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Climate change threatens the future viability of translocated populations

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Abstract

Aim: The dynamic nature of climate change diminishes the effectiveness of static approaches to nature conservation. Areas that were once suitable for species may no longer be suitable, and areas that are suitable now, may 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. In this study, we project changes in climate suitability for populations of ectothermic species that have been successfully established through translocation efforts.

Location: Biogeographical realms: Australasia, Holarctic, Palearctic and Nearctic.

Methods: We use species distribution models (SDMs) to project changes in macroclimatic suitability across 65 translocation recipient sites involving 38 ectothermic species. We consider optimistic (SSP126) and pessimistic (SSP370) scenarios of climate change for five general circulation models spanning three time horizons from 2021–2040 up to 2061–2080.

Results: Our models predict that at least 74% of recipient sites are projected to decline in climate suitability, regardless of the SSP scenario or time horizon. While recipient site suitability, scaled from 0 to 1 (low–high), was typically very high (>0.75, 39% of sites) under baseline climate conditions (1960–2010), models project a marked shift towards low suitability climates (<0.25, 40% of sites) by the middle of the century (2041–2060) onwards under the more pessimistic scenario. Relative to species' ranges, recipient sites located closer to the equator are projected to experience the most significant declines in suitability.

Main Conclusions: Our results call for greater consideration of spatiotemporal factors during the recipient site selection process, so that translocated populations are more strategically placed for long-term persistence under climate change.

KEYWORDS

amphibians, assisted colonisation, climate change, conservation translocation, insects, reintroduction, reptiles, species distribution models

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1 | 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 already 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 1°C, yet without major reductions in greenhouse gas emissions, a rise of 2°C or more is increasingly probable (Liu & Raftery, 2021). Consequently, many more declines and extinctions are likely (Hoegh-Guldberg et al., 2019), leading to a deterioration in ecosystem health and functioning (Pecl et al., 2017).

In the past, conservation has predominantly relied on a static approach, whereby protected areas are managed to maintain their species assemblages (McLaughlin et al., 2022). 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 static approach (Prober et al., 2019), as areas that were once suitable for a species may not continue to be, and areas that are suitable now, may be unsuitable in the future. These shifting conditions under climate change leave populations with four possible responses: migrate, adapt, decline, or face extinction (Davis et al., 2005). To effectively prevent species from local extinction, 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., Butt et al., 2020; Hoegh-Guldberg et al., 2008; Thomas, 2011). When selecting a recipient 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 with translocation programmes 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 S1). Of the 369 translocation programmes examined, 2% explicitly mentioned that climate change had been a consideration during the recipient site selection process (see Appendix S1 for list of projects). While recognising that papers and reports do not always provide detailed accounts

of translocation planning and implementation processes, this figure remains alarmingly low.

Currently, species distribution models (SDMs) represent the most widely proposed approach for assessing climate change impacts at prospective recipient sites (Chauvenet et al., 2013; IUCN, 2013; Krause & Pennington, 2012; Osborne & Seddon, 2012). Thoughtfully constructed 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., Butt et al., 2020; Chauvenet et al., 2013; Hoegh-Guldberg et al., 2008), there are very few cases where SDMs have been applied to reintroductions (but see Bellis et al., 2021; Maes et al., 2019) despite reintroductions being attempted far more frequently than assisted colonisation (e.g., Bellis et al., 2019; Bricchieri-Colombi & Moehrenschrager, 2016). Because assisted colonisation is often motivated by threats that are expected to increase in severity in the future (Chauvenet et al., 2013), the need to consider how changing climatic conditions may affect translocated populations is perhaps more discernible than for reintroductions, which are motivated by the recreation of historical conditions. Some reintroduction practitioners may also be deterred by 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). Nonetheless, when validated on previous translocation attempts (in both experimental and practical conservation settings), outputs from SDMs have correlated well with benchmarks of successful establishment (Bellis et al., 2020; Lee-Yaw et al., 2016), or with recent climate change-induced changes in abundance and distribution (Gregory et al., 2009; Stephens et al., 2016).

