Fred & Brommer 2015; Haycock 2016). However, a large proportion of useful information on translocations of amphibians, reptiles and insects remains in unpublished internal reports, or requires costly journal subscriptions, making it difficult for managers to access and utilise as an evidence base. The creation of a freely accessible and shareable database would help to remedy this problem and facilitate more evidence-based decision making.

Representation of translocations in the tropics

The translocation programmes analysed in Chapters 2, 3 and 4 had a strong bias towards species in temperate climates. For insects, this seems to be representative of current translocation practice, at least in terms of what is reported in the peer-reviewed and grey English-speaking literature. According to the literature search conducted in *Chapter 2*, 95% of insect translocations are undertaken in temperate regions. However, many translocation programmes involving amphibians and reptiles have been undertaken in the tropics, particularly in the Caribbean and South America (e.g. Goodyear & Lazell 1994; Dickinson & Fa 2000; Antelo et al. 2010; Gibbs et al. 2014; Fitzgerald et al. 2015). In fact, the database that I created and analysed for *Chapter 3* and *Chapter 4* contained 42 conservation translocations of herpetofauna in tropical regions, but none of these were eligible for further analyses. There were two main reasons for this, the first relates to a lack of available information online; many translocations in the tropics were poorly documented in the years following release. The second relates to the size of the occurrence datasets for tropical species, which were much smaller than for species in temperate regions. As small sample sizes are known to reduce the accuracy of SDMs (Wisz et al. 2008), most species had to be excluded from the analyses because they fell below the minimum threshold of 30 records.

While species in the tropics are generally less well represented on biodiversity data platforms (Feeley & Silman 2011; Feeley 2015), they also tend to have smaller distributions than temperate species due to narrower physiological tolerance ranges and acclimation capacities (Janzen 1967; Gaston et al. 2009; McCain 2009). In tropical ectotherms, which are especially sensitive to temperature (Angilletta 2009), the climatic conditions of recipient sites will be fundamental to the outcome of a translocation. Significant climate change impacts have already been recorded in tropical ectotherms (Sánchez-Bayo & Wyckhuys 2019), despite lower rates of projected climatic warming in the tropics (IPCC 2014). For example, in the tropical forest of Luquillo in Puerto Rico, climate change was found to be the main driver of a huge reduction in arthropod abundance between 1975 and 2012 (Lister & Garcia 2018). Fortunately for future research and translocation management planning, the field of spatial modelling is constantly advancing, and SDM techniques tailored to species with small range sizes, such as those in the tropics, have become available in recent years. For example, Breiner et al. (2015) developed a technique called an 'ensemble of small models', which overcomes the limitations of modelling species with small occurrence datasets (e.g. reduces overfitting) by averaging bivariate models to an ensemble. This method was successfully used to assess the habitat requirements of two rare flying fox species in the Comoros archipelago (Ibouroi et al. 2018). This method, coupled with the rapidly expanding coverage of biogeographic data, should facilitate both further comparative analyses such as those conducted for Chapters 3 and 4, as well as the increased use of SDMs to inform translocation decision making for tropical species.

Conclusion

This thesis illustrates the importance of macroclimate as a determinant of conservation translocation success for amphibian, reptile, and terrestrial insect species. Using multiple lines of evidence, the research identifies a positive association between the success of translocation programmes and the climatic suitability of recipient sites, predictable using global species distribution models (SDMs). This association indicates that generally, past translocation attempts failed to adopt a strategy as effective as SDMs for the selection of climatically suitable recipient sites, which likely contributed to higher rates of programme failure. While greater integration of climate into management plans can help to improve translocation outcomes, the findings of *Chapter 4* suggest that models of current suitability will be insufficient to gauge the viability of populations under future climate change. Consequently, translocation managers will need to be more forward-looking in their approach to recipient site selection, by proactively choosing sites that are forecast to retain their suitability under climate change. The research presented in *Chapter 5* demonstrates, as a proof of concept, how translocation programmes can adopt species distribution modelling techniques to incorporate climate change into management decision-making.

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Appendices

Appendix 2.1: List of terms used to search for articles relevant to terrestrial insect translocation.

Web of Science search method

We performed a literature search on the Web of Science on 26/07/2018. Literature published between 1970 (earliest possible date) and July 2018 was searched for using the following advanced search criteria:

TS=((translocat* OR conservation translocat* OR reintro* OR re-intro* OR reinforce* OR re-inforce* OR reenforce* OR re-enforce* OR assisted migration OR assisted colonization OR assisted colonisation OR conservation introduction OR managed relocation OR ecological replacement OR augment* OR restor* OR restock* OR re-stock*) AND (insect OR insecta))

Web of Science search method (additional search)

In order to ensure our original search terms were not too restrictive, we performed an additional search on 11/12/2018 that included the list of insect Orders identified in Wheeler *et al.* (2001), with the addition of termitidae based on more recent molecular phylogenetic analyses (Inward *et al.* 2007). Literature published between 1970 and December 2018 was searched for using the following advanced search criteria:

TS=((reintro* OR re-intro* OR translocat* OR conservation translocat* OR reinforce* OR re-inforce* OR reenforce* OR re-enforce* OR assisted migration OR assisted colonization OR assisted colonisation OR conservation introduction OR managed relocation OR ecological replacement OR augment* OR restor* OR restock* OR re-stock*) AND (insect OR insecta OR blattodea OR coleoptera OR collembola OR dermaptera OR diplura OR diptera OR embiidina OR ephemeroptera OR grylloblattodea OR hemiptera OR hymenoptera OR isoptera OR termitidae OR lepidoptera OR mantodea OR mantophasmatodea OR mecoptera OR microcoryphia OR neuroptera OR odonata OR orthoptera OR phasmatodea OR phthiraptera OR plecoptera OR protura OR psocoptera OR siphonaptera OR strepsiptera OR thysanoptera OR thysanura OR trichoptera OR zoraptera))

Using this set of search terms, we retrieved an additional 418 articles (24,582 total) compared to a search performed on the same day using the original set of search terms, however, none of the additional articles were relevant to terrestrial insect translocation.

Directory of Open Access Journals search method

We performed a literature search on the Directory of Open Access Journals on 07/10/2018. Literature published at the earliest possible date (1875) until October 2018 was searched for using the same set of search terms applied in the Web of Science search.

Conservation Evidence search method

We performed a literature search on the Conservation Evidence Individual Studies repository on 08/10/2018. Literature published at the earliest possible date (1912) until October 2018 was searched for using the following individual search terms ‘translocation’, ‘translocate’, ‘reintroduction’, ‘reintroduce’, ‘re-introduction’, ‘re-introduce’, ‘introduction’, ‘introduce’, ‘assisted colonisation’, ‘assisted colonization’, ‘assisted migration’, ‘managed relocation’, ‘ecological replacement’, ‘reinforcement’, ‘reinforce’, ‘re-inforcement’, ‘re-inforce’, ‘reenforcement’, ‘reenforce’, ‘re-enforcement’, ‘re-enforce’, ‘augmentation’, ‘augment’, ‘restoration’, ‘restore’, ‘restock’ and ‘re-stock’.

Appendix 2.2: List of terrestrial insect translocations from around the world

Species	Order	Continent	Country	No. of conservation translocation release sites (Outcome: S = Success F = Failure U = Uncertain)	Min. no. of years between most recent release and most recent monitoring for successful translocations	Reference(s)
Anagotus fairburnii	Coleoptera	Oceania	New Zealand	3(SSU)	8, 12	RSG Oceania, 2008; Sherley et al.,, 2010; C. Miskelly pers. comm.
Anagotus turbotti	Coleoptera	Oceania	New Zealand	1(F)	4	Sherley et al., 2010 N. Miller pers. comm.
Cerambyx cerdo	Coleoptera	Europe	Czech Republic	1(S)	24	Drag & Cizek, 2014; L. Drag pers. comm.
Ceruchus chrysomelinus	Coleoptera	Europe	Sweden	1(S)	17	Karlsson et al., 2013; M. Jonsell pers. comm.
Cicindela dorsalis	Coleoptera	North America	USA	2(FF)	-	Knisley et al., 2005; B. Knisley pers. comm.
Cicindela formosa generosa	Coleoptera	North America	USA	1(F)	-	Brust, 2002; Brust pers. comm.
Cryptocephalus decemmaculatus	Coleoptera	Europe	United Kingdom	-	-	Piper PhD Thesis, 2002
Hadramphus stilbocarpae	Coleoptera	Oceania	New Zealand	1(U)	-	Sherley et al., 2010
Lyperobius huttoni	Coleoptera	Oceania	New Zealand	1(S)	9	Sherley et al., 2010; C. Miskelly pers. comm.
Megadromus guerini	Coleoptera	Oceania	New Zealand	1(S)	13	Sherley et al., 2010; M. Bowie pers. comm.
Mimopeus opaculus	Coleoptera	Oceania	New Zealand	2(FU)	-	Sherley et al., 2010; N. Miller pers. comm.
Nicrophorus americanus	Coleoptera	North America	USA	2(SF)	10	Amaral et al., 1997; Mckenna-Foster et al., 2016; Center for Biological Diversity, 2006; L. Perotti pers. comm.

Paragymnopleurus maurus	Coleoptera	Asia	Malaysia	-	-	Qie et al., 2012
Oligoneuriella rhenana	Ephemeroptera	Europe	Germany	3(FFF)		Rupprecht ,2009
Bombus subterraneus	Hymenoptera	Europe	United Kingdom	1(U)	-	Brown et al., 2016; RSPB, 2016
Dinoponera lucida	Hymenoptera	SA	Brazil	-	-	Simon et al., 2016
Formica rufibarbis	Hymenoptera	Europe	United Kingdom	1(F)	-	Gammans, 2008; S. Dodd pers. comm.
Megachile parietina	Hymenoptera	Europe	Germany	1(S)	17	Westrich, 2007; P. Westrich pers. comm.
Messor barbarus	Hymenoptera	Europe	France	-	-	Bulot et al., 2014
Aphantopus hyperantus	Lepidoptera	Europe	Sweden	-	-	Söderström & Hedblom, 2007
Capricornia boisduvaliana	Lepidoptera	Europe	Finland	1(F)	-	Välimäki & Itämies, 2002; P. Välimäki pers. comm.
Carterocephalus palaemon	Lepidoptera	Europe	United Kingdom	1(F)	-	Warren, 1995
Coenonympha arcania	Lepidoptera	Europe	Sweden	-	-	Söderström & Hedblom, 2007
Cyclargus thomasi bethunebakeri	Lepidoptera	North America	USA	1(F)	-	Daniels, 2009
Eumaeus atala	Lepidoptera	North America	USA	1(S)	8	Smith et al., 2002
Euphydryas aurinia	Lepidoptera	Europe	United Kingdom	4(SSSS)	2, 2, 2, 2	Porter & Ellis, 2010
Euphydryas editha quino	Lepidoptera	North America	USA	-	-	Pratt & Emmel, 2010
Eustroma reticulatum	Lepidoptera	Europe	United Kingdom	2(SS)	10, 7	Hooson & Haw, 2008; J. Hooson pers. comm.
Glaucopsyche lygdamus paloverdesensis	Lepidoptera	North America	USA	1(U)	-	Mattoni & Powers, 2000
Gortyna borelii lunata	Lepidoptera	Europe	United Kingdom	1(S)	3	Ringwood et al., 2004
Lycaena dispar batava	Lepidoptera	Europe	United Kingdom	-	-	Nicholls & Pullin, 2000
Lycia zonaria britannica	Lepidoptera	Europe	United Kingdom	1(F)	-	Howe et al., 2004; M. Howe pers. comm.
Maculinea arion	Lepidoptera	Europe	United Kingdom	4(SSSF)	16, 19, 24	Thomas et al., 2009; Andersen et al., 2014
Maculinea nausithous	Lepidoptera	Europe	Netherlands	1(S)	10	Wynhoff, 1997; Wynhoff et al., 2008
Maculinea teleius	Lepidoptera	Europe	Netherlands	1(S)	10	Wynhoff, 1997; Wynhoff et al., 2008
Melanargia galathea	Lepidoptera	Europe	United Kingdom	-	-	Willis et al., 2009

Melitaea athalia	Lepidoptera	Europe	United Kingdom	2(SF)	11	Warren, 1991; Carter et al., 2017; C. Bulman pers. comm.
Papilio machaon	Lepidoptera	Europe	United Kingdom	1(F)	-	Dempster & Hall, 1980; Moore, 2004
Parnassius apollo	Lepidoptera	Europe	Finland & Poland	4* (SFFF)	11	Witkowski et al., 1997; Adamski & Witkowski, 1998; Adamski et al., 2007; Fred & Brommer, 2015; P. Adamski pers. comm.; J. Brommer pers. comm.
Parnassius mnemosyne	Lepidoptera	Europe	Finland	2(SF)	13	Kuussaari et al., 2015; M. Kuussaari pers. comm.
Plebejus argus	Lepidoptera	Europe	United Kingdom	1(S)	11	Harris, 2008; J. Harris pers. comm.
Plebejus melissa samuelis	Lepidoptera	North America	USA	6(FUUUUU)	-	USFWS, 2003; Pascale & Thiet, 2016; H. Holman pers. comm.
Polyommatus icarus	Lepidoptera	Europe	Sweden	-	-	Söderström & Hedblom, 2007
Polyommatus semiargus	Lepidoptera	Europe	Sweden	-	-	Söderström & Hedblom, 2007
Proclossiana eunomia	Lepidoptera	Europe	France	2(SS)	24, 21	Neve et al., 1996; Barascud & Baguette, 2001
Scolitantides vicrama	Lepidoptera	Europe	Finland	1(F)	-	Marttila et al., 1997; Saarinen pers. comm.
Speyeria idalia	Lepidoptera	North America	USA	1(S)	17	Shepherd & Debinski, 2005; S. Shepherd pers. comm.
Thymelicus sylvestris	Lepidoptera	Europe	United Kingdom	-	-	Willis et al., 2009
Trapezites symmomus	Lepidoptera	Oceania	Australia	1(S)	23	Braby, 2012
Aeshna viridis	Odonata	Europe	Germany	1(U)	-	Kastner et al., 2016
Coenagrion mercuriale	Odonata	Europe	United Kingdom	1(S)	6	Thompson, 2010; Panter et al., 2016
Ischnura gemina	Odonata	North America	USA	1(F)	-	Hannon & Hafernik, 2007
Leucorrhinia dubia	Odonata	Europe	United Kingdom & Czech Republic	2(SU)	4	Clarke, 2014 (unpublished); British Dragonfly Society, 2017; Meredith, 2017; Dolny et al., 2018; C. Meredith pers. comm.; D. Clarke pers. comm.
Megalagrion xanthomelas	Odonata	North America	Hawaii (USA)	2(FU)	-	Preston et al., 2007
Urothemis edwardsii	Odonata	Africa	Algeria	2(SS)	3, 3	Khelifa et al., 2016; R. Khelifa pers. comm.

Decticus verrucivorus	Orthoptera	Europe	United Kingdom	3(SSU)	15, 19	The Species Recovery Trust, 2016; Natural England Wildlife Report, 2016; J. Curson pers. comm.
Deinacrida mahoenui	Orthoptera	Oceania	New Zealand	7(SSSFFFF)	7, 13, 15	Watts et al., 2008; Watts & Thornburrow, 2009; C. Watts pers. comm.
Deinacrida rugosa	Orthoptera	Oceania	New Zealand	7(SSSUUUU)	15, 19, 3	Watts et al., 2008; 2012; 2017; Sherley et al., 2010; White et al., 2017; C. Watts pers. comm.
Euthystira brachyptera	Orthoptera	Europe	Switzerland	-	-	Knop et al., 2007
Gryllus campestris	Orthoptera	Europe	Germany	1(S)	17	Hochkirch et al., 2006; M. Schmedes pers. comm.
Hemideina crassidens	Orthoptera	Oceania	New Zealand	1(S)	9	Watts et al., 2008a; C. Watts pers. comm.
Hemideina ricta	Orthoptera	Oceania	New Zealand	1(S)	12	Watts et al., 2008a; M. Bowie pers. comm.
Hemideina thoracica	Orthoptera	Oceania	New Zealand	2(SS)	8, 10	Watts et al., 2008; Sherley et al., 2010; C. Watts pers. comm.; G. Brackenbury pers. comm.
Mecostethus parapleurus	Orthoptera	Europe	Switzerland	-	-	Knop et al., 2007
Metrioptera roeseli	Orthoptera	Europe	Sweden	-	-	Berggren 2001; Berggren et al., 2001; Berggren et al., 2005
Motuweta isolata	Orthoptera	Oceania	New Zealand	6(SSSSSS)	4, 4, 5, 5, 8, 10	Watts et al., 2008; Sherley et al., 2010; Stringer et al., 2014
Myrmeleotettix maculatus	Orthoptera	Europe	United Kingdom	1(S)	7	Gardiner, 2010; T. Gardiner pers. comm.
Oedipoda caerulescens	Orthoptera	Europe	Switzerland	2(SS)	21, 21	Baur et al., 2017
Oedipoda germanica	Orthoptera	Europe	Germany	1(F)	-	Wagner et al., 2005
Tetrix subulata	Orthoptera	Europe	Sweden	-	-	Forsman et al., 2012
Isoperla goertzi	Plecoptera	Europe	Germany	1(F)	-	Rupprecht, 2009
Isoperla grammatica	Plecoptera	Europe	Germany	1(F)	-	Rupprecht, 2009
Isoperla oxylepis	Plecoptera	Europe	Germany	1(F)	-	Rupprecht, 2009
Perla marginata	Plecoptera	Europe	Germany	1(S)	10	Rupprecht, 2009

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* *Parnassius apollo* was released on 25 Finnish islands contained within 3 Island archipelago zones referred to in Fred & Brommer (2015) as the ‘Inner archipelago zone’, the ‘Middle archipelago zone’ and the ‘Outer archipelago zone’. We made the decision to define these releases as three conservation translocations rather than 25 for two reasons: i) the islands within each archipelago zone were within very close proximity to each other and this species can disperse well, ii) treating these as 3 translocations rather than 25 avoided introducing bias towards one species that would have resulted in ca.40% of the insect translocation failure data being represented by a single species with very similar predictor variable values.

Appendix 3.1: Inclusion criteria and predictor variable data extraction

Inclusion criteria

Of the translocation projects found in the literature search, only those that were motivated by conservation were included. This decision was made because conservation translocations principally aim to establish a viable population (IUCN 2013), which is in line with the definition of success adopted for our study. In contrast, translocations motivated by other factors such as mitigation, research or biological control, often have different core objectives. For example, Brown, Bishop and Brooks (2009) describes the effects of short-distance translocation on the spatial ecology, body condition and behaviour of Western Rattlesnakes *Crotalus oreganus*; this research-driven translocation was excluded because its objective was not population establishment. For translocation projects where we could not obtain all the required information by examining relevant articles, we contacted authors directly to acquire missing information. If the authors were unresponsive, the project was excluded from our analysis.

For failed translocations, the potential causes of failure, as perceived by authors, were documented. Multiple factors can decouple the population dynamics of translocated populations from predicted climate suitability (e.g. predation or competition), potentially leading to erroneous inferences regarding the causes of translocation failure. In order to reduce the effects of false positive detection (i.e. translocation technique and climate both suitable but population was extirpated) on our statistical analyses, we excluded translocation projects where the perceived causes of failure were not directly related to one of our predictor variables. For example, two translocated Sand Lizard *Lacerta agilis* populations in the U.K. looked to be performing well until outbreaks of fire wiped out both populations (M. Wilkie pers. comm.); in these cases, the detection of a climate signal (or any of our other four variables) would have been obscured by this abnormal cause of population extirpation.

Assessing eligibility for inclusion in our statistical analyses involved a two-step procedure that also considered how confidently authors described the potential causes of failure (detailed below). Independence to our variable set was decided on a case-by-case basis by two of the co-authors (J. B. and S. D.), and this led to the exclusion of 22 failed translocation projects that would have otherwise been eligible for inclusion (Table A3.1.1). To evaluate the sensitivity of our results to this decision, we conducted the same statistical analyses (GLMM and hierarchical partitioning) but with all failures. The results are presented in Appendix S6.

Step 1: Does at least one of the perceived causes of failure directly relate to climate, number of individuals released, number of release years, life stage at release or origin? Yes/No
If 'Yes' then retain, if 'No' then go to Step 2

Step 2: Does the author appear confident regarding the cause(s) of failure? Yes/No
If 'Yes' then omit, if 'No' then retain

Table A3.1.1. Failed conservation translocation projects excluded from statistical analyses based on independence to predictor variables. The superscript after the species name denotes the number of sites that were excluded for the same rationale.