In this study, we use SDMs to estimate changes in the macroclimatic suitability of recipient 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 completed full lifecycles at their locations of release, demonstrating an alignment between recent environmental conditions and the species' physiological preferences (Bellis et al., 2020). However, with so few translocation programmes (<2%) explicitly factoring climate change into recipient site selection processes (Appendix S1), there is a risk that sites were chosen in areas where species' physiology and climate will misalign in the future (e.g., Soroye et al., 2020). Biogeographical theory suggests that misalignments caused by rising temperatures should pose the greatest threat to translocated populations located in the equatorial or lower elevational portions of the species range, since they are temporally closer to breaching thermal tolerances (Hampe & Petit, 2005). But it is unclear how much these elements of biogeographical theory have influenced the choice of recipient sites for ectotherms or other animal taxa (limited evidence in plant translocations, see Diallo et al., 2021). Here, we focus on three questions about climate change in the context of translocation. (1) What

percentage of translocated populations are threatened by projected climate change in the short (2021–2040), medium (2041–2060) and long-term (2061–2080)? (2) Are projected changes in recipient site suitability concordant with changes projected across species' global ranges? (3) Do spatial attributes of recipient sites associated with latitude and elevation influence the climate change exposure of translocated populations?

2 | METHODOLOGY

Our dataset comprises a subset of the amphibian, reptile and terrestrial insect conservation translocations that were defined as 'successful' in a peer-reviewed study by Bellis et al. (2020). This study established that conservation translocations had a higher probability of success in areas where SDMs predicted higher macroclimatic suitability. In the present study, we assume that this association between macroclimatic suitability and translocation outcome will hold true under future climate change.

The definition of success adopted in Bellis et al. (2020) was based on three criteria: (1) ≥ 10 years had elapsed between the time of most recent release and most recent monitoring, (2) the period between the most recent release and most recent monitoring exceeded the generation time of the species, and (3) the results of the most recent monitoring indicated individuals were still present. This is a generalised definition of translocation success, 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 65 recipient sites involving 38 species, including 9 amphibians (to 14 sites), 12 reptiles (to 26 sites), and 17 insects (to 25 sites).

Our sample predominantly consisted of species with temperate distributions (there were no tropical species), mostly centred in the Palearctic ($n=19$) and Nearctic ($n=13$) biogeographical realms (Table 1). Typically, species had large range sizes (e.g., 1,000,000–5,000,000 km²; $n=24$) and were distributed over wide latitudinal extents (e.g., 20–30°, $n=19$).

2.1 | Overview of species distribution models

To ensure that our work is transparent and reproducible, we complied with the Overview, Data, Model, Assessment, and Prediction protocol (ODMAP; Zurell et al., 2020). This metadata summary provides a detailed key to the steps of our SDM-based analyses and is presented in Appendix S3, alongside the full SDM methodology.

We compiled a database of occurrences for each species using records from the Global Biodiversity Information Facility (GBIF), New Zealand Department of Conservation, and relevant articles in the academic and grey literature (see Appendix S2). Each species

TABLE 1 Spatial summary of species translocated.

Parameter	Number of species
Biogeographical realm	
Australasia	4
Holarctic	2
Palearctic	19
Nearctic	13
Range size (km ²)	
<100,000	3
100,000–1,000,000	5
1,000,000–5,000,000	24
>5,000,000	6
Latitudinal extent (decimal degrees)	
<10°	3
10–20°	11
20–30°	19
>30°	5

occurrence dataset was carefully cleaned to account for coordinate imprecision, duplications of points, spatial biases and the presence of historical records. 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, 2022). All presence locations excluded during spatial thinning were then subsampled again (following the same approach) and used for ensemble model evaluation.