Species	Class	Reference(s)	Rationale for exclusion
Ambystoma maculatum	Amphibia	Cook (in prep)	High predation pressure and insufficient wintering habitat caused extirpation of the translocated population.
Epidalea calamita^{2}	Amphibia	R. Rannap pers. comm.	Absence of wintering habitat within dispersal capability of species caused extirpation of the translocated population.
Lithobates pipiens	Amphibia	Johnston (2013)	High predation pressure, which the authors note is also likely to have caused the absence of other locally common amphibian species, caused extirpation of the translocated population.

Litoria aurea	Amphibia	Daly et al. (2008); G. Daly pers. comm.	Chytrid fungus outbreak caused extirpation of the translocated population.
Litoria aurea	Amphibia	White and Pyke (2008)	No suitable microhabitat available to meet the species wintering niche requirements caused extirpation of the translocated population.
Litoria aurea	Amphibia	White and Pyke (2008)	Cessation of habitat management caused extirpation of the translocated population.
Pelobates fuscus[2]	Amphibia	Scali et al. (2002); S. Scali pers. comm.; F. Bernini pers. comm.	Alien species invasion caused extirpation of the translocation population.
Pseudacris crucifer	Amphibia	Cook (in prep)	Intolerable salinity levels caused by damaging coastal storms caused the local extirpation of the translocated population.
Rana muscosa[4]	Amphibia	Fellers et al. (2007)	Chytrid fungus outbreak caused extirpation of the translocated population.
Carterocephalus palaemon	Insecta	Warren (1995); Moore (2004)	Breeding habitat of insufficient quality due to lack of management caused the local extirpation of the translocated population.
Gryllus campestris[2]	Insecta	Edwards (1999; 2007); R. Edwards pers. comm.	Cessation of habitat management caused extirpation of the translocated population.

Gryllus campestris	Insecta	Edwards (2000)	Quality and extent of suitable microhabitat caused extirpation of the translocated population.
Heterodon platirhinos[2]	Reptilia	Cook (in prep)	Extirpation of the translocated population coincided with extirpation of prey species.
Lacerta agilis[2]	Reptilia	Woodfine et al. (2017); M. Wilkie pers. comm. (unpublished data)	Fire outbreak caused extirpation of the translocated population.

Variable extraction and categorization

For every conservation translocation, we collected data on five predictor variables in addition to climate suitability (Table 3.1). Data on NRelYears, NumRel, LifeStageRel and Origin was extracted from each relevant article. In order to maximise the amount of data available for analyses, translocation projects that released individuals between the egg and adult stages of their lifecycle were grouped into one variable level termed ‘immatures’. There were two translocation projects, both involving amphibians, which only released eggs (Muths et al. 2001; Beebee 2002); we chose to exclude these projects from our analyses to reduce model overfitting and obscured parameter estimates. If the source individuals originated from both wild and captive-bred populations (*n* = 4), we treated the source population as ‘captive-bred’. Translocations that used headstarted individuals or a combination of wild and headstarted were also grouped with ‘captive-bred’ (*n* = 7), as at least part of their lifecycle had been spent under captive conditions (see Table A3.4.1 for data summary). For the Position predictor variable, we applied a simple metric to categorize the release site as ‘core’ or ‘edge’ with respect to the species global range. Each species range was delimited using minimum convex polygons in ArcMap v.10.5, generated with the corresponding quality-checked species occurrence dataset. Sites were categorized as ‘core’ if they were positioned inside the inner 80% of the minimum convex polygon, while sites outside of the inner 80% were categorized as 'edge'. In order to avoid variable categories with small sample sizes and to maximize the number of translocations eligible for statistical analyses, we categorized assisted colonization attempts (i.e. outside of indigenous range) as range 'edge'. In cases where we could not obtain all the required information by examining relevant articles, we contacted authors directly to acquire missing information.

Appendix 3.2: Species and climate data

Species occurrence data

We downloaded species occurrence data from the Global Biodiversity Information Facility (GBIF.org 2019; accessed May 2019). For all species, we considered their whole global range in order to model the full extent of their climatic niche (Barbet-Massin et al. 2012a; Raes 2012). There are a number of limitations to using occurrence records from big data repositories in species distribution modelling (Beck et al. 2014), therefore we carefully cleaned the GBIF data and selected locality records as reliably as possible, including only occurrences reported to at least two digits (precision of ca. 1 km), deleting non-native occurrences, duplicated records and records explicitly collected prior to 1950. As GBIF occurrence data were very limited for endemic New Zealand species, we supplemented the GBIF data with records from the New Zealand Department of Conservation. SDMs were not run for species with less than 30 occurrences in their final cleaned datasets because accuracy metrics have been shown to decline severely beyond this point (15 species were omitted based on this threshold; see Table A.3.2.1 for number of occurrences in each SDM) (Wisz et al. 2008).

In order to reduce spatial bias caused by unequal sampling (Boria et al. 2014; Radosavljevic & Anderson 2014), we thinned the occurrence data for each species at a 20 km resolution using the Spatial Rarefy Tool in the SDM ToolBox v2.2 (Brown 2014) in ArcMap v.10.5. This approach has been shown to improve species distribution model (SDM) predictions by reducing sampling bias, spatial autocorrelation and overfitting (Boria et al. 2014; Galante et al. 2018). We did not use the translocation site locations to build SDMs and any occurrence points that overlapped with translocation sites were removed. In order to maximise our sample size, cleaned species occurrence datasets were not thinned if this procedure caused the number of unique records to fall below 30.

Climate data

Climate data averaged for the period 1960-2010 was downloaded from the WorldClim Database (Version 2) at a 30 arc-second resolution (Fick & Hijmans 2017). As increasing the number of predictor variables increases the risk of model overfitting (Collevatti et al. 2013), we selected *a priori* eight standard bioclimate predictors known/presumed to be important in structuring the distributions of ectotherms (Wiens et al. 2006; Kozak & Wiens 2007; Clusella-Trullas et al. 2011) and commonly used in SDMs, describing annual averages (Bio1 and Bio12), seasonality (Bio4 and Bio15) and highest/lowest monthly values of temperature (Bio5 and Bio6) and precipitation (Bio13 and Bio14) (Williams et al. 2003; Barbet-Massin et al. 2012b; Bucklin et al. 2015 used similar predictors).

The geographical background extent in which pseudo-absences are selected and models are developed, tested and compared influences model predictions (VanDerWal et al. 2009; Lobo et al. 2010). Pseudo-absences selected from too small an area can produce spurious models while pseudo-absences selected from too large of an area can lead to artificially inflated evaluation metric values and predictions of suitable area (VanDerWal et al. 2009). Therefore, we delimited the background area for each SDM based on the ecoregions a species is/has been known to occur in (Barve et al. 2012). Ecoregions are smaller biogeographical units than biomes, are more climatically homogeneous, lack major geographical barriers to species movement and are comprised of similar vegetation communities (Olson et al. 2001). We clipped the climate data based on the ecoregions that overlapped with each species cleaned occurrence dataset. In order to preserve climate cells situated at the edge of ecoregions (especially coastal), we created a 1 km buffer around the ecoregion shapefile and used this to clip the climate data.

We used the Variance Inflation Factor (VIF) as a measure of the degree of multicollinearity between predictor variables for each species background extent. Multicollinearity describes the situation where two or more predictor variables in a statistical model are linearly related. Including collinear variables in a statistical model causes variable effects to be inseparable and extrapolation to be potentially erroneous. Therefore, variables that presented a VIF of >10 (Quinn & Keough 2002) were eliminated from the set of variables used to run each SDM in R with the package *usdm* (v. 1.1-18) (Naimi 2015).

Table A3.2.1. List of the species included in the species distribution model-based analyses. The number of occurrences after spatial thinning (*n*) and the climate variables used to construct each species distribution model are also presented.

Species	***n***	**bio1**	**bio4**	**bio5**	**bio6**	**bio12**	**bio13**	**bio14**	**bio15**
Ambystoma maculatum	654		✓	✓			✓		✓
Anaxyrus boreas	327		✓	✓			✓	✓	✓
Anaxyrus fowleri	612		✓	✓			✓		✓
Boloria eunomia	595		✓	✓			✓	✓	✓
Bolria euphrosyne	1286		✓	✓			✓	✓	
Cerambyx cerdo	137		✓	✓			✓	✓	✓
Ceruchus chrysomelinus	41		✓	✓			✓		✓
Cicindela dorsalis	41			✓	✓	✓	✓	✓	
Coluber constrictor	1497		✓	✓			✓	✓	✓
Crotaphytus collaris	681		✓	✓			✓	✓	✓
Decticus verrucivorus	645		✓	✓			✓		✓
Emys orbicularis	379			✓	✓		✓	✓	✓
Eustroma reticulatum	235		✓	✓			✓		✓
Gryllus campestris	687			✓	✓		✓	✓	✓
Heterodon platirhinos	610		✓	✓			✓	✓	✓
Hoplodactylus duvaucelii	63		✓	✓				✓	✓
Hyla arborea	1302			✓	✓		✓	✓	✓
Hyla versicolor	824		✓	✓			✓		✓
Lacerta agilis	797			✓	✓		✓		✓
Lampropeltis triangulum	822		✓	✓			✓	✓	✓
Lithobates clamitans	1691		✓	✓			✓		✓
Lithobates pipiens	1317		✓	✓			✓	✓	✓

Lithobates sylvaticus	1639		✓	✓			✓	✓	✓
Lycia zonaria	52	✓	✓				✓		✓
Melitaea athalia	1247		✓	✓			✓		✓
Nerodia sipedon	1001		✓	✓			✓		✓
Notophthalmus viridescens	1073		✓	✓			✓		✓
Oedipoda caerulescens	674			✓	✓		✓	✓	✓
Oedipoda germanica	188		✓	✓			✓		✓
Oligoneuriella rhenana	50			✓	✓		✓		✓
Oligosoma lineoocellatum	136		✓	✓				✓	✓
Opheodrys vernalis	253		✓	✓			✓	✓	✓
Papilio machaon	2653		✓	✓			✓	✓	✓
Parnassius apollo	337		✓	✓			✓	✓	✓
Parnassius mnemosyne	260		✓	✓			✓	✓	✓
Pelobates fuscus	859	✓	✓				✓		✓
Pelobates syriacus	54			✓	✓		✓	✓	✓
Perla marginata	125		✓	✓			✓	✓	✓
Phengaris nausithous	180		✓	✓			✓	✓	✓
Phengaris teleius	154		✓	✓			✓	✓	✓
Plebejus argus	1324		✓	✓			✓	✓	✓
Plethodon cinereus	1024		✓	✓			✓		✓
Psammodromus algirus	616			✓	✓		✓	✓	✓
Pseudacris crucifer	1254		✓	✓			✓	✓	✓
Pseudophilotes vicrama	93		✓	✓			✓	✓	✓
Psophus stridulus	255		✓	✓			✓	✓	✓
Sistrurus catenatus	235		✓	✓			✓	✓	✓
Storeria dekayi	973		✓	✓			✓	✓	✓
Terrapene carolina	561		✓	✓			✓	✓	
Trapezites symmomus	58		✓	✓		✓		✓	✓

Appendix 3.3: Modelling and climate suitability extraction approach

Species distribution models

We used an ensemble of species distribution model algorithms in order to minimise the uncertainty associated with single modelling techniques (Buisson et al. 2010). We used Random Forests (RF), Generalised Boosted Models (GBM) and MaxEnt, which have each been shown to perform well when modelling species distributions (Elith et al. 2006; Elith & Graham 2009). The default settings in the *biomod2* package (v. 3.3-7) (Thuiller et al. 2016) in R were applied to each algorithm.

For each species, we replicated five runs with 70% of occurrences randomly selected for model training and cross-validation, and the remaining 30% set aside for model testing and independent validation. We evaluated model performance using the receiver operating characteristic to determine an area under the curve (AUC). Models are considered to have reliable prediction performances with AUC values >0.70 (Swets 1998). Therefore, our ensemble models retained only models with AUC scores of >0.70 and the contribution of each of the selected models to the final ensemble was proportional to its goodness-of-fit statistic. This procedure minimizes uncertainties since weak models receive less weight in the final ensemble. For one species (*Cicindela formosa*), none of the model runs reached the selected AUC threshold of 0.7, therefore this species was not considered for further analysis.

Based on recommendations made in (Barbet-Massin et al. 2012a), we sampled pseudo-absence records at random from the background extent for each species, weighted to reach an equal prevalence with presence records. After spatial thinning, the number of presences for our species ranged from 41 to 2,653. The optimum number of absences varies depending on the selected model algorithm, with MaxEnt performing best when a larger number of absences (background points) are selected (e.g. 10,000; Phillips & Dudík 2008), and GBM and RF performing best when the number of absence records is similar to the number of presence records (Barbet-Massin et al. 2012a). As we adopted an ensemble modelling approach consisting of different algorithm families which differ in the number of absences required to achieve optimum performance, we followed the approach of (Bellard et al. 2016), where models with <1,000 occurrence records were fitted with 1,000 pseudo-absences and models with $\geq$1,000 occurrence records were fitted with 10,000 pseudo-absences.

Climate suitability extraction

Our approach to extracting and calculating climate suitability for each translocation release site was dependent on the availability of post-release distributional monitoring data and the comprehensiveness of the release site details provided by authors. Ideally, we aimed to calculate climate suitability values based on the area used by the translocated population, but this was only achievable with up-to-date distribution monitoring data (see Scenario 1 of Table A3.3.1). In the absence of this, we calculated climate suitability using two approaches that were dependent on whether or not a precise release location could be identified for the translocation. If it could, then we extracted the climate suitability value from the grid cell(s) on which the precise release location was situated within (see Scenario 2 of Table A3.3.1). If a precise release location could not be determined, then the climate suitability calculation was based on the mean average across the grid cell(s) overlapping with the reserve (see Scenario 3 of Table A3.3.1).

Table A3.3.1. Alternative approaches for defining release site and subsequent selection method for climate suitability extraction.

Scenario	Selection method for extraction	Sample size
1	Distribution data on the translocated population for the period of most recent monitoring was available. Climate suitability was calculated based on the cell(s) that overlapped with the distribution of the translocated population.	*n* = 44
2	Either the coordinates of the release site were available (must have had a minimum coordinate precision of one digit), location of release site was given on a map, or the release location was described with precision and with reference to an identifiable physical feature (e.g. lake). In	*n* = 45

	the latter case, satellite imagery in ArcMap v.10.5 was used to pinpoint the geographic feature. Climate suitability was calculated based on the cell(s) corresponding to the release site locality.	
3	Only the name of the release reserve was provided. Climate suitability was calculated based on an average of the cell(s) contained within the boundary of the reserve. For one translocation project involving *Leipelma archeyi* (Haigh et al. 2011; A. Quinnell pers. comm.), we had to omit the sample from further analysis because the release reserve was very large and the sensitivity of the species meant we were unable to obtain a more precise location.	*n* = 13

Appendix 3.4: Data summary

Table A3.4.1. Summary of sample sizes and mean (min – max) for variables included in statistical analyses. Variable abbreviations are in Table 3.1.

Variable	Type	Level or mean (min – max)	Success	Failure
Origin	Categorical	Captive-bred	*n* = 18	*n* = 18
		Wild-caught	*n* = 43	*n* = 23
LifeStageRel	Categorical	Adult	*n* = 15	*n* = 9
		Immature	*n* = 19	*n* = 24
		Mixed	*n* = 27	*n* = 8
Position	Categorical	Core	*n* = 34	*n* = 20
		Edge	*n* = 27	*n* = 21
ClimSuit	Continuous	Mean (min – max)	0.572 (0.123 – 0.946)	0.362 (0.012 – 0.924)
NRelYears	Continuous	Mean (min – max)	2.9 (1 – 12)	2.0 (1 – 6)
NumRel	Continuous	Mean (min – max)	844 (4 – 10009)	2329 (9 – 53240)

Appendix 3.5: Results with all failures included

Table A3.5.1. Generalized Linear Mixed Model results used to assess the effect of each parameter on translocation outcome with all failures included for amphibians, reptiles and terrestrial insects. Variable abbreviations are in Table 3.1.

Parameter	**β**	**β SE**
(Intercept)	0.564	0.752
ClimSuit	0.985**	0.308
NRelYears	0.506*	0.294
NumRel	-0.665	0.557
LifeStageRel (Immature)[a]	-1.066	0.673
LifeStageRel (Mixed)[b]	-0.540	0.734
Origin (Captive)[c]	-1.040*	0.564
Position (Edge)[d]	0.948*	0.530

[a] Estimates for LifeStageRel = Immature versus Adult

[b] Estimates for LifeStageRel = Mixed versus Adult

[c] Estimates for Origin = Captive-bred versus Wild-caught

[d] Estimates for Position = Edge versus Core

* Significance at 0.1 level

** Significance at 0.01 level

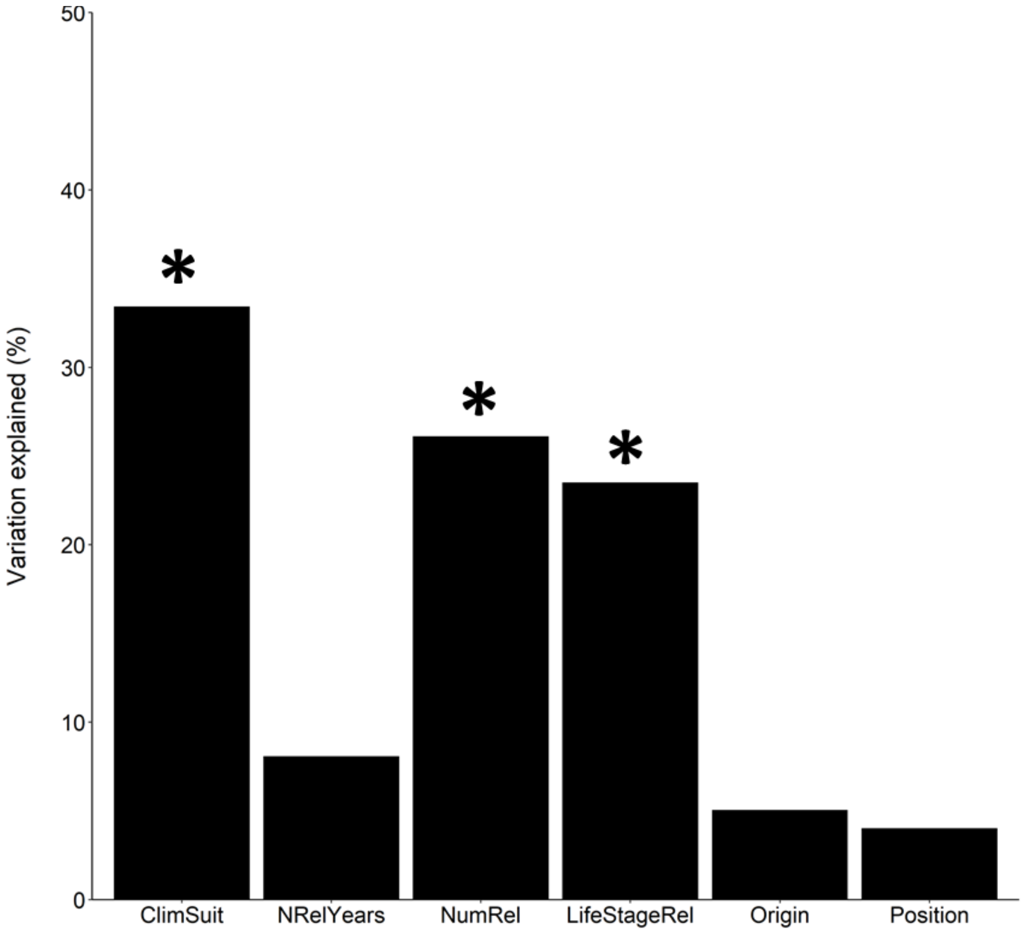


Figure A3.5.1. The percentage independent contribution of each explanatory variable derived by hierarchical partitioning to translocation outcome when all failures are included for amphibians, reptiles and terrestrial insects. Explanatory variables with significant ($P < 0.05$) independent contributions to translocation outcome are denoted with an asterisk.

Appendix 4.1: Search of translocation literature

We conducted an indicative assessment of the academic and grey literature to establish the proportion of conservation translocation programmes that factor climate change into the recipient site selection process. To do this, we examined 338 translocation reports from the IUCN SSC Conservation Translocation Specialist Group database published between 2008 and 2018 (Soorae 2008, 2010, 2011, 2013, 2016, 2018), as well as a mixture of academic papers and practitioner reports from 31 translocations found in Bellis et al. 2020. If reports/papers documented the translocation of multiple species to the same (or adjacent) sites, we considered this as a single record. We examined all instances of “climat”, “chang” and “warm” to determine whether the authors had considered potential future climate change (also considering global change and global warming) impacts when selecting their recipient site.

Appendix 4.2: Species data preparation and model evaluation summary

Table A4.2.1. Species data preparation and model evaluation summary. The listed sources of occurrence data are in addition to records from the global biodiversity information facility (GBIF). Where available, we used polygons from the IUCN and Global Assessment of Reptile Distributions (GARD) database to delimit ranges and select pseudo-absences. If unavailable, α-hulls were created from the cleaned occurrence data. The number of occurrences represents the number of records used to run the SDMs (i.e. post-cleaning and thinning).

		Species data preparation				**Model evaluation**	
Species	Additional sources of occurrence data	Reference(s) consulted for range delimitation	Polygon source	No. occurrences	AUC	TSS	CBI
Anaxyrus fowleri	-	IUCN distribution map	IUCN	796	0.864	0.569	0.994
Boloria eunomia	Neve et al. (1996); Turlure et al. (2011)	Nève et al. (2008); Maresova et al. (2019)	α-hull	817	0.920	0.648	0.987
Boloria euphrosyne	-	Haahtela et al. (2019)	α-hull	1742	0.902	0.640	0.997
Cerambyx cerdo	-	IUCN Red List profile (countries listed)	α-hull	161	0.896	0.645	0.973
Ceruchus chrysomelinus	Kašák et al. (2019)	IUCN distribution map	IUCN	57	0.969	0.842	0.939
Coluber constrictor	-	Roll et al. (2017)	GARD	1949	0.911	0.633	0.996
Crotaphytus collaris	A. Templeton pers. comm.	Roll et al. (2017)	GARD	663	0.932	0.700	0.998
Decticus verrucivorus	J. Curson pers. Comm.	IUCN Red List profile (countries listed)	α-hull	788	0.904	0.629	0.996
Dryophytes versicolor	-	IUCN distribution map	IUCN	1146	0.852	0.511	0.994
Emys orbicularis	Fritz & Chiari (2013)	Roll et al. (2017)	GARD	235	0.941	0.725	0.896
Epidalea calamita	-	IUCN distribution map	IUCN	785	0.865	0.595	0.993
Eumaeus atala	Miller & Steinhauser (1992)	Smith et al. (1994); Minno et al. (2005)	α-hull	55	0.978	0.903	0.515
Eustroma reticulatum	J. Hooson pers. comm.	-	α-hull	318	0.907	0.641	0.990
Gryllus campestris	-	Panagiotopoulou et al. (2016); IUCN Red List profile (countries listed)	α-hull	832	0.917	0.631	0.993
Hemideina thoracica	Morgan-Richards et al. (2000)	Bulgarella et al. (2014)	α-hull	65	0.903	0.668	0.839
Heterodon platirhinos	-	Roll et al. (2017)	GARD	783	0.855	0.546	0.992
Hoplodactylus duvaucelii	BioWeb Herpetofauna (2019)	Roll et al. (2017)	GARD	38	0.928	0.731	0.887
Hyla arborea	-	IUCN distribution map	IUCN	1241	0.911	0.642	0.993

Lacerta agilis	-	Roll et al. (2017)	GARD	1024	0.929	0.697	0.998
Lampropeltis triangulum	-	Roll et al. (2017)	GARD	921	0.890	0.600	0.999
Lithobates pipiens	-	IUCN distribution map	IUCN	1400	0.888	0.588	0.999
Notophthalmus viridescens	-	IUCN distribution map	IUCN	1337	0.810	0.480	0.994
Oedipoda caerulescens	-	IUCN Red List profile (countries listed)	α-hull	827	0.909	0.649	0.991
Oligosoma lineoocellatum	BioWeb Herpetofauna (2019)	Roll et al. (2017)	GARD	48	0.906	0.666	0.896
Opheodrys vernalis	-	Roll et al. (2017)	GARD	348	0.912	0.660	0.960
Parnassius apollo	-	Collins & Morris (1985); Haahtela et al. (2019)	α-hull	385	0.919	0.657	0.993
Parnassius mnemosyne	Välimäki & Itämies (2003); Kuussaari et al. (2015)	IUCN Red List profile (countries listed)	α-hull	407	0.947	0.742	0.991
Pelobates syriacus	Tarkhnishvili (1996); Mazanaeva & Askenderov (2007); Székely et al. (2010)	IUCN distribution map	IUCN	53	0.963	0.844	0.979
Perla marginata	Fenoglio et al. (2008)	-	α-hull	145	0.927	0.682	0.937
Phengaris arion	-	Haahtela et al. (2019); IUCN Red List profile (countries listed)	α-hull	529	0.925	0.706	0.997
Phengaris nausithous	Wynhoff 1998; Jubete & Román (2016)	Wynhoff (1998); Ritter et al. (2013)	α-hull	286	0.939	0.709	0.953
Phengaris teleius	Witek et al. (2010)	Wynhoff (1998); Ritter et al. (2013)	α-hull	282	0.940	0.733	0.990
Plebejus argus	-	Haahtela et al. (2019); IUCN Red List profile (countries listed)	α-hull	1922	0.962	0.794	0.946
Plethodon cinereus	-	IUCN distribution map	IUCN	1143	0.871	0.546	0.998
Psammodromus algirus	-	Roll et al. (2017)	GARD	311	0.908	0.657	0.993
Pseudacris crucifer	-	IUCN distribution map	IUCN	1581	0.853	0.514	0.996
Storeria dekayi	-	Roll et al. (2017)	GARD	1297	0.868	0.571	0.991
Terrapene carolina	-	Roll et al. (2017)	GARD	570	0.908	0.658	0.974
Trapezites symmomus	-	-	α-hull	107	0.977	0.876	0.869

Appendix 4.3: ODMAP protocol

ODMAP element	Contents
OVERVIEW	
Authorship	• **Authors:** Joe Bellis, David Bourke, Joyce Maschinski and Sarah Dalrymple • **Contact email:** joebellis7@gmail.com • **Title:** Climate change threatens the viability of populations at sites of successful translocation
Model objective	• **Objective:** Transfer • **Target outputs:** Change in predicted suitability from current conditions to three separate time horizons.
Taxon	Amphibians, reptiles and terrestrial insects
Location	Global
Scale of analysis	• **Spatial extent (Lon/Lat):** Global (90, -180, 180, -60; ymax, xmin, xmax, ymin) • **Spatial resolution:** 2.5 arc-minutes • **Temporal extent/time period**: 1960-2010, 2021-2040, 2041-2060, 2061-2080 • **Type of extent boundary**: N/A
Biodiversity data overview	• **Observation type:** Citizen science, peer-reviewed papers, NZ Department of Conservation • **Response/Data type:** Presence-only
Type of predictors	Climatic
Conceptual model / Hypotheses	• **Hypotheses:** i) Projected future conditions will be worse than current conditions at most existing translocation recipient sites. ii) There will be no statistically significant difference between changes in recipient site suitability and average suitability at regional and global scales. iii) Recipient sites at higher latitudes (Northern Hemisphere) and altitudes relative to the species global average, will be predicted to fare better under climate change.
Assumptions	**We assumed that:** After data cleaning and thinning, species occurrence data are free of bias. After running a variance inflation factor analysis on the macroclimatic predictor variables, the model predictions are free from collinearity issues.
SDM algorithms	• **Algorithms**: GAM, GBM, RF, MARS and Maxent

	• **Model complexity**: Default configurations in the biomod2 package were set for each SDM algorithm. These are detailed in the Model Settings section. • **Model averaging:** Weighted mean
Model workflow	Prior to model building, we spatially thinned the species presence data and selected pseudo-absences from within an extended (2-degree buffered) version of the species expert-drawn range. We used variance inflation (VIF) analysis to avoid highly correlated variables. Ensemble models were constructed using the weighted mean based on five SDM algorithms, five test/training splits and a single pseudo-absence selection. Predictive model performance was evaluated using a 5-fold cross-validation and calibration capacity based on independent data.
Software	• **Software**: R v3.5.1 (packages: biomod2, raster, dismo, rangeBuilder, usdm, envirem, ecospat) • **Code availability**: code not shared, available on request. • **Data availability**: data not shared, some available on request.
DATA	
Biodiversity data	• **Taxon names:** *Anaxyrus fowleri, Boloria eunomia, Boloria Euphrosyne, Cerambyx cerdo, Ceruchus chrysomelinus, Coluber constrictor, Crotaphytus collaris, Decticus verrucivorus, Dryophytes versicolor, Emys orbicularis, Epidalea calamita, Eumaeus atala, Eustroma reticulatum, Gryllus campestris, Hemideina thoracica, Heterodon platirhinos, Hoplodactylus duvaucelii, Hyla arborea, Lacerta agilis, Lampropeltis Triangulum, Lithobates pipiens, Notophthalmus viridescens, Oedipoda caerulescens, Oligosoma lineoocellatum, Opheodrys vernalis, Parnassius apollo, Parnassius Mnemosyne, Pelobates syriacus, Perla marginate, Phengaris arion, Phengaris nausithous, Phengaris teleius, Plebejus argus, Plethodon cinereus, Psammodromus algirus, Pseudacris crucifer, Storeria dekayi, Terrapene Carolina and Trapezites symmomus.* • **Taxonomic reference system:** As described in relevant translocation study (data for basionyms were also checked on GBIF). • **Ecological level:** Species • **Data source**: Species occurrence data was primarily downloaded from GBIF, extracted from relevant literature (shown in Table A4.2.1), and provided by the New Zealand Department of Conservation for NZ endemic species. • **Sampling design**: Spatial thinning to 20 km. • **Sample size**: min = 38, max = 1949 (post-cleaning) • **Data cleaning/filtering**: We maximised occurrence precision by retaining only records reported to at least two digits (precision of ca. 1 km) and deleting redistributed records, duplicated records and those explicitly collected prior to 1960. We consulted expert-drawn range maps and distribution descriptions where possible to remove records outside of the indigenous range (Table A4.2.1). • **Background data**: Pseudo-absences. We extended expert-drawn range maps (e.g. IUCN and GARD), or cleaned occurrences if these were not available (using an alpha hull), using a 2 degree buffer (ca. 200km), in order to define the area from which to select PAs from. We randomly selected PAs from unoccupied cells within the newly extended polygons according to the number of presences after spatial thinning *N* (if *N* ≤ 1000 then 1000 PAs were selected, otherwise 10,000 PAs were selected). • **Absence data:** N/A

Data partitioning	• **Selection of training data:** 5-fold cross-validation with 70% set aside for training and 30% set aside for validation. • **Selection of validation data:** (see above) • **Selection of truly independent test data:** the occurrences that were removed during spatial thinning were set aside and used for model evaluation using the Continuous Boyce Index (CBI).
Predictor variables	• **Predictor variables:** - Temperate species: Mean annual temperature (BIO1), temperature seasonality (BIO4), maximum temperature of the warmest month (BIO5), minimum temperature of the coldest month (BIO6), precipitation of the wettest month (BIO13), precipitation of the driest month (BIO14), precipitation seasonality (BIO15) and growing degree days. - Tropical species: Mean annual temperature (BIO1), isothermality (BIO3), temperature seasonality (BIO4), maximum temperature of the warmest month (BIO5), minimum temperature of the coldest month (BIO6), precipitation of wettest quarter (BIO16) and precipitation of driest quarter (BIO17).
	• **Data sources:** WorldClim.org • **Spatial resolution and extant of raw data:** 2.5 arc-minutes (90, -180, 180, -60; ymax, xmin, xmax, ymin) • **Geographic projection:** +proj=longlat +datum=WGS84 +no_defs • **Temporal extent:** 1960-2010, 2021-2040, 2041-2060, 2061-2080 • **Temporal resolution**: 50 years for current and three 20 year time slices for future. • **Data processing:** N/A
MODEL	
Variable pre-selection	We selected nine bioclimatic variables known or presumed to be important in structuring the distributions of temperate ectotherms and that had been selected *a priori* in previous SDM studies on the same taxonomic groups. The selection of variables for tropical species was slightly different than for temperate species.
Multicollinearity	We removed variables that were highly inter-correlated according to the results of a variance inflation factor (VIF) test. Variables with a VIF of >10 were removed.

Model settings

```
GBM = list( distribution = 'bernoulli',
            n.trees = 2500,
            interaction.depth = 7,
            n.minobsinnode = 5,
            shrinkage = 0.001,
            bag.fraction = 0.5,
            train.fraction = 1,
            cv.folds = 3,
            keep.data = FALSE,
            verbose = FALSE,
            perf.method = 'cv')
GAM = list( algo = 'GAM_mgcv',
            type = 's_smoother',
            k = -1,
            interaction.level = 0,
```

```
          myFormula = NULL,
          family = binomial(link = 'logit'),
          method = 'GCV.Cp',
          optimizer = c('outer','newton'),
          select = FALSE,
          knots = NULL,
          paraPen = NULL,
          control = list(nthreads = 1, irls.reg = 0, epsilon = 1e-07, maxit = 200, trace =
FALSE, mgcv.tol = 1e-07, mgcv.half = 15, rank.tol = 1.49011611938477e-08
, nlm = list(ndigit=7, gradtol=1e-06, stepmax=2, steptol=1e-04, iterlim=200,
check.analyticals=0), optim = list(factr=1e+07)
, newton = list(conv.tol=1e-06, maxNstep=5, maxSstep=2, maxHalf=30, use.svd=0),
outerPIsteps = 0, idLinksBases = TRUE, scalePenalty = TRUE, efs.lspmax = 15
, efs.tol = 0.1, keepData = FALSE, scale.est = fletcher, edge.correct = FALSE) )
MARS = list( type = 'simple',
           interaction.level = 0,
           myFormula = NULL,
           nk = NULL,
           penalty = 2,
           thresh = 0.001,
           nprune = NULL,
           pmethod = 'backward')
RF = list( do.classif = TRUE,
         ntree = 500,
         mtry = 'default',
         nodesize = 5,
         maxnodes = NULL),
MAXENT.Phillips = list( path_to_maxent.jar = 'C:/Users/Joe/Documents',
            memory_allocated = 512,
            background_data_dir = 'default',
            maximumbackground = 'default',
            maximumiterations = 200,
            visible = FALSE,
            linear = TRUE,
            quadratic = TRUE,
            product = TRUE,
            threshold = TRUE,
            hinge = TRUE,
            lq2lqptthreshold = 80,
            l2lqthreshold = 10,
            hingethreshold = 15,
            beta_threshold = -1,
            beta_categorical = -1,
            beta_lqp = -1,
            beta_hinge = -1,
            betamultiplier = 1,
            defaultprevalence = 0.5)
```

Model estimates	• **Coefficients:** N/A • **Parameter uncertainty:** N/A • **Variable importance:** Calculated for all five algorithms in biomod2. Repeated procedure 10 times for each SDM

Model averaging / Ensembles	• **Model selection:** N/A • **Model averaging:** N/A • **Model ensembles:** SDM outputs were averaged according to the weighted mean. Coefficient of variation (CV) was also calculated and examined for each species' SDM.
Non-independence	• **Spatial autocorrelation:** Model residuals were not tested for spatial autocorrelation (SA) as the relatively coarse resolution (20km) of the spatial thinning was assumed to mitigate the effect of SA. • **Temporal autocorrelation:** N/A • **Nested data:** N/A
ASSESSMENT	
Performance statistics	• **Performance statistics estimated on training data:** AUC and TSS. We also evaluated the ensemble model using the CBI.
Plausibility checks	• **Response plots:** Response plots were produced and examined for every species using the response.plot2 function in biomod2.
PREDICTION	
Prediction output	To make predictions comparable across species we standardised the continuous predicted climate suitability values to range between 0 and 1 with the following formula: (x – min)/(max – min).
Uncertainty quantification	In SDMs, we accounted for algorithmic uncertainty by applying an ensemble approach averaging over five different SDM algorithms.

Appendix 4.4: Multivariate Environmental Similarity Surface (MESS) analysis outputs

Table A4.4.1. MESS outputs for each recipient site under current and future climate projections. Min_value is the minimum MESS prediction across all projections (i.e. highest extrapolation). Each column represents a climate change projection, coded according to: GCM - SSP scenario - time period (e.g. can126_30 = CanESM5, SSP126, 2021-2040).