We downloaded baseline climate data from the WorldClim Database (v2.1) at a resolution of 2.5 arc-minutes (~4 km at the equator) for the period 1960–2010 (Fick & Hijmans, 2017). We selected nine bioclimatic variables known or presumed to be important in structuring the distributions of temperate ectotherms (Clusella-Trullas et al., 2011; Kozak & Wiens, 2007) and that had been selected a priori in previous SDM studies on the same taxonomic groups (Cabrelli et al., 2014; Carvalho et al., 2010; Ihlw et al., 2012). These variables describe annual averages of temperature and precipitation, seasonality, highest and lowest monthly values of temperature and precipitation, and growing degree days (GDD) (sum of all monthly temperatures greater than 5°C). We removed highly inter-correlated variables for each species based on the variance inflation factor (VIF) test, using a value of >10 (Dormann et al., 2013; Guisan et al., 2017) as an indicator of multicollinearity.

To simulate scenarios of future societal development under climate change, we focused on two shared socioeconomic pathways (SSP126 and SSP370) from the sixth phase of the Coupled Model Intercomparison Project (CMIP6) for three time horizons: 2021–2040, 2041–2060 and 2061–2080. The SSP126 scenario corresponds to a sustainable future in which there are low challenges to mitigation and adaptation, while the SSP370 scenario predicts

a future of regional rivalry in which there are high challenges to mitigation and adaptation (Riahi et al., 2017). We selected these two scenarios in order to represent two alternative, but realistic (Hausfather & Peters, 2020), futures: one highly optimistic future where global average warming is limited to 2°C by the end of the century (SSP126), and a more pessimistic future where warming may reach 4.4°C (SSP370) (Tebaldi et al., 2020). We selected five general circulation models (GCMs) with available data on WorldClim for our SSP scenarios from five separate research institutes based in Europe (CNRM-CM6-1, IPSL-CM6A-LR), Asia (MIROC6, MRI-ESM2-0), and North America (CanESM3). These five GCMs represent a wide range of equilibrium climate sensitivity values from 2.6°C (MIROC6) up to a maximum of 5.6°C (CanESM3) (Meehl et al., 2020). Equilibrium climate sensitivity is defined as the global mean surface air temperature change due to a rapid doubling of carbon dioxide concentrations as soon as the associated ocean-atmosphere-sea ice processes reach equilibrium.

For each time horizon and SSP scenario, we calculated the mean average of predictions across the individual GCMs to produce an ensemble and calculated the level of agreement using the coefficient of variation. The degree of model extrapolation under baseline and individual climate change projections was assessed for each species using a multivariate environmental similarity surface (MESS) analysis (Elith et al., 2010). The MESS analysis measures the similarity of any given point (grid cell in projected climate data) to a reference set of points (grid cells in baseline climate data used to fit SDMs), with respect to the chosen predictor variables. It reports the closeness of the point to the distribution of reference points, assigning negative values for dissimilar points and maps these values across the whole prediction region.

We adopted an ensemble SDM approach with five algorithms implemented in the package *biomod2* (v. 3.3-7) in R. Evidence in the tree ensemble literature suggests that ensembles work best when the component models are not highly correlated (Elith, 2019), therefore, we selected a set of algorithms with a range of fitted functions and model fitting approaches: Generalised Additive Model (GAM), Multivariate Adaptive Regression Splines (MARS), Generalised Boosted Model (GBM), Random Forest (RF) and Maxent (Thuiller et al., 2016). As we were reliant on presence-only data, we generated pseudo-absences for each SDM by randomly selecting unoccupied cells within an extended version of the species range extent (see Appendix S3) according to the number of presences after spatial thinning N (if $N \leq 1000$ then 1000 pseudo-absences were selected, otherwise 10,000 pseudo-absences were selected) (Barbet-Massin et al., 2012; Bellard et al., 2016). Because we used pseudo-absences instead of true absence data and suitability values were not real occurrence probabilities (Guillera-Aroita 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: $(x - \min) / (\max - \min)$.

The accuracy of individual models was evaluated using the area under the curve (AUC) and the true skill statistic (TSS) based on a

cross-validation procedure with five repetitions (70% of records selected for model calibration and 30% set aside for model testing). To assess the calibration accuracy of our SDMs, we evaluated the final ensemble model with the continuous Boyce index (CBI) (Hirzel et al., 2006), according to the independent set of records that had been removed from each species occurrence dataset during spatial thinning.

2.2 | Quantifying and comparing suitability change

Suitability change was calculated by measuring the difference between the baseline and future predicted suitability at each recipient site (the cells selected to represent sites were defined according to the methodology described in Bellis et al., 2020). To account for the varying magnitude of suitability declines across recipient localities, we categorised losses into “minor decline” (<0.25), “moderate decline” (0.25–0.50), and “severe decline” (>0.50).

To establish whether site-level changes in suitability were concordant with wider trends, we compared recipient site suitability change with species' global averages. 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 computing the median average across suitability predictions. To statistically compare recipient site-scale suitability change with global predictions, we computed multiple paired Wilcoxon Signed-Rank tests (significance set at $p < .05$).

2.3 | Spatial attributes of recipient sites

We selected two spatial attributes of recipient sites that could potentially be associated with climate change exposure: Latitude relative to latitudinal mean of distribution (LatDiff) and elevation relative to elevational mean of distribution (ElevDiff). We calculated LatDiff for each translocation by measuring 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 reversed to negative and vice versa, to allow comparison with translocations in the northern hemisphere.

We calculated ElevDiff using the same approach as for LatDiff. As our sample did not consist of any alpine specialists, which are highly vulnerable to climate change (Habel et al., 2011), we expected a positive relationship between ElevDiff and the favourability of predicted suitability change at recipient sites.

2.4 | 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 baseline and projected future conditions. LatDiff and ElevDiff were fixed effects (explanatory variables in standard linear regression), and species was set as a random effect. We tested for multicollinearity among the spatial attributes using the Variance Inflation Factor (VIF), implemented in R with the package *car* (v. 3.0–2) (Fox, Weisberg, et al., 2019). Each spatial attribute had a VIF of <2, indicating minimal correlation between predictors (Quinn & Keough, 2002). We standardised LatDiff and ElevDiff in order to 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). We also ran LMMs without standardisation, since the absolute values of latitude and elevation improved interpretation. In the ElevDiff 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* was visually identified as an outlier in the LatDiff dataset, thus this record was also omitted from our statistical analyses.

3 | RESULTS

3.1 | Model evaluation

The SDMs of the final species set ($n=38$) generally had high discrimination metric values (AUC: mean [minimum–maximum]=0.909 [0.810–0.978]; TSS: 0.659 [0.480–0.903]) (Table A2.1), indicating good discrimination capacity. Similarly, evaluations of calibration accuracy indicated that ensemble models performed well on average (CBI: 0.971 [0.839–0.999]).

3.2 | Model extrapolation

The MESS analyses indicated that 87% of the recipient sites had no extrapolation issues under baseline climate conditions or future projections. Among the recipient 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. The remaining 3% of translocations covered two recipient sites involving *Boloria eunomia* and in both cases the extrapolation (<-20) was detected under the CanESM5 model based on the SSP370 scenario for the period 2061–2080.

3.3 | Predicted suitability and projected changes

Our SDMs predicted that translocated populations were most commonly located at recipient sites with very high macroclimatic suitability (0.75–1; $n=25$) (Figure 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 the middle of the century onwards, more translocated populations were projected to be in the lowest suitability classification (0–0.25) than in any other classification, with 34% ($n=22$) of recipient sites under SSP126 (Figure 1a) and 40% ($n=26$) under SSP370 (Figure 1b) falling within this bracket.

Climatic suitability at recipient sites is predicted to decline for most species regardless of SSP scenario, GCM, or time horizon (Table 2; Appendix S4). By the middle of the century, SDM outputs indicated that around three quarters of recipient sites will undergo a deterioration of climate suitability, irrespective of the SSP scenario. While the direction and magnitude of predicted suitability change varied greatly across recipient sites (Figure 2; Table 2), a minor decline (<0.25) in suitability was the most commonly projected consequence of climate change (33.8%–47.7% of sites depending on the scenario/time period). However, there was a notable increase in the proportion of recipient sites projected to undergo a moderate decline (0.25–0.50) in both 2041–2060 and 2061–2080 under the SSP370 scenario, where this was the most represented category (Table 2; Table A4.1).