Species	Min_value	Current	can126_30	can370_30	can126_50	can370_50	can126_70	can370_70	cnrm126_30	cnrm370_30	cnrm126_50	cnrm370_50	cnrm126_70	cnrm370_70	ipsl126_30	ipsl370_30	ipsl126_50	ipsl370_50	ipsl126_70	ipsl370_70	miroc126_30	miroc370_30	miroc126_50	miroc370_50	miroc126_70	miroc370_70	mri126_30	mri370_30	mri126_50	mri370_50	mri126_70	mri370_70
Anaxyrus fowleri	5.80	14.72	39.13	41.25	33.78	36.68	33.67	6.69	24.30	34.78	9.92	5.80	14.94	11.37	34.78	31.55	53.18	16.95	47.71	32.55	41.47	61.09	57.19	51.95	42.92	38.35	51.95	62.54	52.06	46.71	62.54	39.46
Boloria eunomia	-27.52	1.21	0.22	0.22	-0.59	-12.70	-3.19	-27.52	0.44	0.66	0.33	0.33	0.33	0.11	0.55	0.33	0.22	0.11	0.22	-14.06	0.33	0.44	0.33	0.22	0.33	-1.77	0.33	0.33	0.44	0.33	0.44	0.22
Boloria eunomia	-30.83	1.32	0.22	-1.63	-3.93	-16.07	-6.23	-30.83	0.33	0.33	0.33	0.22	0.22	-2.85	0.33	0.33	0.22	-2.17	0.11	-17.28	0.33	0.33	0.22	0.22	0.22	-4.90	0.33	0.33	0.33	0.22	0.33	-0.42
Boloria euphrosyne	0.73	6.36	3.99	3.61	2.59	1.86	2.37	0.73	8.91	7.92	9.22	8.66	9.34	4.74	7.74	8.38	6.44	3.63	4.75	1.93	8.91	8.38	8.26	6.20	8.67	4.00	8.72	7.62	8.96	8.52	10.67	7.28
Cerambyx cerdo	3.10	53.70	21.69	19.62	18.24	9.29	16.52	3.10	28.40	30.64	26.33	22.55	25.82	16.52	29.09	27.19	23.06	19.45	20.65	8.43	25.65	26.51	22.03	20.31	21.00	14.97	26.16	27.19	26.85	23.58	22.55	18.76
Ceruchus chrysomelinus	0.95	38.60	6.81	6.62	5.87	3.22	5.11	0.95	21.38	22.71	18.73	14.00	16.65	5.87	19.11	18.54	11.16	6.24	9.46	3.22	18.54	21.38	12.87	9.84	12.49	5.87	16.65	17.79	17.98	12.11	17.98	6.62
Coluber constrictor	3.26	5.29	13.83	17.14	13.09	19.99	12.15	10.75	9.73	13.73	3.33	3.26	7.60	5.74	13.78	10.29	18.06	8.02	17.22	13.66	10.80	17.56	21.68	23.65	14.14	10.80	24.74	20.77	15.48	10.80	13.84	15.47
Coluber constrictor	1.96	4.22	12.29	13.66	11.42	17.69	10.73	15.63	7.78	11.28	2.66	1.96	5.11	3.87	11.43	8.84	15.48	5.09	15.40	10.43	7.06	17.56	21.68	15.48	13.02	7.06	25.63	22.65	15.48	7.06	13.84	12.71
Crotaphytus collaris	3.61	8.91	10.23	9.63	10.11	9.63	9.15	3.61	11.68	9.75	9.15	9.75	9.15	8.91	10.84	10.84	10.36	9.15	8.67	8.07	9.63	9.15	11.44	6.26	9.63	8.91	16.50	8.19	8.07	7.59	15.41	7.59
Crotaphytus collaris	3.37	10.84	10.84	10.11	10.23	9.75	9.63	3.37	12.76	10.11	9.63	10.11	9.63	9.15	11.44	11.44	11.56	9.63	9.63	8.19	9.75	9.63	11.68	7.59	9.75	9.15	17.10	9.63	8.67	7.83	16.50	7.83
Crotaphytus collaris	4.21	9.75	10.23	9.63	10.11	9.75	9.15	4.21	11.68	9.75	9.15	9.75	9.15	8.91	10.84	10.84	10.84	9.15	9.15	8.07	9.63	9.15	11.44	7.10	9.63	8.91	16.50	8.31	7.95	7.59	15.41	7.59
Decticus verrucivorus	0.67	0.67	2.69	3.14	3.03	4.37	3.14	6.83	2.58	2.02	2.91	2.58	3.14	3.59	2.13	2.46	2.46	2.69	2.13	2.58	2.69	2.24	3.59	3.25	3.59	3.59	2.58	2.13	2.91	3.14	4.37	3.47
Decticus verrucivorus	2.46	2.46	3.59	4.37	4.26	6.95	4.37	11.43	3.59	3.03	3.81	3.59	3.81	4.71	3.14	3.25	3.25	3.59	3.03	3.47	3.59	3.14	4.37	4.37	4.37	4.48	3.70	3.25	4.37	4.26	7.17	4.93
Dryophytes versicolor	3.07	8.47	23.67	29.10	22.21	19.29	20.28	3.07	16.26	23.43	5.02	4.99	12.42	9.31	23.52	17.17	30.74	13.26	29.27	23.17	24.06	25.28	20.19	17.94	24.24	17.94	29.82	34.67	27.60	24.01	28.24	26.65
Dryophytes versicolor	3.19	6.37	20.58	23.18	18.77	29.64	17.87	8.42	12.85	18.54	4.04	3.19	8.22	5.76	18.93	14.88	30.58	8.22	26.59	17.35	20.72	25.28	20.19	17.94	22.02	17.94	21.28	28.24	27.92	24.01	28.24	21.57
Dryophytes versicolor	3.25	6.48	21.59	25.17	19.63	31.37	18.21	15.83	13.37	19.49	3.91	3.25	8.94	6.82	19.33	15.34	31.81	8.90	27.02	19.02	21.26	22.54	18.95	17.10	22.43	16.13	22.54	29.82	27.33	22.54	25.28	22.79
Dryophytes versicolor	2.96	6.37	21.21	23.76	18.25	27.76	17.32	13.74	12.26	18.43	3.98	2.96	7.46	5.47	18.59	15.16	31.15	7.88	27.27	16.92	20.92	22.54	18.95	17.10	22.14	17.10	17.94	25.28	24.01	22.54	25.28	21.77
Emys orbicularis	3.09	34.63	21.46	19.19	16.91	8.62	14.63	3.09	29.11	30.73	26.18	21.95	24.23	13.33	30.08	27.97	22.11	17.40	19.19	6.18	26.50	26.50	21.79	19.84	16.59	11.87	26.50	28.29	26.67	24.07	28.78	16.59
Epidalea calamita	0.34	0.34	1.91	2.36	2.25	2.93	2.14	2.70	2.14	1.46	2.25	2.36	2.36	3.15	2.03	2.14	2.36	2.59	2.03	1.01	2.03	1.58	2.59	2.59	2.36	2.36	1.24	0.45	2.03	1.58	2.59	1.91
Eumaeus atala	-26.05	3.03	3.03	3.03	3.03	-7.35	3.41	-26.05	2.46	3.03	1.90	1.90	2.84	-10.75	2.46	2.84	2.46	2.84	3.03	-9.05	3.03	3.41	3.79	3.41	3.41	3.41	2.84	2.84	3.41	3.60	2.84	-5.65
Eustroma reticulatum	0.31	3.36	3.05	3.05	2.14	1.22	1.68	0.31	6.86	5.95	7.63	5.95	7.32	3.81	5.64	5.64	4.42	3.05	3.66	1.37	6.25	6.25	5.80	4.42	6.25	3.20	6.56	5.64	7.63	5.64	9.61	5.49
Gryllus campestris	1.53	31.00	9.83	9.17	7.10	4.48	6.33	1.53	16.05	16.70	14.96	13.21	14.63	8.41	15.28	14.96	11.68	8.62	9.61	3.82	13.65	14.85	11.79	8.08	11.90	6.77	15.07	14.96	16.05	13.10	16.70	9.83
Gryllus campestris	1.09	5.57	6.33	6.22	4.69	2.84	4.04	1.09	9.28	7.64	10.37	9.28	10.70	6.55	7.75	8.62	8.62	6.33	7.10	3.06	9.93	8.30	10.37	9.39	11.46	7.10	8.84	7.21	9.28	9.61	14.19	8.52
Gryllus campestris	1.42	7.75	7.64	6.99	5.90	3.38	5.13	1.42	12.66	10.59	13.43	11.90	13.10	7.64	10.37	11.35	9.93	7.53	8.62	3.93	12.88	11.35	13.10	11.14	13.65	9.06	11.90	10.04	13.10	11.14	16.27	9.83
Hemideina thoracica	-12.75	25.19	14.66	12.22	7.52	-1.62	5.64	-12.75	19.74	19.74	12.22	5.64	7.52	-3.64	25.56	19.74	12.22	3.20	12.22	-5.67	20.49	28.38	22.18	19.74	28.38	4.14	17.11	12.22	9.96	-1.62	4.14	-12.75
Heterodon platirhinos	2.69	8.30	23.89	24.68	20.53	22.55	20.42	9.98	14.92	21.20	5.38	2.69	8.75	5.95	21.20	19.63	33.31	10.88	29.05	16.15	24.79	42.85	45.65	38.59	25.80	23.44	44.76	43.63	31.41	28.27	41.28	24.12
Hoplodactylus duvaucelii	0.96	1.54	4.82	3.08	4.82	6.94	4.82	10.02	1.73	1.35	1.35	1.35	1.73	1.35	1.35	1.54	1.35	2.31	1.16	1.73	2.31	2.31	1.73	0.96	1.73	1.35	4.82	5.39	1.73	5.78	3.08	8.67
Hyla arborea	8.23	8.23	31.37	30.45	28.95	23.58	27.98	14.39	33.72	30.24	33.92	35.27	41.84	33.43	38.92	37.29	34.72	35.27	40.37	25.90	33.72	27.37	38.92	32.26	44.17	34.11	36.67	32.89	29.98	33.56	24.54	22.97
Lacerta agilis	0.04	3.43	1.07	0.89	0.53	0.29	0.47	0.04	2.76	3.41	2.74	2.21	2.54	1.11	2.54	2.32	1.72	1.02	1.34	0.38	2.98	3.85	2.67	2.05	3.27	1.47	2.72	2.32	3.77	2.07	5.01	1.65
Lacerta agilis	0.09	3.39	1.76	1.65	1.05	0.47	0.85	0.09	4.19	3.96	4.36	4.23	4.50	1.76	3.90	4.03	2.85	1.72	2.05	0.54	4.25	4.03	4.92	3.92	4.94	2.25	4.07	3.88	4.30	3.94	5.99	2.60
Lacerta agilis	0.04	2.50	1.11	0.91	0.56	0.29	0.47	0.04	2.96	3.25	2.98	2.25	2.69	1.22	2.67	2.41	1.72	1.07	1.45	0.38	2.98	3.36	2.49	2.00	3.03	1.45	3.01	2.49	3.58	2.18	4.34	1.72
Lacerta agilis	0.04	2.65	1.18	0.98	0.56	0.31	0.49	0.04	3.09	3.28	3.10	2.36	2.85	1.23	2.78	2.47	1.81	1.11	1.47	0.38	3.16	3.45	2.58	2.05	3.25	1.47	3.21	2.65	3.65	2.23	4.36	1.78
Lacerta agilis	0.05	3.19	1.43	1.18	0.60	0.38	0.56	0.05	3.76	3.81	3.72	2.70	3.41	1.42	3.50	2.98	2.05	1.29	1.62	0.45	3.85	3.85	3.39	2.41	4.08	1.65	3.76	3.03	4.07	2.47	5.41	1.92
Lacerta agilis	-0.70	2.81	0.85	0.65	0.47	0.18	0.45	-0.70	2.30	2.58	2.29	1.89	2.18	0.89	2.21	2.03	1.56	0.87	1.14	0.33	2.30	2.90	2.14	1.72	2.43	1.18	2.27	2.05	3.07	1.83	4.30	1.49
Lacerta agilis	0.05	3.19	1.43	1.18	0.60	0.38	0.56	0.05	3.76	3.81	3.72	2.70	3.41	1.42	3.50	2.98	2.05	1.29	1.62	0.45	3.85	3.85	3.39	2.41	4.08	1.65	3.76	3.03	4.07	2.47	5.41	1.92
Lacerta agilis	-1.78	2.23	0.67	0.58	0.45	0.13	0.38	-1.78	2.07	2.25	2.11	1.76	2.03	0.85	1.92	1.76	1.38	0.60	0.98	0.24	2.05	2.45	1.85	1.56	2.11	0.91	2.12	1.85	2.90	1.65	3.96	1.42
Lacerta agilis	0.04	1.09	0.91	0.83	0.49	0.29	0.45	0.04	2.25	1.76	2.41	2.21	2.54	1.23	1.87	2.09	1.65	0.98	1.29	0.38	2.41	2.05	2.21	1.65	2.54	1.18	2.01	1.47	2.25	2.16	3.19	1.80
Lampropeltis triangulum	2.11	14.53	12.74	10.63	9.47	6.11	8.63	2.11	14.95	15.37	9.58	9.68	13.37	7.79	14.63	14.63	10.95	8.74	10.53	3.58	14.95	16.00	12.11	10.95	13.37	7.79	13.68	13.37	10.95	8.74	10.63	7.37
Lampropeltis triangulum	2.42	10.84	13.89	11.16	10.53	6.42	9.47	2.42	16.00	16.21	7.68	6.00	13.58	8.11	15.37	15.37	11.79	9.89	10.95	4.21	8.74	17.05	13.68	11.79	14.00	8.11	14.74	14.32	11.79	8.74	11.16	7.89
Lithobates pipiens	4.30	42.66	12.74	11.09	9.27	7.07	8.88	4.30	20.82	21.31	17.57	14.71	15.66	9.16	17.55	18.13	14.17	11.71	13.38	7.25	15.75	19.84	14.38	12.46	15.11	8.99	17.36	18.56	16.13	13.22	12.38	9.67
Notophthalmus viridescens	5.56	9.62	29.50	35.50	26.73	20.38	24.77	5.96	18.95	27.24	5.56	5.70	14.79	11.93	27.14	20.84	35.34	15.86	34.27	27.93	26.73	46.16	39.70	37.37	26.94	29.20	47.09	39.01	30.37	37.65	48.47	28.88
Oedipoda caerulescens	0.99	22.26	13.27	10.53	9.43	3.40	8.22	0.99	18.75	19.08	16.23	15.57	16.78	9.21	17.65	17.43	13.60	9.98	11.40	2.85	17.11	17.98	15.57	13.49	15.35	7.57	17.11	17.76	17.11	14.14	13.49	9.98
Oligosoma lineoocellatum	0.43	0.65	1.73	1.73	1.73	2.81	1.51	0.43	0.65	0.65	0.65	0.65	0.86	1.08	0.65	1.51	0.86	1.73	0.65	1.73	0.65	0.65	0.86	0.65	0.65	1.08	0.86	1.73	1.30	1.73	1.73	2.38
Opheodrys vernalis	0.74	11.57	3.41	3.41	3.26	2.52	3.26	0.74	3.71	3.71	3.41	3.41	3.41	2.82	3.41	3.41	3.41	3.26	3.41	1.78	3.71	3.71	3.41	3.41	3.41	2.82	3.41	3.41	3.41	3.26	3.41	2.67
Parnassius apollo	5.20	24.33	11.91	14.37	10.40	10.54	9.89	5.20	22.45	17.47	20.22	20.07	19.06	13.57	15.67	14.15	16.97	15.60	15.88	8.74	16.97	22.89	19.06	18.56	17.18	13.72	14.51	16.39	22.96	13.00	18.63	14.80
Parnassius mnemosyne	10.52	42.08	33.12	30.70	25.44	16.06	21.46	10.52	48.61	51.03	44.63	39.66	41.36	24.45	44.92	46.48	36.25	28.71	36.11	16.20	44.63	47.05	34.68	33.40	35.96	24.88	43.21	45.91	42.93	36.96	42.36	29.85
Pelobates syriacus	1.33	15.59	33.46	27.38	37.83	27.38	40.11	15.40	19.39	14.07	23.38	13.31	11.22	10.08	10.08	11.60	10.08	6.08	9.32	1.33	27.19	36.12	33.27	30.42	28.33	30.61	12.93	10.46	13.88	4.75	4.75	7.98
Perla marginata	0.87	32.14	7.69	6.64	5.76	3.49	5.24	0.87	15.72	17.47	11.18	11.70	12.75	6.11	15.55	12.93	9.43	6.29	6.99	2.97	12.75	10.48	10.48	8.91	10.31	1.75	13.28	13.80	14.15	10.48	15.20	6.64
Phengaris arion	-3.92	3.67	3.14	2.88	1.83	1.05	1.57	-3.92	6.02	5.37	6.16	5.24	5.89	3.27	5.37	5.24	4.19	2.88	3.41	1.18	6.02	6.16	5.50	4.32	6.02	3.27	6.16	4.19	7.33	4.98	9.17	4.19
Phengaris nausithous	-11.35	8.24	0.31	0.31	0.31	-0.63	0.31	-11.35	3.11	4.04	2.80	2.49	2.80	0.31	2.95	2.80	1.56	0.31	0.31	0.16	2.64	2.80	2.49	0.93	2.49	0.31	2.80	2.80	3.89	2.33	4.51	0.31
Phengaris teleius	0.16	0.62	3.12	3.59	3.59	4.68	3.59	0.16	3.43	1.87	3.43	2.81	3.59	5.30	1.25	1.87	1.25	1.72	1.25	1.09	2.81	1.25	3.90	3.43	3.90	3.59	3.43	2.34	3.59	2.81	7.96	3.59
Plebejus argus	0.15	3.02	1.16	1.08	0.78	0.37	0.60	0.15	2.83	2.98	2.83	2.31	2.83	1.45	2.61	2.46	2.05	1.19	1.49	0.37	2.87	3.17	3.09	2.50	3.24	2.05	2.50	2.31	3.09	2.16	3.73	1.98
Plebejus argus	0.19	3.02	1.16	1.12	0.78	0.37	0.60	0.19	2.83	3.02	2.83	2.31	2.83	1.49	2.61	2.39	2.05	1.16	1.49	0.37	2.87	3.17	3.09	2.50	3.24	2.05	2.50	2.31	3.09	2.16	3.73	1.98
Plebejus argus	0.15	3.13	1.12	0.97	0.75	0.37	0.45	0.15	2.50	2.83	2.57	2.16	2.50	1.19	2.39	2.27	1.98	1.12	1.27	0.37	2.68	2.98	2.83	2.27	3.09	1.83	2.31	2.16	2.91	2.09	3.58	1.75
Plebejus argus	0.26	2.42	1.49	1.38	0.82	0.37	0.78	0.26	3.24	2.83	3.24	2.83	3.21	1.94	2.91	2.83	2.16	1.49	1.86	0.48	3.21	3.32	3.47	2.83	3.65	2.09	2.91	2.72	3.62	2.50	4.33	2.16
Plethodon cinereus	-6.88	12.60	9.51	3.48	2.98	-1.18	2.55	-6.88	16.77	18.08	8.15	7.36	12.01	1.53	19.42	18.08	12.01	5.49	9.51	0.07	24.18	16.77	14.00	6.28	14.49	0.77	19.42	18.08	13.10	6.28	15.56	1.27
Plethodon cinereus	-4.53	9.87	18.08	10.75	9.51	0.14	7.36	-4.53	19.28	26.77	6.28	5.06	12.17	4.70	28.18	22.30	20.79	12.12	19.42	1.92	22.22	17.90	14.00	12.62	24.18	3.48	14.86	20.90	20.90	14.49	20.90	4.70
Psammodromus algirus	23.95	26.54	30.66	30.97	33.87	34.02	35.39	35.09	30.97	29.44	29.14	27.77	28.53	30.36	28.53	29.44	28.53	30.36	36.46	30.36	30.97	29.44	41.19	35.85	39.05	37.68	34.17	23.95	29.44	43.02	28.07	28.99
Pseudacris crucifer	0.81	8.07	21.95	27.14	20.73	8.20	19.09	0.81	15.23	21.71	5.03	4.99	11.45	8.55	21.78	16.15	28.76	12.16	27.31	15.29	22.37	35.36	29.97	28.21	22.58	20.64	39.66	32.84	25.79	29.19	38.71	24.58
Pseudacris crucifer	2.92	6.18	19.26	21.61	17.76	17.12	16.70	3.35	11.83	17.55	4.01	2.92	7.77	5.70	17.77	13.87	28.59	7.72	24.80	16.31	19.36	35.36	29.97	28.21	20.59	17.89	31.32	36.05	26.08	25.43	38.71	20.14
Pseudacris crucifer	2.99	6.37	20.21	23.53	18.26	29.38	17.15	6.62	12.25	18.19	3.82	2.99	8.34	6.58	18.05	14.34	29.86	8.29	25.13	17.88	19.88	32.68	29.02	27.20	20.85	20.45	32.68	34.86	25.63	26.62	35.36	21.16
Storeria dekayi	10.36	30.54	33.55	30.54	20.38	41.47	20.38	16.84	20.38	36.35	20.38	12.18	25.28	12.18	27.94	27.94	22.63	18.52	48.35	25.28	10.36	25.28	30.54	22.63	30.54	10.36	38.81	48.35	22.63	10.36	20.38	33.55
Storeria dekayi	8.30	30.54	38.81	38.81	27.94	31.75	25.28	8.30	27.94	46.14	20.38	16.41	36.35	20.38	27.94	30.54	33.55	30.54	54.39	36.35	16.41	25.28	30.54	33.55	30.54	16.41	38.81	48.35	22.63	16.41	20.38	41.47
Storeria dekayi	10.36	27.94	33.55	30.54	20.38	41.47	20.38	26.66	20.38	38.81	18.52	10.36	27.94	16.41	25.28	25.28	25.28	20.38	50.46	30.54	10.36	22.63	27.94	25.28	27.94	10.36	36.35	46.14	20.38	12.18	16.41	33.55
Terrapene carolina	12.11	30.08	65.90	61.70	43.72	42.19	43.72	12.11	47.42	59.40	30.21	27.92	59.53	38.50	43.72	53.54	57.87	53.54	64.24	57.23	27.92	43.72	47.42	57.87	47.42	24.98	57.87	59.40	34.29	27.92	27.92	61.70
Trapezites symmomus	0.36	8.49	1.81	3.61	1.99	0.72	4.16	0.36	8.31	6.14	8.31	11.74	12.10	7.77	8.31	7.77	0.90	0.36	8.49	0.72	8.85	10.12	10.30	10.30	6.68	15.72	16.26	6.50	1.08	0.72	4.16	7.77

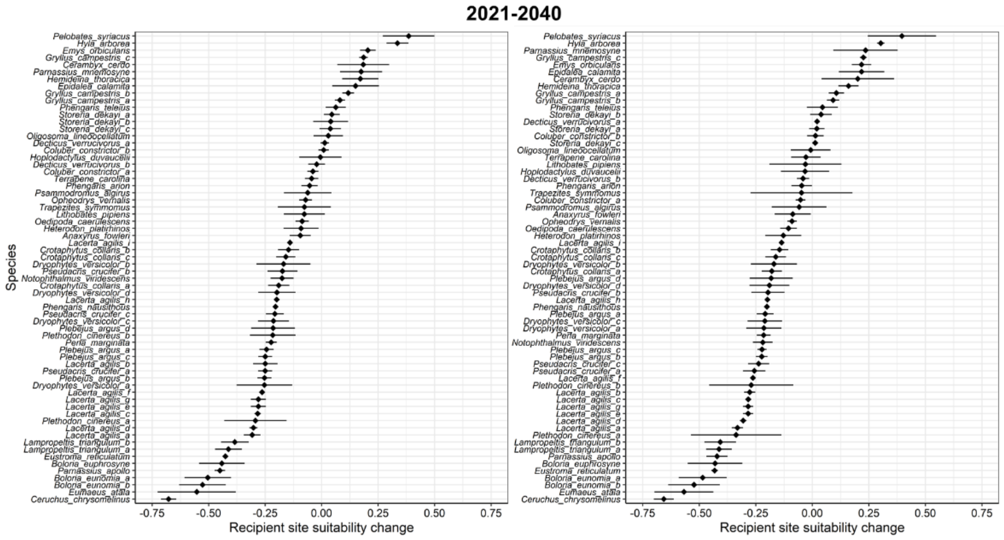
Appendix 4.5: Proportion of declining recipient sites across GCMs

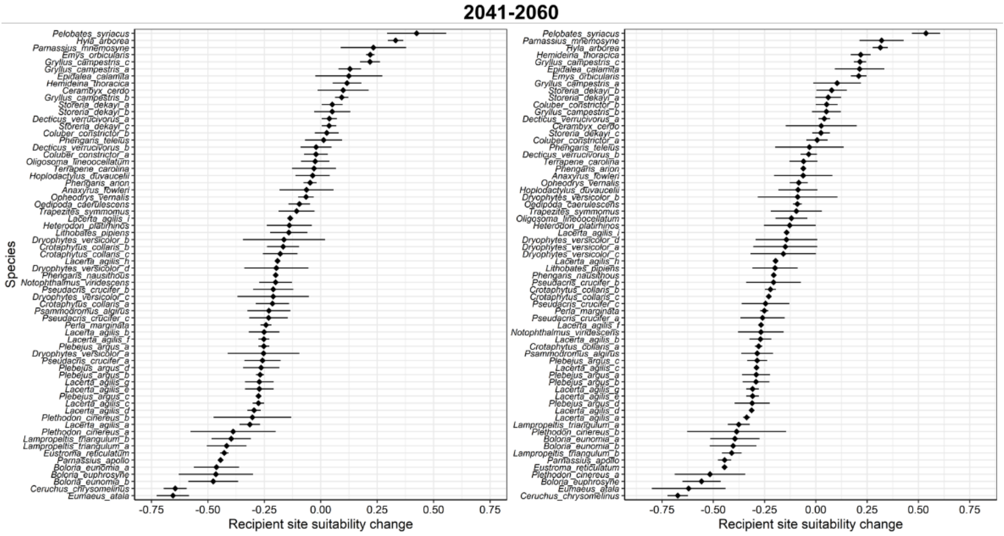
Table A4.5.1. Percentage of recipient sites predicted to decline in suitability across six climate change projections. Results are compared across three suitability change categorisations (decline = 0 – 0.25, medium decline = 0.25 – 50, and large decline = >0.5). Future projections have been averaged across 5 GCMs for each SSP scenario.