3.4 | Comparing suitability change across spatial scales

On average, suitability was projected to decline across most species' global ranges in the future (Figure 3; Figure A4.2). The magnitude of projected suitability change tended to be less severe for recipient sites than changes projected across the rest of species' ranges, with 64.6%–69.2% of recipient sites faring better than the global median, depending on the time horizon and SSP scenario (Figure A4.2). Differences in predicted suitability change between recipient sites and species' global medians were statistically significant under all climate change projections according to Wilcoxon signed-rank tests ($p < .01$, $n=6$).

3.5 | Spatial attributes of recipient sites

The latitudinal distance between recipient site and distribution centre (LatDiff) indicated slightly more sites were located in the poleward half (54%; $n=35$) of species' ranges. Recipient sites were on average 1.24 decimal degrees (median=0.62°) polewards of species' latitudinal centres, with a notable proportion of sites located close to latitudinal centres (37%; $n=24$, falling within $\pm 1^\circ$ of the centre). Outputs from LMMs consistently predicted a statistically significant association between LatDiff and recipient site suitability change

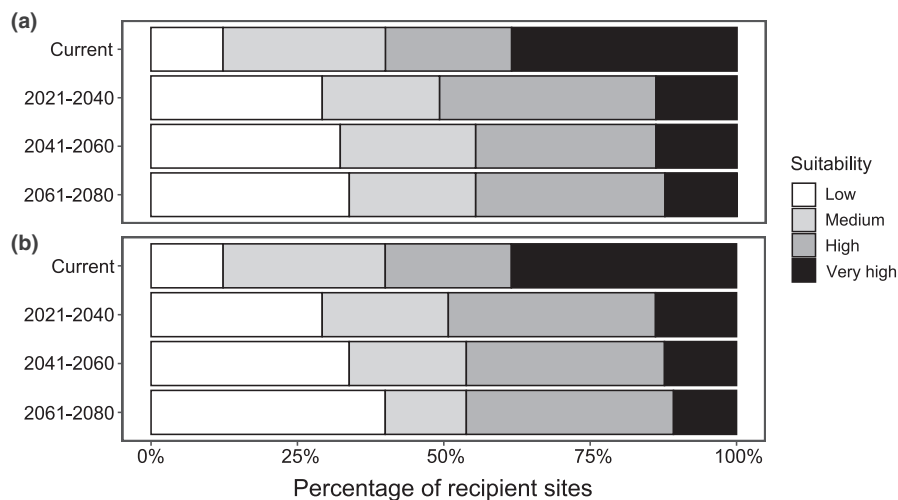


FIGURE 1 Predicted standardised suitability of translocation recipient sites ($n=65$) under baseline macroclimatic conditions and future projected conditions for 2041–2060 under SSP126 (a) and SSP370 (b). Future projections have been averaged across 5 GCMs for each SSP scenario. Suitability categorisations are as follows: Low = <0.25 , Medium = $0.25-0.50$, High = $0.51-0.75$ and Very high = >0.75 .

(Table A4.2), with the favourability of suitability change increasing as the poleward distance from distribution centre increased (Figure 4; Figure A7.3). By the middle of the century, recipient sites oriented close to the latitudinal centre of species' distributions were generally projected to experience minor or moderate declines in suitability (Figure 4). In contrast to the LatDiff variable, the effect of elevation relative to the elevational mean of distribution (ElevDiff) was considerably weaker and was not statistically significant under any climate change scenario (Table A4.2). The majority of recipient sites (91%; $n=59$) were located below the elevational mean of species' ranges at an average of 238m lower (median = 242m). The translocation of *Pelobates syriacus* to an elevation of 1609m above the species average represented a notable outlier, with this population projected to experience the largest gains in suitability of any translocation considered (e.g., Figure 2).

4 | DISCUSSION

While our sample of 65 recipient sites have supported the successful establishment of translocated populations, three quarters are projected 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 majority of recipient sites are in areas of very high suitability under baseline climates (>0.75). However, our SDMs predict a marked shift in suitability, with more than a third of recipient sites projected to be located in low suitability (<0.25) by the middle of the century onwards. These findings are concerning given that 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).

Due to the physiological sensitivities of ectotherms to temperature and other components of climate (e.g., rainfall), their fitness is expected to be particularly threatened by climate change (Kingsolver

TABLE 2 Percentage of recipient sites predicted to decline in suitability across six climate change projections (percentages are calculated from a total of 65 sites).

Scenario	Minor decline	Moderate decline	Severe decline	Total
2021–2040				
SSP126	46.2 (8.3)	23.1 (8.0)	4.6 (0.7)	73.8 (2.5)
SSP370	47.7 (6.1)	24.6 (7.5)	3.1 (2.3)	75.4 (3.5)
2041–2060				
SSP126	40.0 (4.7)	33.8 (8.0)	1.5 (1.4)	75.4 (6.1)
SSP370	35.4 (4.6)	35.4 (8.9)	4.6 (1.3)	75.4 (7.8)
2061–2080				
SSP126	44.6 (5.3)	27.7 (5.6)	1.5 (1.7)	73.8 (4.2)
SSP370	33.8 (3.6)	38.5 (5.0)	6.2 (2.3)	78.5 (4.0)

Note: Results are compared across three suitability change categorisations (minor decline = <0.25 , moderate decline = $0.25-0.50$, and severe decline = >0.50). Future projections have been averaged across five GCMs for each SSP/time period combination. Numbers in parentheses show the variability of predicted declines according to the standard deviation of the five GCMs.

et al., 2013). Rising mean temperatures along with increasing inter-annual variability and extreme temperature events threaten organismal performance by exceeding thermal optima and critical thermal maximum levels (Clusella-Trullas et al., 2011; Ma et al., 2021; Vasseur et al., 2014). While global mitigation efforts aim to reduce the severity and frequency of these climate alterations, similarities in the direction of suitability change between the scenario with low challenges to mitigation and adaptation (SSP126) and the scenario with high challenges (SSP370) (Table 2; Figure 2) indicate that these efforts will be insufficient to prevent suitability declines for the majority of our sample of translocated populations. Nonetheless, in the more optimistic scenario, the magnitude of suitability decline is projected to be less severe towards the end of our modelling period (2061–2080), indicating that global mitigation efforts could help to reduce the number of species that will experience moderate ($0.25-0.50$) to severe (>0.50) deterioration of climate conditions.