Scenario	Decline	Medium decline	Large decline	Total
2021-2040 SSP126				
CanESM5	34.8	33.3	6.1	74.2
CNRM-CM6-1	47.0	17.0	6.1	69.7
IPSL-CM6A-LR	51.5	20.0	4.5	75.8
MIROC6	33.3	33.3	4.5	71.2
MRI-ESM2-0	36.4	31.8	6.1	74.2
2021-2040 SSP370				
CanESM5	33.3	34.8	10.6	78.8
CNRM-CM6-1	47.0	19.7	4.5	71.2
IPSL-CM6A-LR	47.0	19.7	4.5	71.2
MIROC6	37.9	28.8	6.1	72.7
MRI-ESM2-0	39.4	31.8	6.1	77.3
2041-2060 SSP126				
CanESM5	28.8	40.9	7.6	77.3
CNRM-CM6-1	39.4	16.7	6.1	62.1
IPSL-CM6A-LR	40.9	33.3	4.5	78.8
MIROC6	34.8	30.3	7.6	72.7
MRI-ESM2-0	40.9	30.3	4.5	75.8
2041-2060 SSP370				
CanESM5	37.9	40.9	6.1	84.8
CNRM-CM6-1	37.9	19.7	6.1	63.6
IPSL-CM6A-LR	33.3	34.8	4.5	72.7
MIROC6	27.3	39.4	6.1	72.7
MRI-ESM2-0	31.8	40.9	4.5	77.3
2061-2080 SSP126				

CanESM5	30.3	39.4	7.6	77.3
CNRM-CM6-1	42.4	24.2	3	69.7
IPSL-CM6A-LR	40.9	33.3	3	77.3
MIROC6	36.4	28.8	4.5	69.7
MRI-ESM2-0	42.4	30.3	4.5	77.3
2061-2080 SSP370				
CanESM5	28.8	39.4	10.6	78.8
CNRM-CM6-1	27.3	34.8	7.6	69.7
IPSL-CM6A-LR	34.8	37.9	6.1	78.8
MIROC6	27.3	42.4	7.6	77.3
MRI-ESM2-0	25.8	47.0	6.1	78.8

Appendix 4.6: Predicted recipient site suitability change


2021-2040


2041-2060

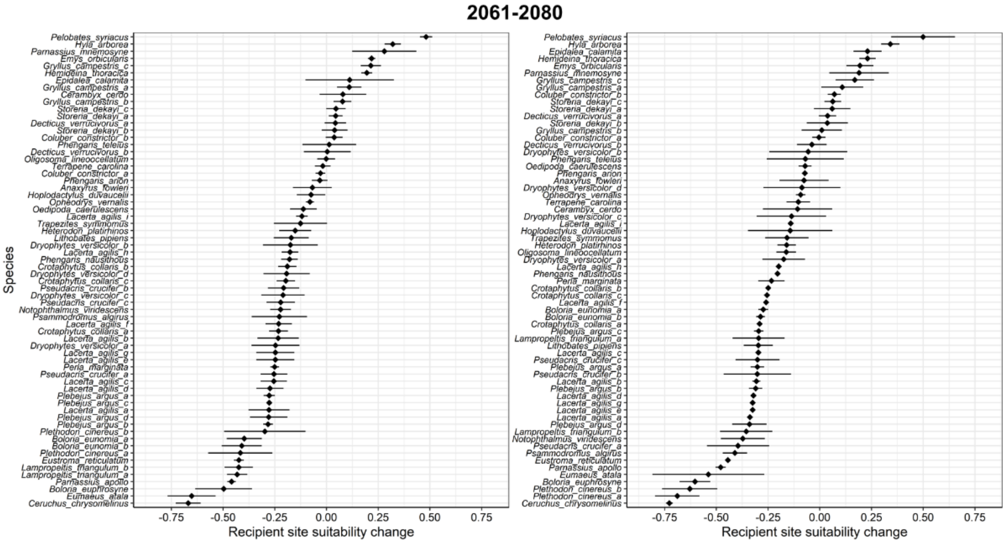

2061-2080

Figure A4.6.1. Mean (SD) predicted changes in standardised suitability at 66 translocation recipient sites between current conditions and those projected for 2021-2040, 2041-2060, and 2061-2080, according to two different climate change scenarios: SSP126 (left) and SSP370 (right). Future projections have been averaged across 5 GCMs for each SSP scenario.

Appendix 4.7 – Difference in suitability change predictions across spatial scales

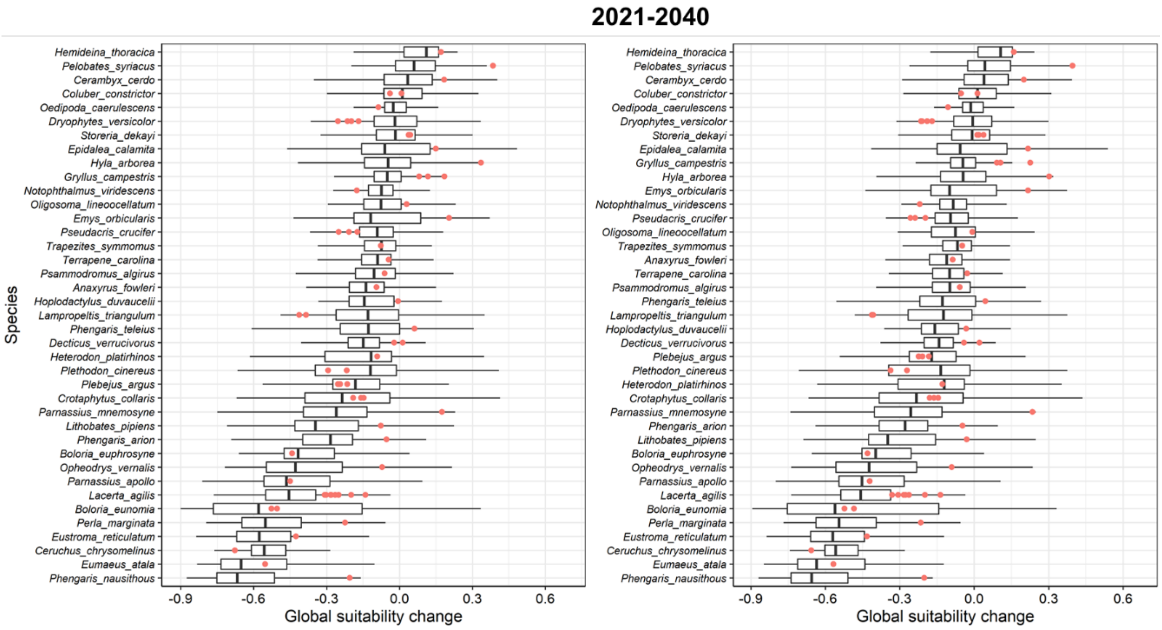
Table A4.7.1. Percent of recipient sites in each boxplot distribution category under each climate change projection. Boxplots were created for every species, according to the distribution of suitability change across their global ranges. Minimum is Q1 – 1.5*IQR and Maximum is Q3 + 1.5*IQR.

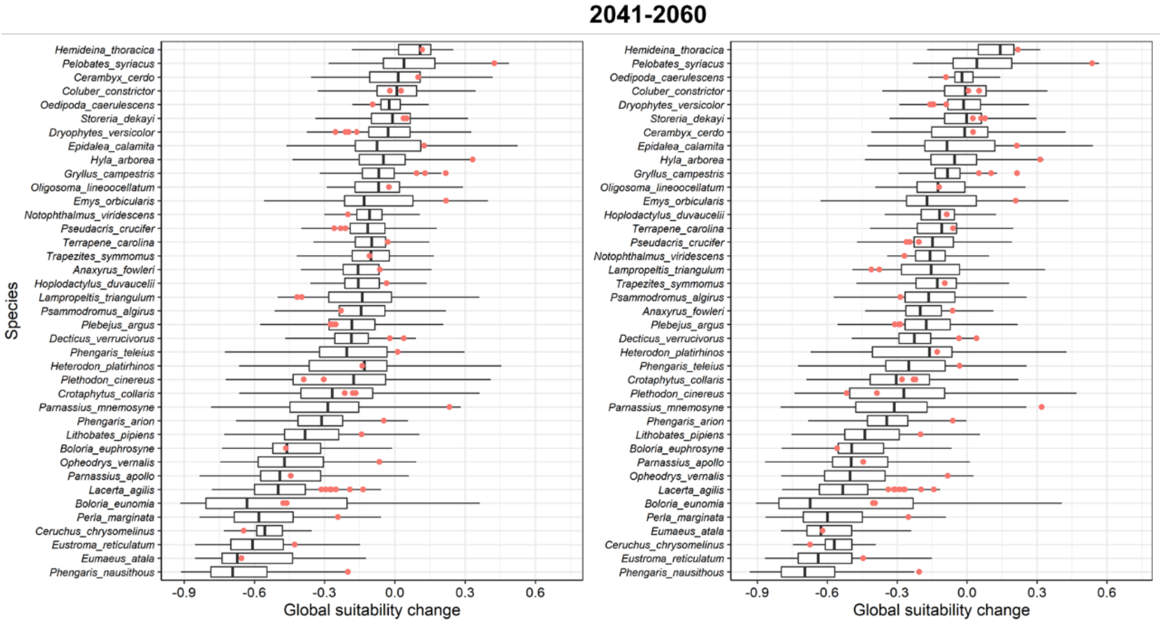
Scenario	< Minimum (outliers)	Minimum to Q1	Q1 to median	Median to Q3	Q3 to maximum	> Maximum (outliers)
2021-2040 – SSP126	0	18.2	15.2	21.2	40.9	4.5
2021-2040 – SSP370	0	18.2	13.6	22.7	42.4	3.0
2041-2060 – SSP126	0	18.2	16.7	21.2	42.4	1.5
2041-2060 – SSP370	0	27.3	3.0	25.8	39.4	4.5
2061-2080 – SSP126	0	24.2	7.6	22.7	39.4	6.1
2061-2080 – SSP370	0	22.7	12.1	15.2	40.9	9.1

Table A4.7.2. Percent of recipient sites in each boxplot distribution category under each climate change projection. Boxplots were created according to the distribution of suitability change across species' regional ranges. Minimum is Q1 – 1.5*IQR and Maximum is Q3 + 1.5*IQR. Translocations with less than six occurrences in the focal region were excluded (*n* = 11).

Scenario	< Minimum (outliers)	Minimum to Q1	Q1 to median	Median to Q3	Q3 to maximum	> Maximum (outliers)
2021-2040 – SSP126	1.8	41.8	16.4	23.6	14.5	1.8

2021-2040 – SSP370	5.5	38.2	16.4	21.8	14.5	3.6
2041-2060 – SSP126	5.4	32.7	23.6	27.3	7.3	3.6
2041-2060 – SSP370	1.8	40.0	23.6	21.8	9.1	3.6
2061-2080 – SSP126	1.8	36.4	20.0	29.1	9.1	3.6
2061-2080 – SSP370	1.8	41.8	20.0	20.0	9.1	7.3





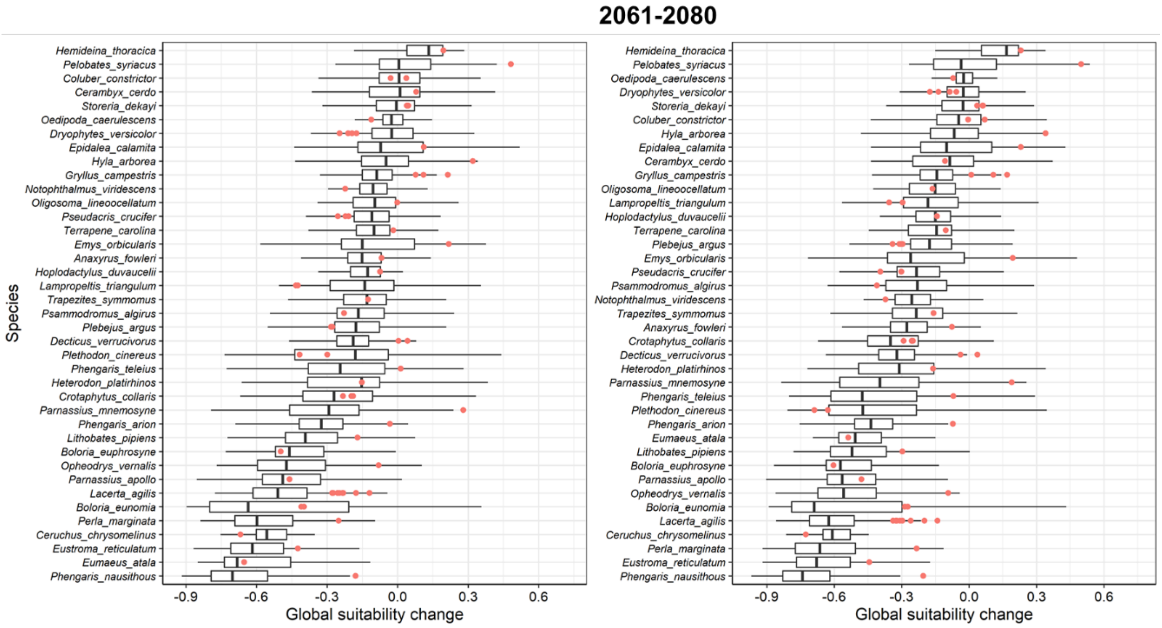
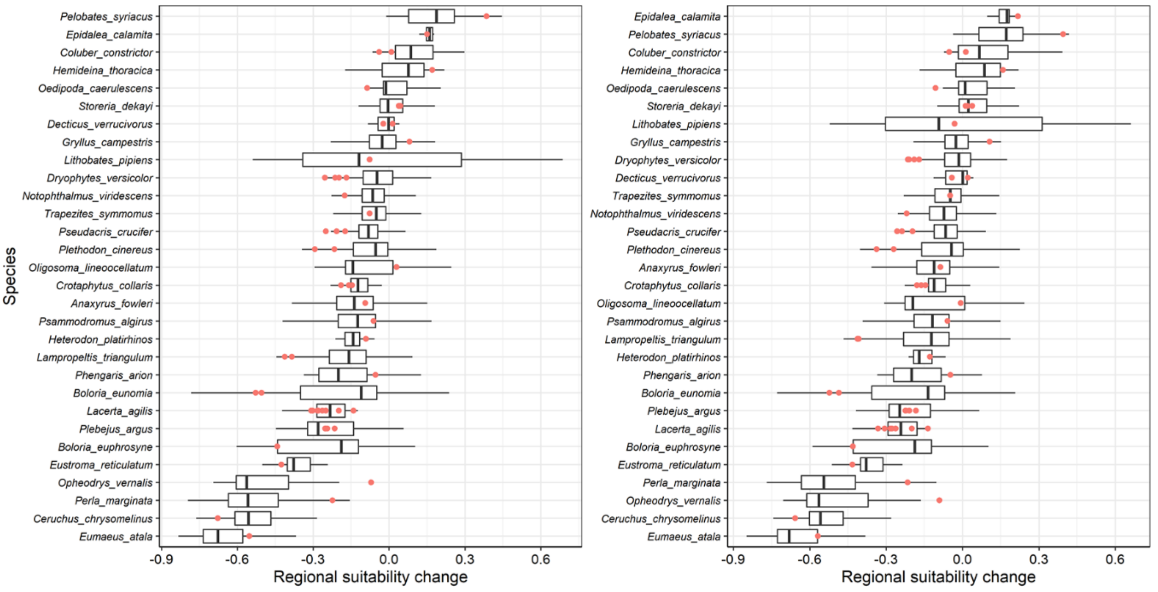
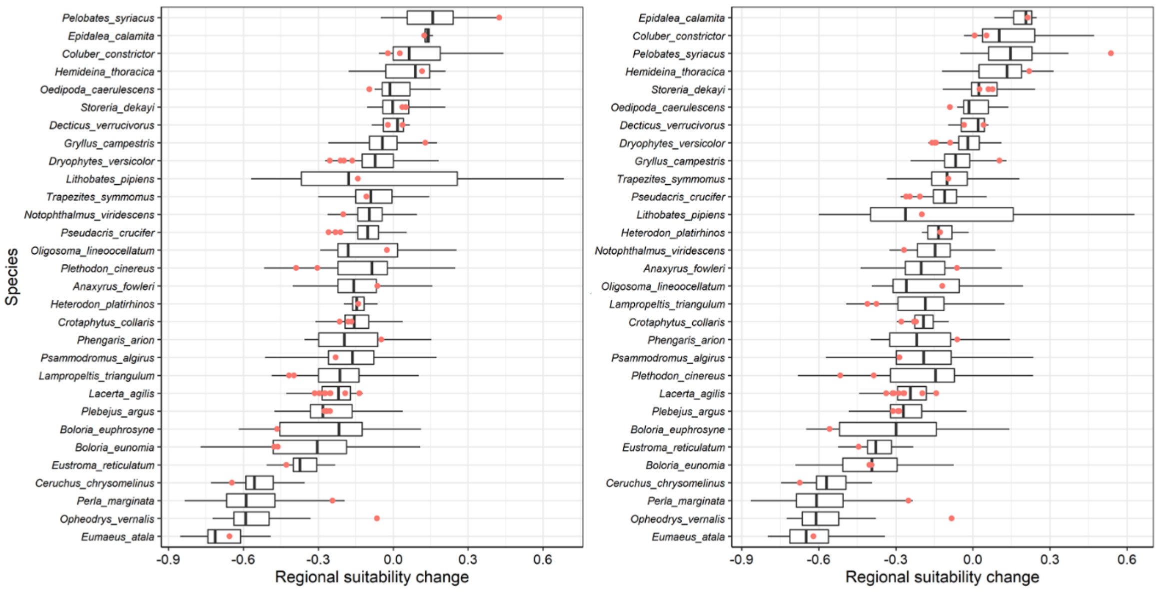


Figure A4.7.1. Average predicted change in suitability across species global ranges according to two different climate change scenarios: SSP126 (left) and SSP370 (right). Red dots represent predicted suitability change for translocated populations. Future projections have been averaged across 5 GCMs for each SSP scenario.



2021-2040



2041-2060

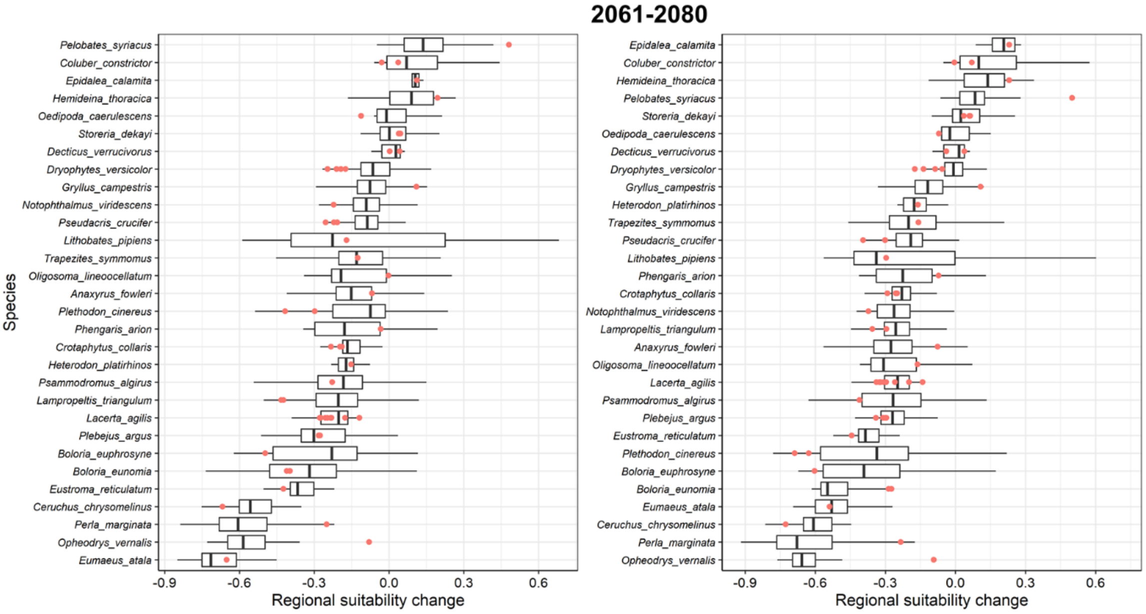
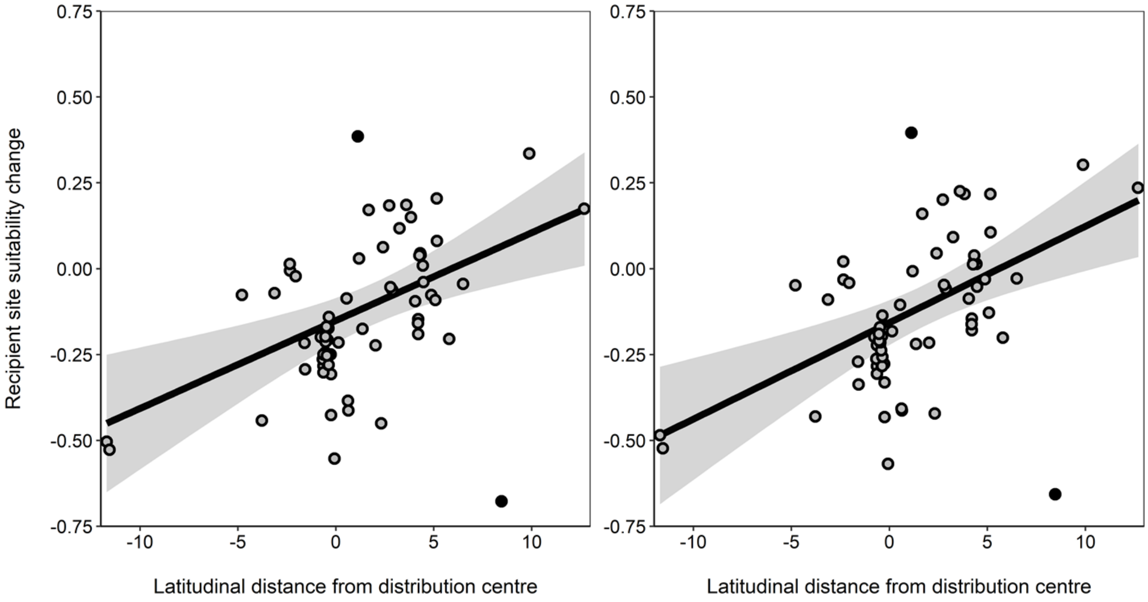


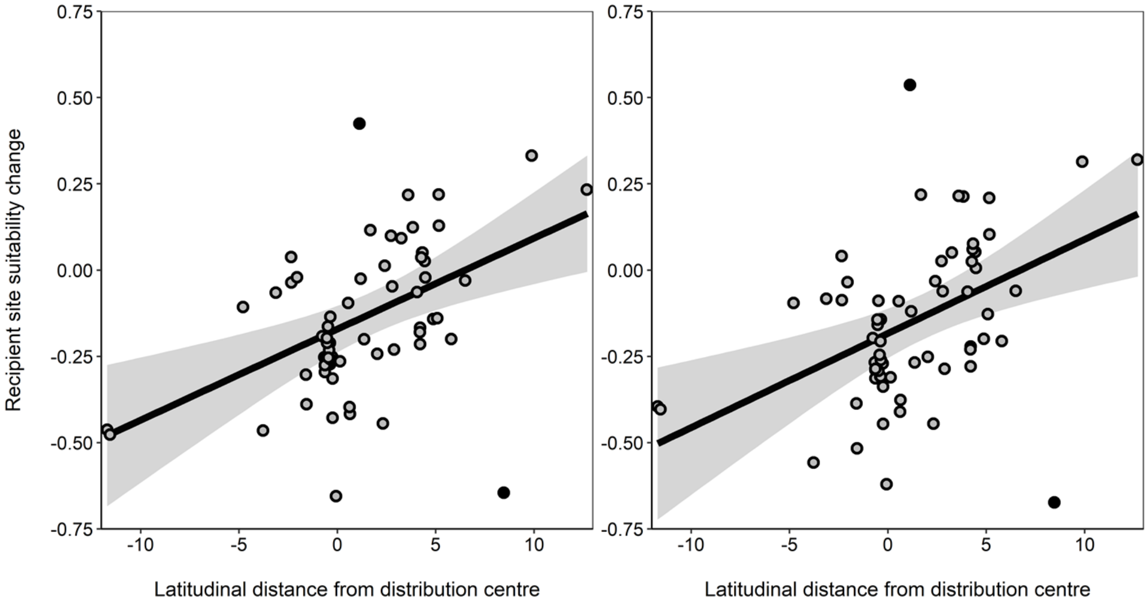
Figure A4.7.2. Average predicted change in suitability across species regional ranges according to two different climate change scenarios: SSP126 (left) and SSP370 (right). Red dots represent predicted suitability change for translocated populations. Future projections have been averaged across 5 GCMs for each SSP scenario. Translocations with less than six occurrences in the focal region were excluded (*n* = 11).

Appendix 4.8: Outputs from LMMs

2021-2040



2041-2060



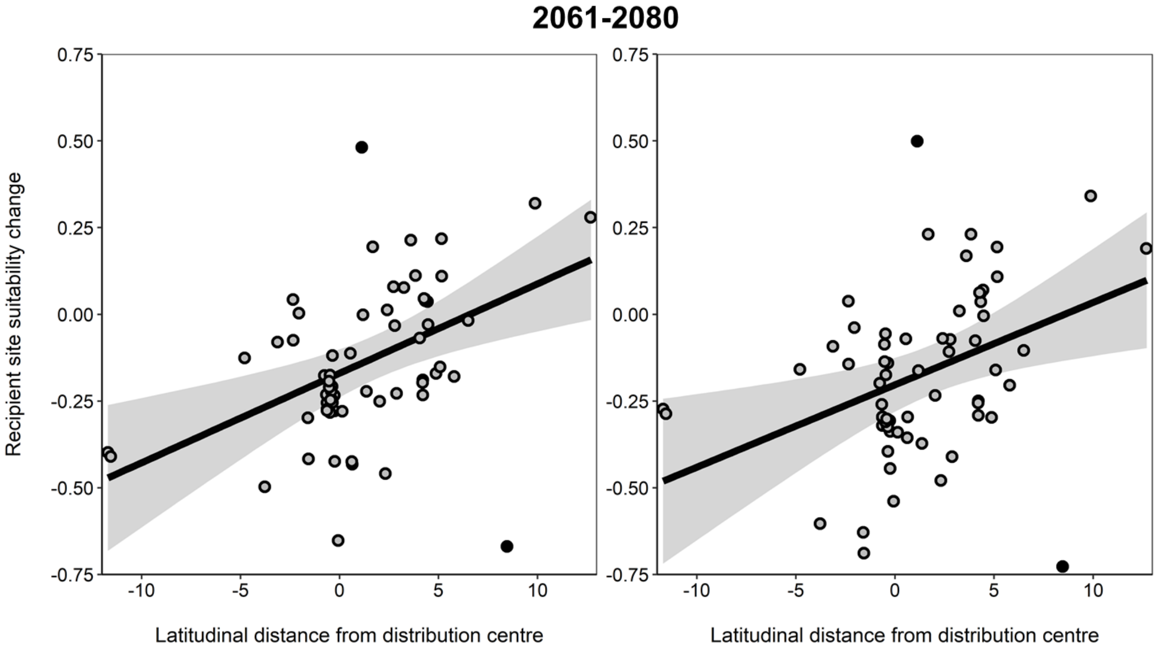


Figure A4.8.1. Effect of distance from latitudinal centre (decimal degrees) on predicted changes in macroclimatic suitability at recipient sites across three time horizons, according to SSP126 (left) and SSP370 (right). The two black dots (upper = *Pelobates syriacus*; lower = *Ceruchus chrysomelinus*) on each plot represent outliers that were omitted from the LMM.

Table A4.8.1. Sensitivity of LMM outputs when *Eumaeus atala* is omitted from the analysis. Beta coefficients (β), standard error and 95% confidence intervals of the spatial attributes influencing predicted changes in macroclimatic suitability at recipient sites.

Spatial attribute	**β**	**β SE**	**95% CI**	
2021-2040 – SSP126				
(Intercept)	0.12		-0.18	0.41
Altitudinal difference	0.04		-0.21	0.28
Latitudinal difference	0.53		**0.26**	**0.79**
2021-2040 – SSP370				
(Intercept)	0.11		-0.18	0.40
Altitudinal difference	0.04		-0.20	0.29
Latitudinal difference	0.56		**0.30**	**0.83**

2041-2060 – SSP126			
(Intercept)	0.09	-0.20	0.38
Altitudinal difference	-0.04	-0.28	0.20
Latitudinal difference	0.54	**0.27**	**0.80**
2041-2060 – SSP370			
(Intercept)	0.07	-0.23	0.38
Altitudinal difference	-0.05	-0.31	0.20
Latitudinal difference	0.52	**0.24**	**0.79**
2061-2080 – SSP126			
(Intercept)	0.08	-0.22	0.38
Altitudinal difference	-0.04	-0.29	0.21
Latitudinal difference	0.53	**0.25**	**0.80**
2061-2080 – SSP370			
(Intercept)	0.05	-0.27	0.38
Altitudinal difference	-0.11	-0.38	0.16
Latitudinal difference	0.42	**0.13**	**0.72**

Appendix 5.1: Species distribution modelling methodology

Species data

We compiled a database of occurrences using multiple data repositories where possible for each species; these included the Global Biodiversity Information Facility (GBIF), the Botanical Information and Ecology Network (BIEN) and the Botanical Society for Britain and Ireland (BSBI) (DOIs and links to downloaded data are available at: http://opendata.ljmu.ac.uk/). We utilised worldwide occurrence data for each species to avoid misrepresenting the potential suitability of a site resulting from biased and truncated estimates of a species niche (Barbet-Massin et al. 2010; Sánchez-Fernández et al. 2011).

SDMs constructed from openly available data repositories can achieve accuracy comparable with those constructed from field-sampled data (Jackson et al. 2015), but there are still a number of potential pitfalls (e.g. coordinate imprecision, spatial biases and inclusion of historical records) (Beck et al. 2014). Therefore, we retained only those records reported to at least two digits (precision of ca. 1 km) and deleted redistributed records, duplicated records and those explicitly collected prior to 1950. To reduce the effects of spatial bias caused by unequal sampling (Boria et al. 2014; Radosavljevic & Anderson 2014), we thinned the cleaned occurrence datasets of each species at a 10 km resolution in ArcMap v10.5 using the Spatial Rarefy Tool from the SDM ToolBox v2.2 (Brown 2014). This approach has been widely used (Darwell & Cook 2017; Galante et al. 2018; Guevara et al. 2018) and has demonstrated improved SDM predictions through reductions in sampling bias, spatial autocorrelation and overfitting (Galante et al. 2018). We did not use the reintroduction site locations to construct SDMs and any occurrence points that overlapped with these sites were removed.

We then consulted expert-drawn range maps and distribution descriptions to remove records outside of the indigenous range (Table A5.1.1). Since the global ranges of our focal taxa are coarsely described, limited to Europe (e.g. *Leucorrhinia dubia*), or not formally described at all (e.g. *Carsia sororiata*), we used kernel density estimates to identify and remove outlying presence localities (Gomes et al. 2018). As we aimed to maximise the number of occurrences for each SDM, we selected a large bandwidth (ca.

1,111 km at the equator) and removed records with a kernel density estimate of < 0.05. After data cleaning and thinning, the species presence databases ranged from 615 – 4623 occurrences ready for modelling.

Table A5.1.1. Expert-drawn range maps and distribution descriptions used to spatially refine species occurrence data.

Species	Reference
Andromeda polifolia	Meusel and Jäger (1992)
Genista anglica	Meusel and Jäger (1992)
Gentiana pneumonanthe	Meusel and Jäger (1992)
Drosera anglica	Meusel and Jäger (1992)
Rhynchospora alba	Meusel and Jäger (1992)
Utricularia minor	Meusel and Jäger (1992); IUCN map available
Drosera intermedia	Meusel and Jäger (1992)
Lycopodiella inundata	Meusel and Jäger (1992)
Narthecium ossifragum	Meusel and Jäger (1992)
Leucorrhinia dubia	IUCN map available
Coenonympha tullia	The IUCN describe the distribution of this species but there is no range map available. State-level distribution map for North America available on NatureServe.
Metrioptera brachyptera	The IUCN describe the distribution of this species but there is no range map available
Carsia sororiata	No distribution description could be located.

Environmental data

We considered a combination of climatic variables and soil pH as macroecological predictors in our SDMs. While landcover variables have been shown to improve the accuracy of SDM predictions for some plant and invertebrate species (Pearson et al. 2004; Eskildsen et al. 2013), openly available products were either too coarsely classified (e.g. Li et al. 2017) or too limited in extent (e.g. CORINE Land Cover data) for inclusion in our models.

For climate, we considered nine variables averaged for the period 1950-2000 that have commonly been used in plant and invertebrate SDM studies (Broennimann et al. 2007; Safranyik et al. 2010; Petitpierre, B., Kueffer, C., Broennimann, O., Randin, C., Daehler, C. and Guisan 2012; Estay et al. 2014; Mod et al. 2016) and/or represent different aspects of climate affecting plant and invertebrate eco-physiology (Chown, S. L. and Nicolson 2004; Lambers, H., Chapin, F.S. and Pons 2008). Seven of these were downloaded from the WorldClim dataset (Version 1.4; www.worldclim.org) (Hijmans et al. 2005) at a 30 arc-second resolution and include: mean annual temperature (BIO1), temperature seasonality (BIO4), mean temperature of the warmest quarter (BIO10), mean temperature of the coldest quarter (BIO11), precipitation seasonality (BIO15), precipitation of the wettest quarter (BIO16) and precipitation of the driest quarter (BIO17). We also generated growing degree days (GDD) (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 (SMD), which represents the difference between annual precipitation (Bio12) and potential evapotranspiration (PET) (PET provided by A. Trabucco; Trabucco & Zomer 2009). GDD and SMD are considered to be two of the best default climate predictors for temperate species (Foden et al. 2019).

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) made available by the International Soil Reference and Information Center (ISRIC) at 250 m resolution (Hengl et al. 2017). The inclusion of soil-based variables has improved the spatial modelling results for invertebrates (Titeux et al. 2009), and plants, particularly acidophilic species (Dubuis et al. 2013) such as the ones being considered for translocation. As pH is on a logarithmic scale, resampling the ISRIC-generated 250 m raster to a coarser 1 km grid would have resulted in the loss of potentially important variation between adjacent cells. Therefore, we back-converted pH to hydronium ion H_3O^+ concentration before resampling the raster grid to 1 km resolution using bilinear interpolation. We excluded soil pH from the two Lepidopteran SDMs because the lifecycles of these species do not involve direct contact with the soil.

To avoid multicollinearity between the ten predictors, we removed variables that presented a variance inflation factor (VIF) of >10 (Dormann et al. 2013; Guisan et al. 2017) with the R package *usdm* (v. 1.1-18) (Naimi 2015). VIF estimates the severity of the effect of multicollinearity, by calculating the increase in variance in a regression due to collinearity compared to when uncorrelated variables are used.

General circulation models (GCMs) are known to be highly variable in their projections (Goberville et al. 2015) so we used the following three GCMs to derive projections of the nine climatic variables for the period 2041-2060 : MPI-SM-LR models (Giorgetta et al. 2013), IPSLCM5A-LR (Dufresne et al. 2013) and HadGEM2-ES (Jones et al. 2011). (Goberville et al. 2015) found that these three GCMs caused low, moderate and high levels of projected occurrence changes respectively for two species distributed across Europe. Nonetheless, these three GCMs are only representative of a sample of potential climate change trajectories described by 19 GCMs accessible in the WorldClim v1.4 dataset, thus, outputs presented in our study do not account for every possible projection of climate change effects. Additionally, we used two representative concentration pathways describing low (RCP2.6) and high (RCP8.5) greenhouse gas concentration scenarios. We computed a multivariate environmental similarity surface (MESS), following (Elith et al. 2010), to assess the degree of extrapolation (i.e. the extent to which projected environmental conditions were outside those represented within the model calibration data (Barbosa et al. 2009) for each climate projection. To compute the MESS we used the *dismo* package (v1.1-4) (Hijmans et al. 2017) in R and calculated the proportion of cells in the projection extent with MESS values of < 0.

Species distribution models

Species distribution models (SDMs) were built using the *biomod2* package (v. 3.3-7) (Thuiller et al. 2016) in R using five algorithms from different families: Generalised Additive Model (GAM), Multivariate Adaptive Regression Splines (MARS), Generalised Boosted Model (GBM), Random Forest (RF) and Maxent. Each SDM was parameterised with the default settings from *biomod2*. We applied different algorithms because the variability between different techniques has been identified as an important source of uncertainty (Buisson et al. 2010). For each species, we replicated five runs with 70% of records randomly selected for model calibration and the remaining 30% set aside for model testing. Model performance was evaluated using the receiver operating characteristic to determine an area under the curve (AUC) and the true skill statistic (TSS).

Our ensemble models retained only models with AUC scores of > 0.80, as models are considered to have reliable prediction performances if above this threshold (Swets 1998). The contribution of each of the selected models to the final ensemble was proportional to its AUC score; this approach minimises uncertainties since weak models receive less weight in the final ensemble. All models from different repetitions and algorithms were combined using an ensemble forecasting strategy and their outputs were averaged based on the weighted mean. We also computed a separate model based on the coefficient of variation (Standard Deviation / Mean), which represents a measure of agreement between the combination of models that contributed to the final ensemble.

As we were reliant on presence-only data, we generated pseudo-absences (PAs) for each SDM. The selection of PAs influences model parameterisation and thus, can influence the appropriateness and accuracy of model predictions when extrapolating species distributions across time (Chefaoui & Lobo 2008; VanDerWal et al. 2009). We began by refining each species background extent to terrestrial ecoregions overlapping with their cleaned occurrence datasets. Ecoregions represent geographical units characterised by homogenous climates, geology, fauna and flora (Olson et al. 2001). However, some of the terrestrial ecoregions relevant to the distributions of our focal species are vast (e.g. Scandinavian and Russian Taiga, >2 million km^2). SDMs become increasingly simplified as the area from which PAs are selected increases (VanDerWal et al. 2009), so we further restricted PA selection to a 2-degree buffer zone drawn around an alpha-hull generated from the refined occurrence dataset with the *ConR* package v1.2.4 (Dauby et al. 2017) in R. We then randomly selected 10,000 pseudo-absence records from the buffer zone for each species (Barbet-Massin et al. 2012a).

As 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 standardised the predicted climate suitability values to range between

0 and 1 with the following formula: (x – min)/(max – min). Therefore, the suitability of each grid cell was relative to the maximum predicted suitability value across the projection extent for each species.

To categorise 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 maximises the true skill statistic (TSS; (Allouche et al. 2006). We chose this method because it demonstrated improved reliability over other commonly applied approaches when only presence data is available (Liu et al. 2013).

Relative importance of predictor variables to the SDMs was estimated using a randomisation procedure in *biomod2* (Thuiller et al. 2016). This approach calculates the Pearson's correlation between a prediction using all of the variables and a prediction where one variable has been randomly permutated. If the correlation score between the two predictions is high, then the variable is considered to be of low importance. We repeated this procedure 10 times for each species.

Appendix 5.2: Species distribution model outputs

Table A5.2.1. Mean percent importance of the three most contributing predictor variables for each species SDMs. Variable abbreviations are as follows: BIO4 = temperature seasonality, BIO15 = precipitation seasonality, BIO17 = precipitation of the driest quarter, GDD = growing degree days, SMD = soil moisture deficit and SpH = soil pH.

Species	Predictor	Percent variable importance	Species	Predictor	Percent variable importance
A. polifolia	BIO4	42.8	*D. anglica*	BIO4	36.2
	SMD	17.1		SMD	18.2
	BIO17	11.9		BIO15	12.8
D. intermedia	BIO4	31.7	*G. anglica*	GDD	35.0
	GDD	26.7		BIO4	28.1
	SpH	24.8		SpH	18.1

G. pneumonanthe	BIO4	57.1	*L. inundata*	BIO4	24.6
	GDD	15.9		SMD	20.0
	SMD	14.1		GDD	16.6
N. ossifragum	BIO4	34.9	*R. alba*	BIO4	36.0
	SMD	30.1		SpH	23.8
	GDD	15.7		GDD	23.2
U. minor	BIO4	35.4	*C. sororiata*	GDD	43.8
	GDD	24.3		BIO4	42.2
	BIO17	17.7		BIO15	7.7
C. tullia	BIO4	46.2	*L. dubia*	SpH	32.5
	SMD	17.9		BIO4	28.7
	GDD	17.6		GDD	19.2
M. brachyptera	BIO4	29.7			
	GDD	26.9			
	BIO15	17.0			

Table A5.2.2. Percent of projection extent (U.K. and Ireland) where model extrapolation occurred for each climate scenario according to a multivariate environmental similarity surface (MESS) (MESS values of < 0). Abbreviations for scenarios are as follows: HE2.6 = HadGEM2-ES (RCP2.6), HE8.5 = HadGEM2-ES (RCP8.5), IP2.6 = IPSLCM5A-LR (RCP2.6), IP8.5 = IPSLCM5A-LR (RCP8.5), MP2.6 = MPI-SM-LR (RCP2.6) and MP8.5 = MPI-SM-LR (RCP8.5).

Species	**Current**	**HE2.6**	**HE8.5**	**IP2.6**	**IP8.5**	**MP2.6**	**MP8.5**
A. polifolia	0.00	0.00	0.00	1.10	0.19	0.00	0.00
D. anglica	0.00	0.00	0.00	0.00	0.00	0.00	0.00
D. intermedia	0.00	0.00	0.00	0.33	0.00	0.00	0.00
G. anglica	0.00	0.01	0.02	0.07	0.19	0.00	0.02
G. pneumonanthe	0.00	0.00	0.00	1.15	0.20	0.00	0.00
L. inundata	0.00	0.00	0.00	0.00	0.00	0.00	0.00
N. ossifragum	0.00	0.00	0.00	0.00	0.00	0.00	0.00
R. alba	0.00	0.00	0.00	0.16	0.00	0.00	0.00
U. minor	0.00	0.00	0.00	0.92	0.12	0.00	0.00
C. sororiata	0.00	3.09	3.56	4.49	3.63	0.00	3.56
C. tullia	0.00	0.00	0.00	0.00	0.00	0.00	0.00

L. dubia	0.00	0.00	0.00	3.19	0.60	0.00	0.00
M. brachyptera	0.00	0.44	0.44	10.99	3.32	0.00	0.44

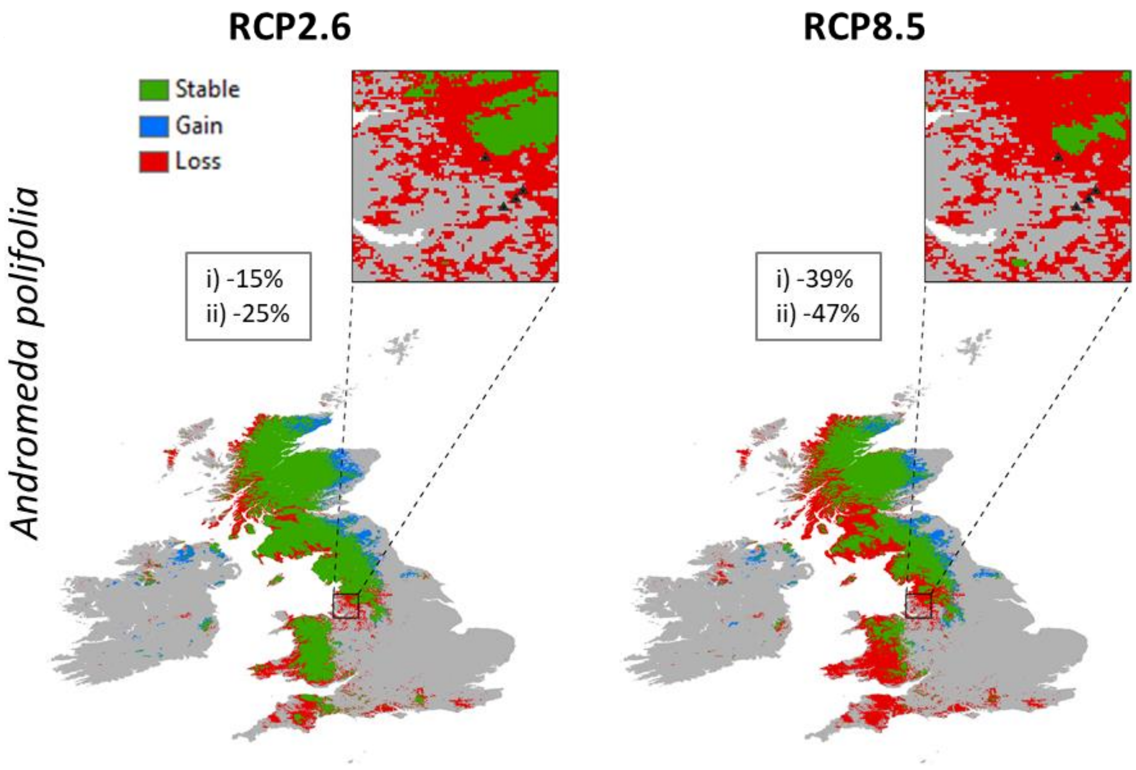
Table A5.2.3. Binary SDM outputs for each potential recipient site under current macroecological (C) conditions and projected future conditions for RCP2.6 (2.6) and RCP8.5 (8.5). A = above statistical suitability threshold and B = below statistical suitability threshold.

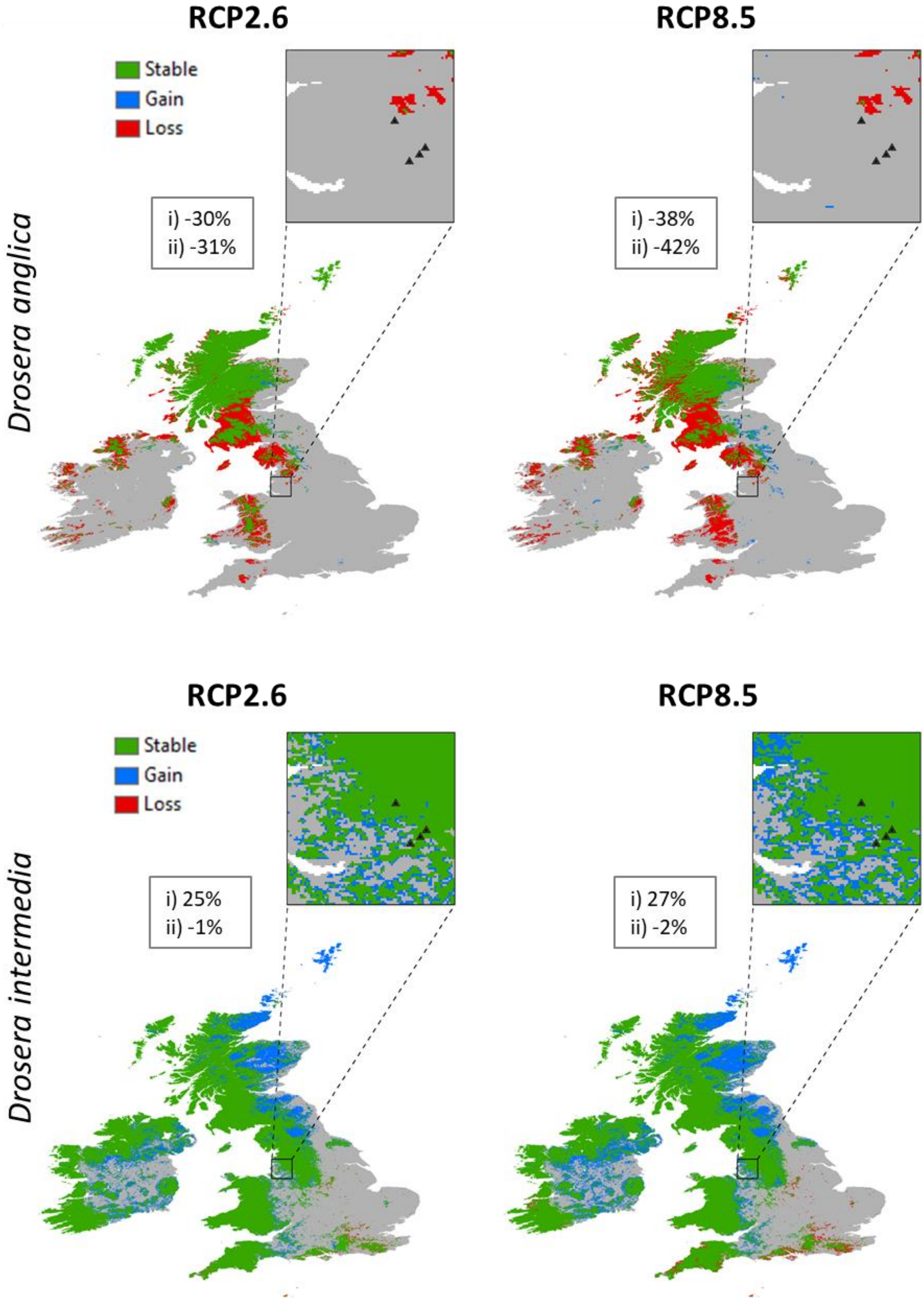
	Astley			**Cadishead**			**Red**			**Risley**		
	C	**2.6**	**8.5**	**C**	**2.6**	**8.5**	**C**	**2.6**	**8.5**	**C**	**2.6**	**8.5**
A. polifolia	A	B	B	A	B	B	A	B	B	A	B	B
D. anglica	B	B	B	B	B	B	B	B	B	B	B	B
D. intermedia	A	A	A	A	A	A	A	A	A	A	A	A
G. anglica	A	A	B	A	A	B	A	A	A	A	A	B
G. pneumonanthe	A	A	A	A	A	A	A	A	A	A	A	A
L. inundata	A	A	A	A	A	A	A	A	A	A	A	A
N. ossifragum	A	A	A	A	A	A	A	A	A	A	A	A
R. alba	A	A	A	A	A	A	A	A	A	A	A	A
U. minor	B	B	B	B	B	B	B	B	B	B	B	B
C. sororiata	B	B	B	B	B	B	B	B	B	B	B	B
C. tullia	A	A	A	A	A	A	A	A	A	A	A	A
L. dubia	B	B	B	B	B	B	B	B	B	B	B	B
M. brachyptera	A	B	B	A	B	B	A	A	B	A	B	B

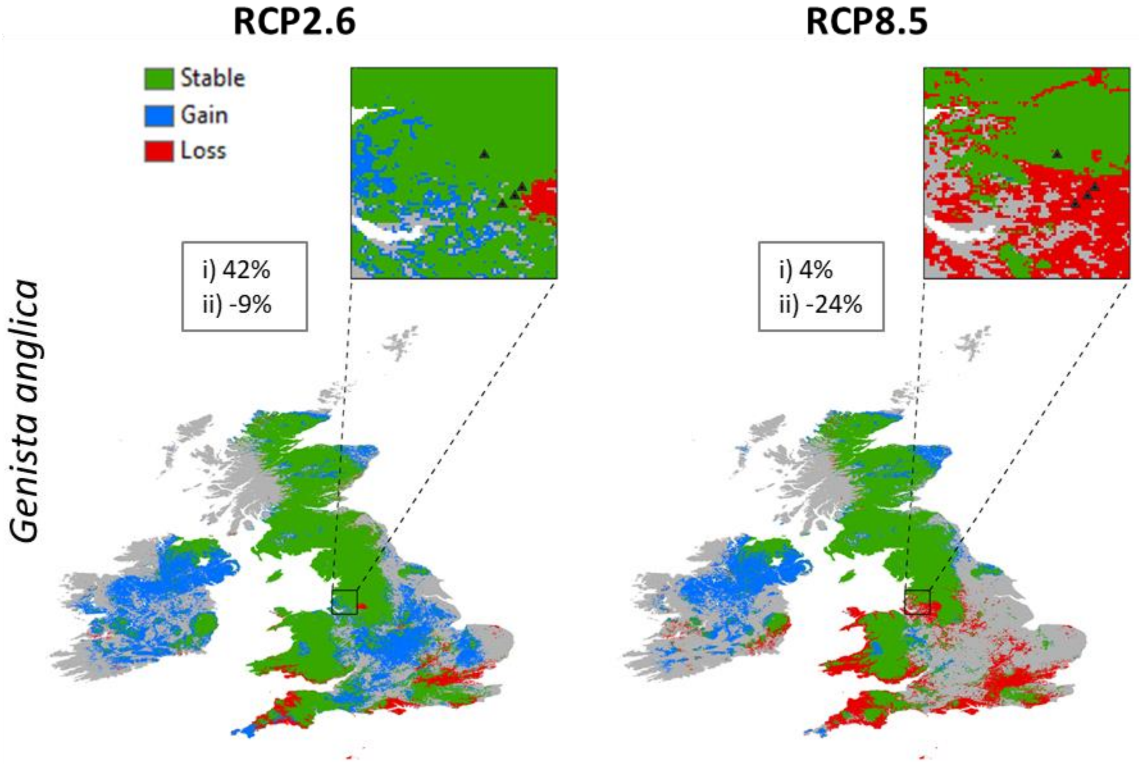
Table A5.2.4. Mean (min - max) coefficient of variation (CV) for suitability predictions at potential recipient sites. Average CV is presented for species distribution models (SDMs) and general circulation models (GCMs). SDM variation represents the mean CV between the 25 different SDMs that made up each species' ensemble model. GCM variation represents the mean CV between the 3 different climate change models for RCP2.6 and RCP8.5.

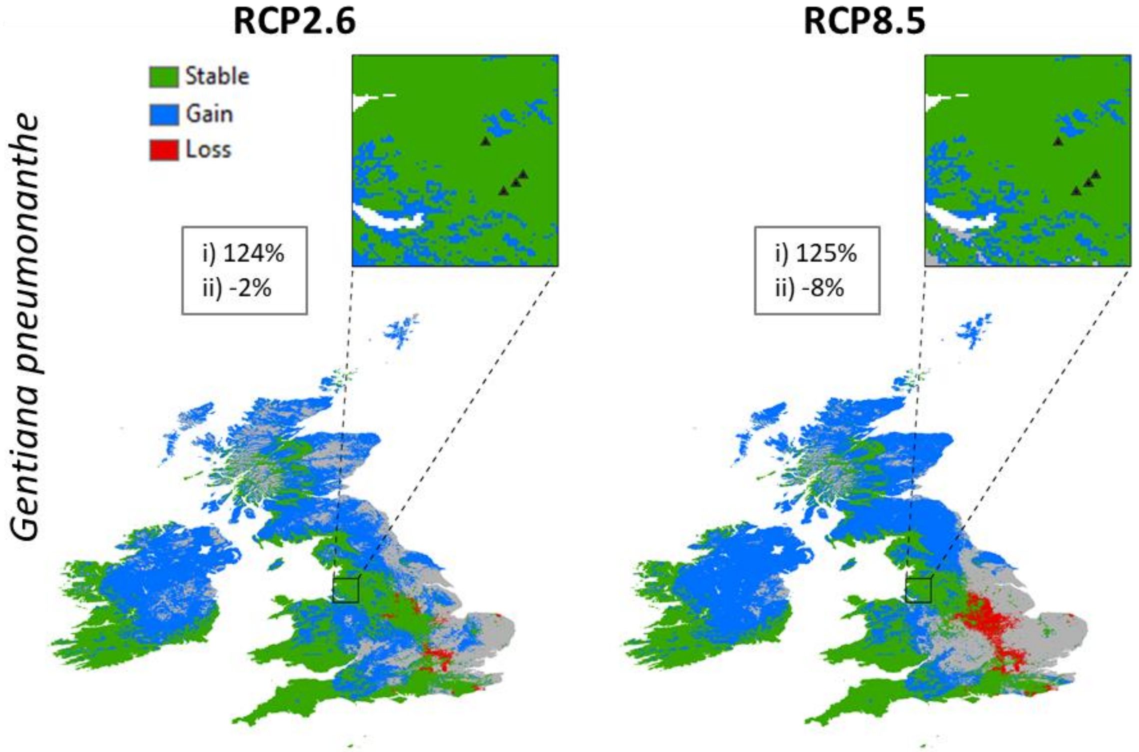
	Current	**RCP2.6**		**RCP8.5**	
	SDM	**SDM**	**GCM**	**SDM**	**GCM**

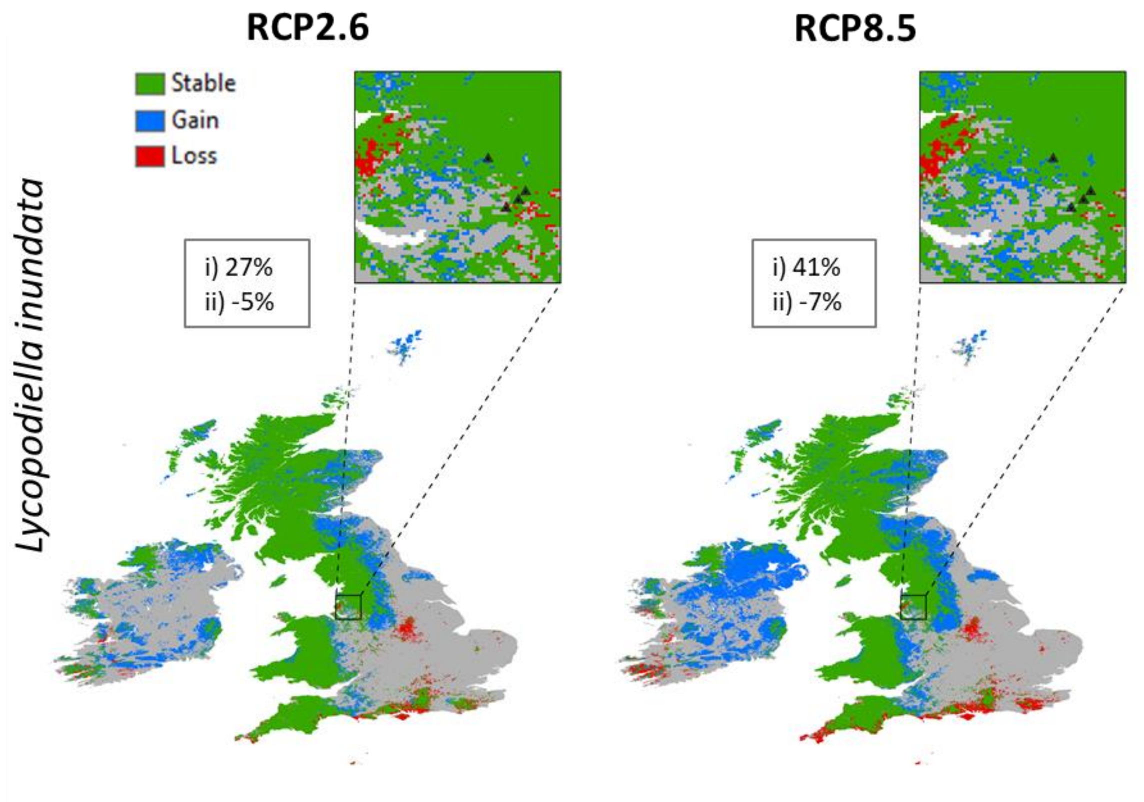
A. polifolia	46 (37-50)	61 (53-66)	25 (23-27)	62 (58-64)	18 (17-20)
D. anglica	69 (66-75)	71 (70-72)	25 (17-42)	78 (68-82)	27 (22-31)
D. intermedia	32 (27-39)	28 (23-36)	17 (15-18)	26 (23-29)	16 (11-19)
G. anglica	22 (8-33)	49 (29-59)	50 (19-74)	54 (52-55)	85 (72-97)
G. pneumonanthe	40 (32-55)	30 (26-35)	11 (10-13)	24 (22-28)	16 (15-17)
L. inundata	42 (36-54)	43 (41-44)	29 (25-34)	43 (42-44)	17 (12-20)
N. ossifragum	12 (9-14)	35 (22-43)	18 (7-23)	40 (29-48)	37 (20-43)
R. alba	46 (45-46)	38 (21-45)	32 (27-36)	30 (14-36)	28 (26-31)
U. minor	43 (40-47)	69 (60-76)	85 (61-99)	79 (77-82)	71 (67-73)
C. sororiata	74 (68-80)	136 (121-146)	43 (31-56)	133 (45-169)	34 (23-39)
C. tullia	38 (24-43)	39 (32-42)	8 (6-9)	40 (34-43)	9 (8-9)
L. dubia	76 (69-93)	114 (111-118)	48 (46-50)	120 (110-130)	46 (41-48)
M. brachyptera	45 (34-58)	71 (55-79)	65 (59-67)	88 (83-91)	51 (44-64)

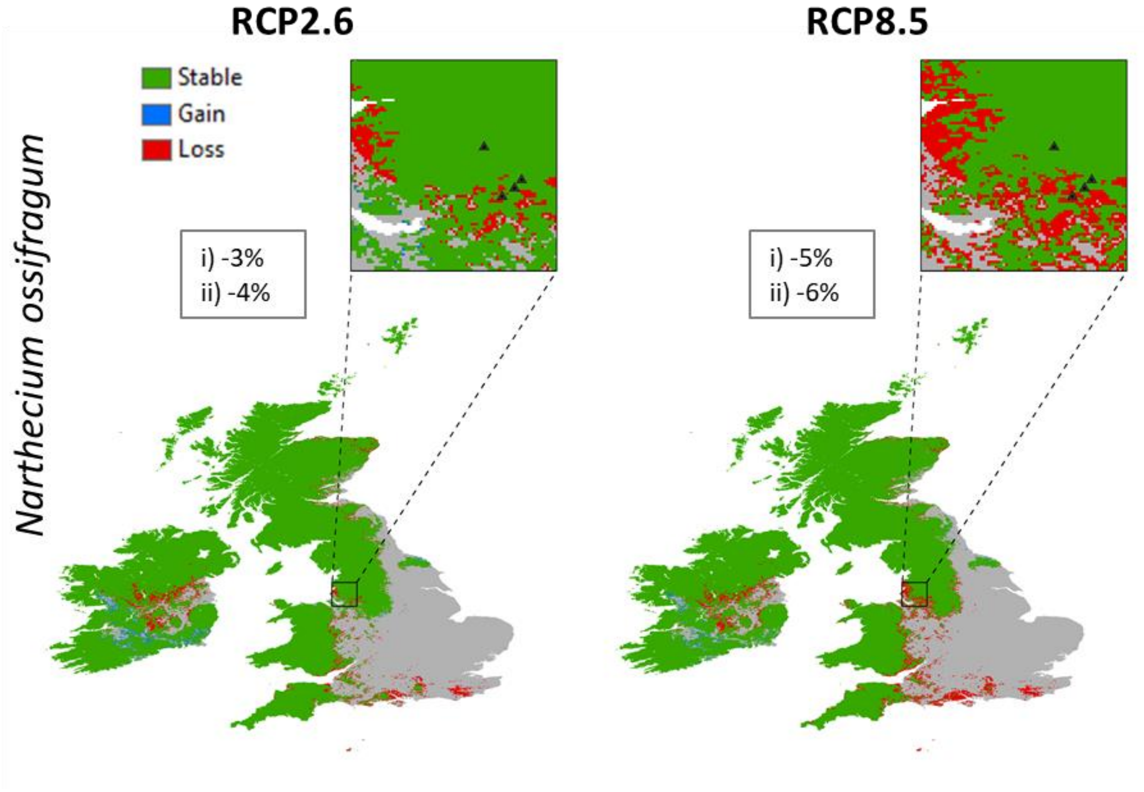


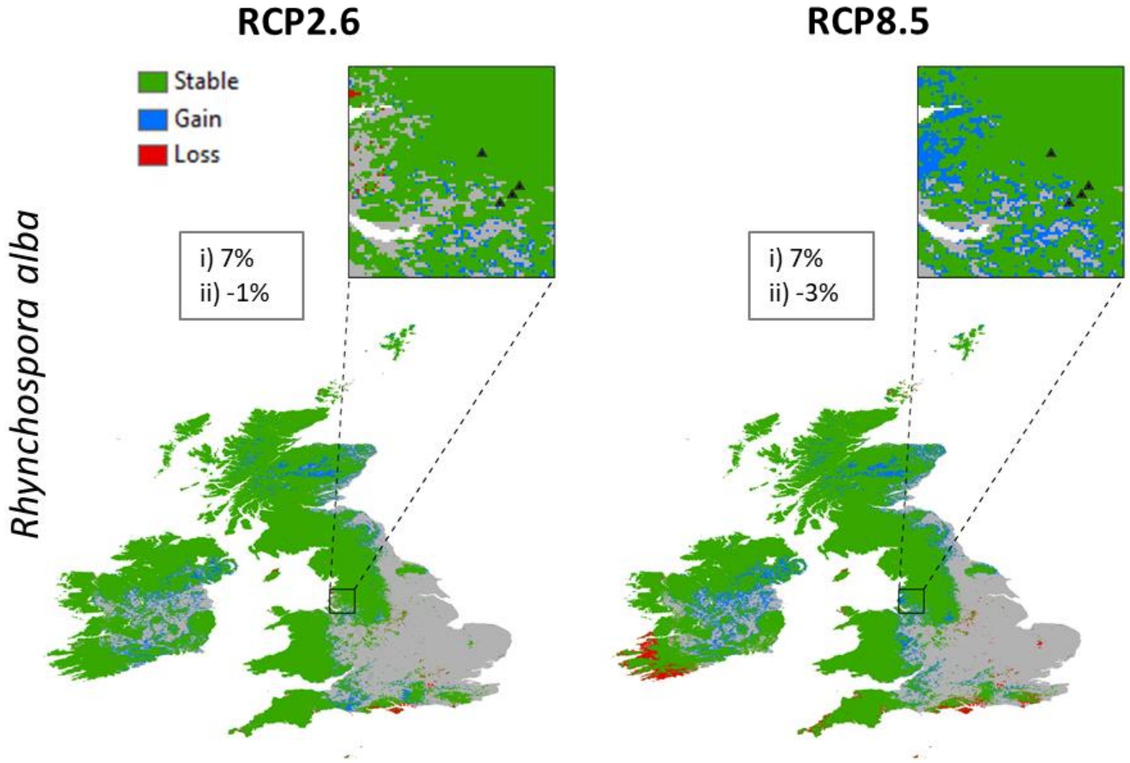

RCP2.6
RCP8.5
🟩 Stable
🟦 Gain
🟥 Loss
Drosera anglica
i) -30%
ii) -31%
i) -38%
ii) -42%
RCP2.6
RCP8.5
🟩 Stable
🟦 Gain
🟥 Loss
Drosera intermedia
i) 25%
ii) -1%
i) 27%
ii) -2%

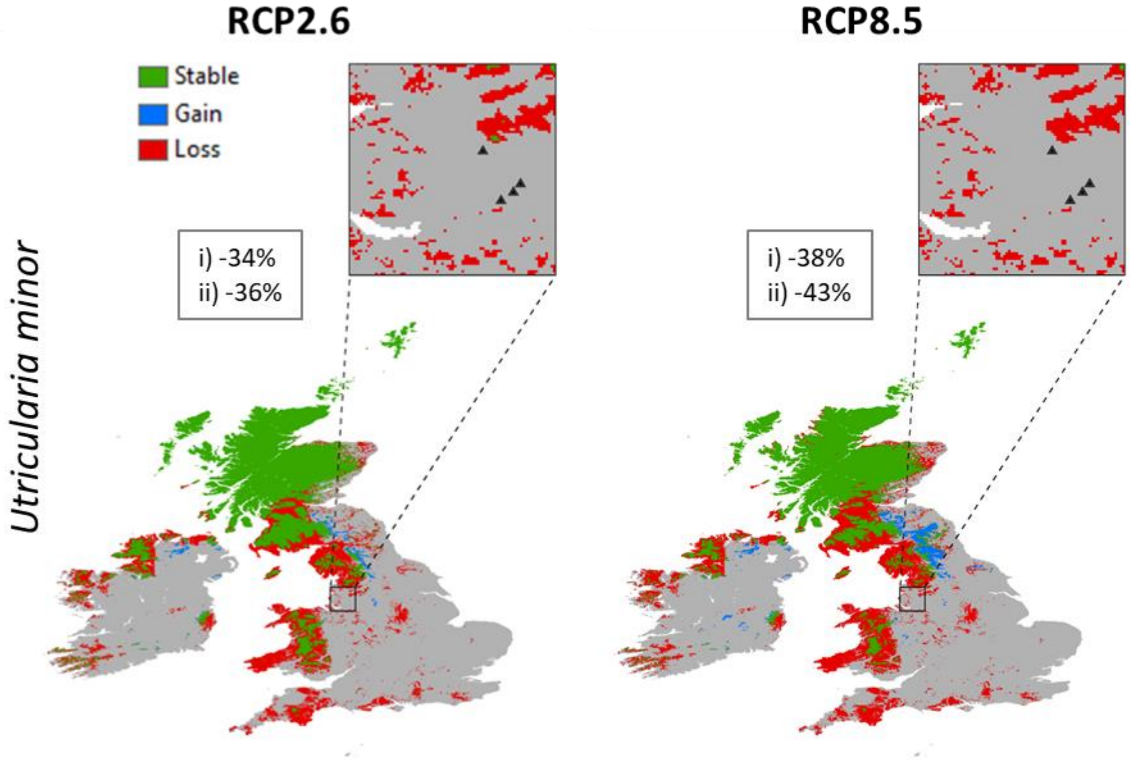

RCP2.6
RCP8.5
Genista anglica
🟩 Stable
🟦 Gain
🟥 Loss
i) 42%
ii) -9%
i) 4%
ii) -24%

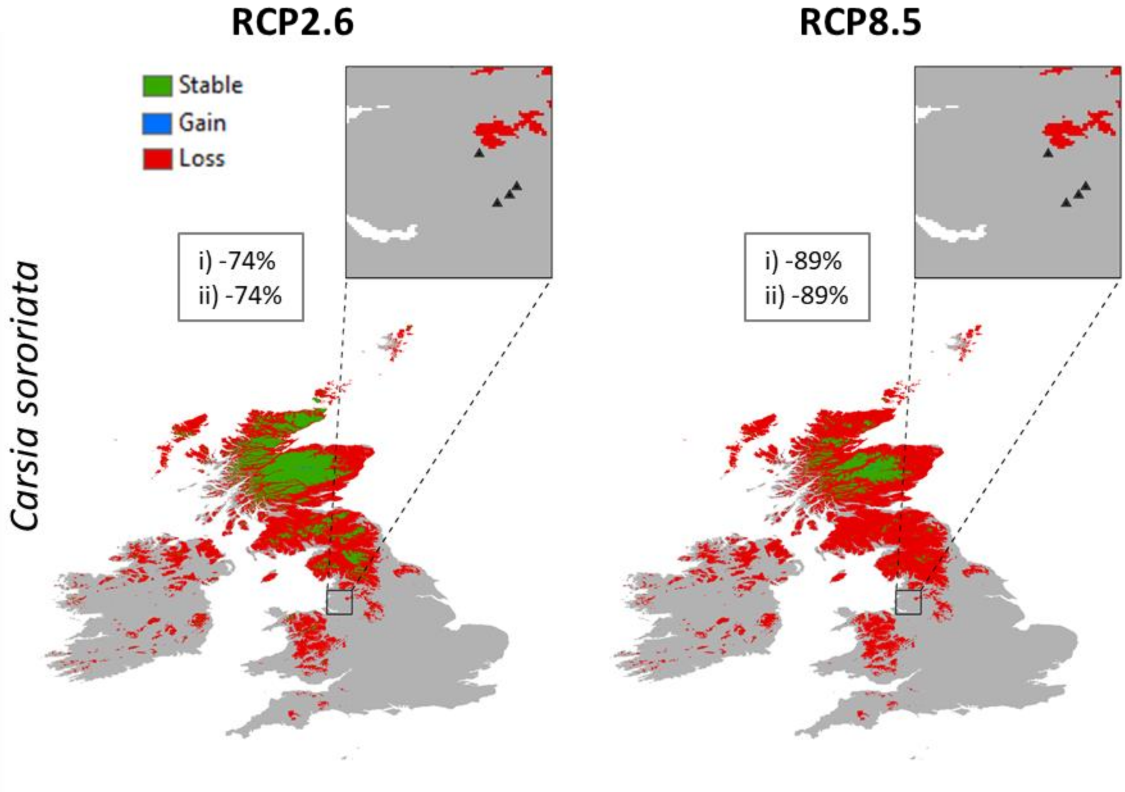

RCP2.6
RCP8.5
Gentiana pneumonanthe
🟩 Stable
🟦 Gain
🟥 Loss
i) 124%
ii) -2%
i) 125%
ii) -8%

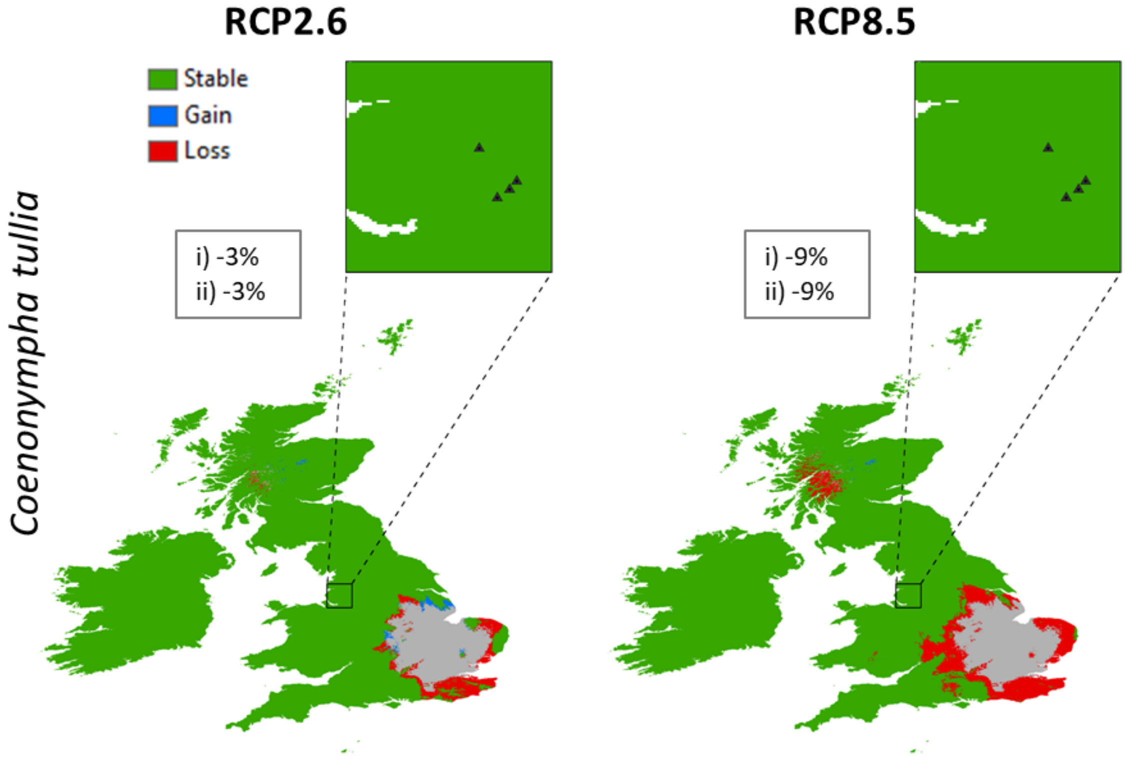

RCP2.6
RCP8.5
Lycopodiella inundata
🟩 Stable
🟦 Gain
🟥 Loss
i) 27%
ii) -5%
i) 41%
ii) -7%


RCP2.6
RCP8.5
Narthecium ossifragum
🟩 Stable
🟦 Gain
🟥 Loss
i) -3%
ii) -4%
i) -5%
ii) -6%


RCP2.6
RCP8.5
Stable
Gain
Loss
Rhynchospora alba
i) 7%
ii) -1%
i) 7%
ii) -3%


RCP2.6
RCP8.5
Stable
Gain
Loss
Utricularia minor
i) -34%
ii) -36%
i) -38%
ii) -43%


RCP2.6
RCP8.5
Carsia sororiata
🟩 Stable
🟦 Gain
🟥 Loss
i) -74%
ii) -74%
i) -89%
ii) -89%


RCP2.6
RCP8.5
Coenonympha tullia
🟩 Stable
🟦 Gain
🟥 Loss
i) -3%
ii) -3%
i) -9%
ii) -9%

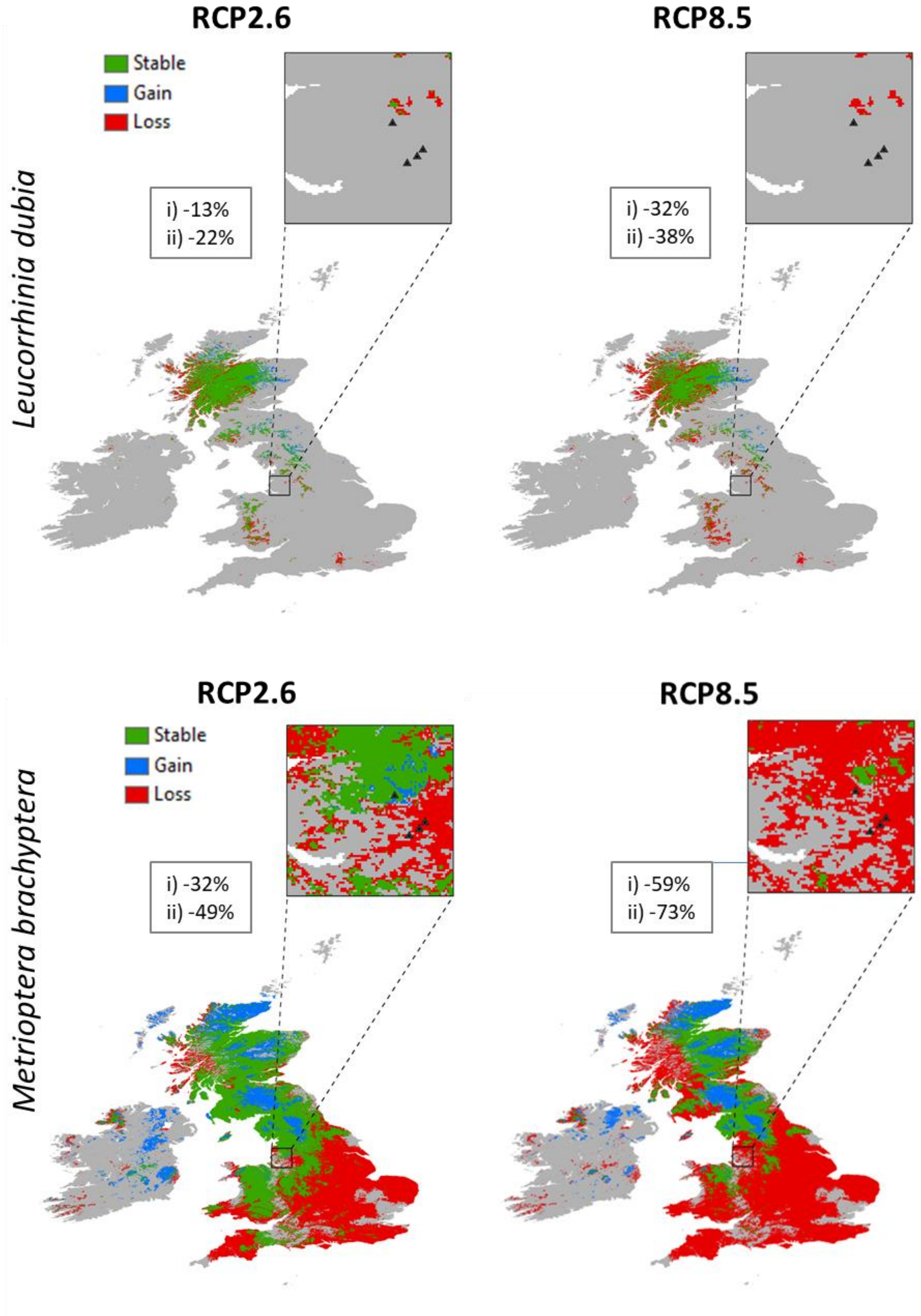


Figure A5.2.1. Predicted changes in suitable area across the U.K. and Ireland by 2041-2060 under RCP2.6 and RCP8.5 for nine plant and four insect species. The proportional change in overall suitability (i) and the proportional change in currently suitable cells (ii) are also shown.

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