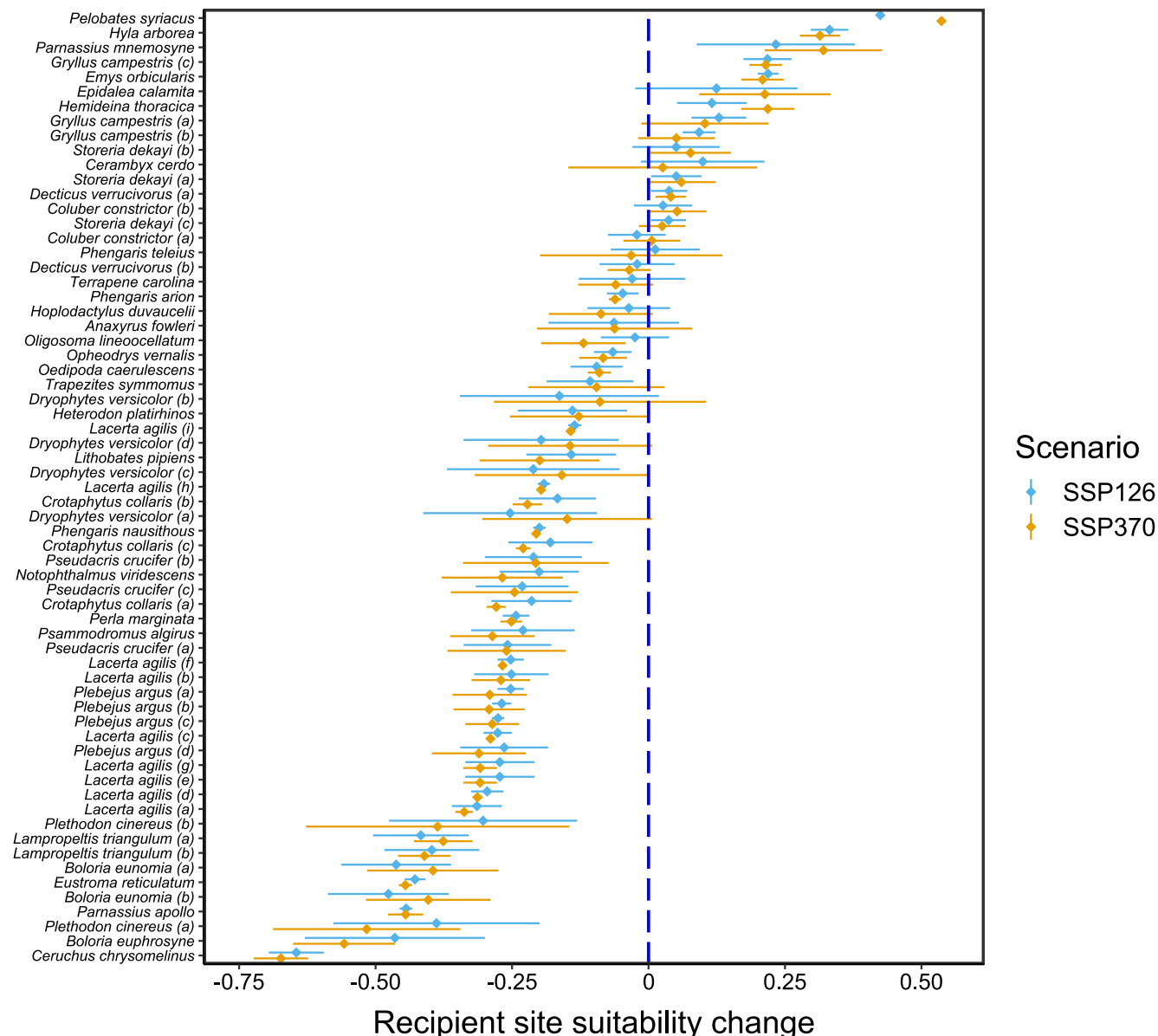


FIGURE 2 Mean (SD) projected changes in standardised climate suitability at 65 translocation recipient sites between baseline conditions and those projected for mid-century (2041–2060), according to two different climate change scenarios: SSP126 and SSP370. Future projections have been averaged across 5 GCMs for each SSP scenario. Letters following species' names indicate different recipient sites for the same species. Outputs for 2021–40 and 2061–2080 are presented in [Figure A4.1](#).

Whether the projected declines will lead to population extirpations will depend on multiple factors, such as the availability of microhabitats (De Frenne et al., 2019), the adaptability of the species (Fox, Donelson, et al., 2019), the effectiveness of management interventions (Greenwood et al., 2016), and the magnitude of suitability decline. Since most terrestrial ectotherms exhibit behavioural thermoregulation that allows them to exploit local heterogeneity in temperature by shifting time or place of activity (Sunday et al., 2014), the persistence of populations in climatically deteriorating environments could be aided via the creation or maintenance of cool microhabitats to avoid heat stress.

Although a majority of recipient sites are projected to decline in suitability, they performed slightly, but significantly, better under

projected climate change than species' averages ([Figure 3](#)). While this is encouraging, the findings from our keyword search ([Appendix S1](#)) suggest that this result is most likely coincidental rather than the outcome of some coordinated forward-looking approach to recipient site selection. Since our sample predominantly consisted of widely distributed species from the Palearctic and Nearctic ([Table 1](#)), with translocations most frequently undertaken in two known translocation hotspots (north-western Europe and the north-eastern United States, Brichieri-Colombi & Moehrensclager, 2016; Diallo et al., 2021), recipient sites generally sit on or above the latitudinal core of species' ranges making them less vulnerable to climate change in the near-term than populations closer to the equator (Araújo et al., 2006). The likelihood that this finding is coincidental is

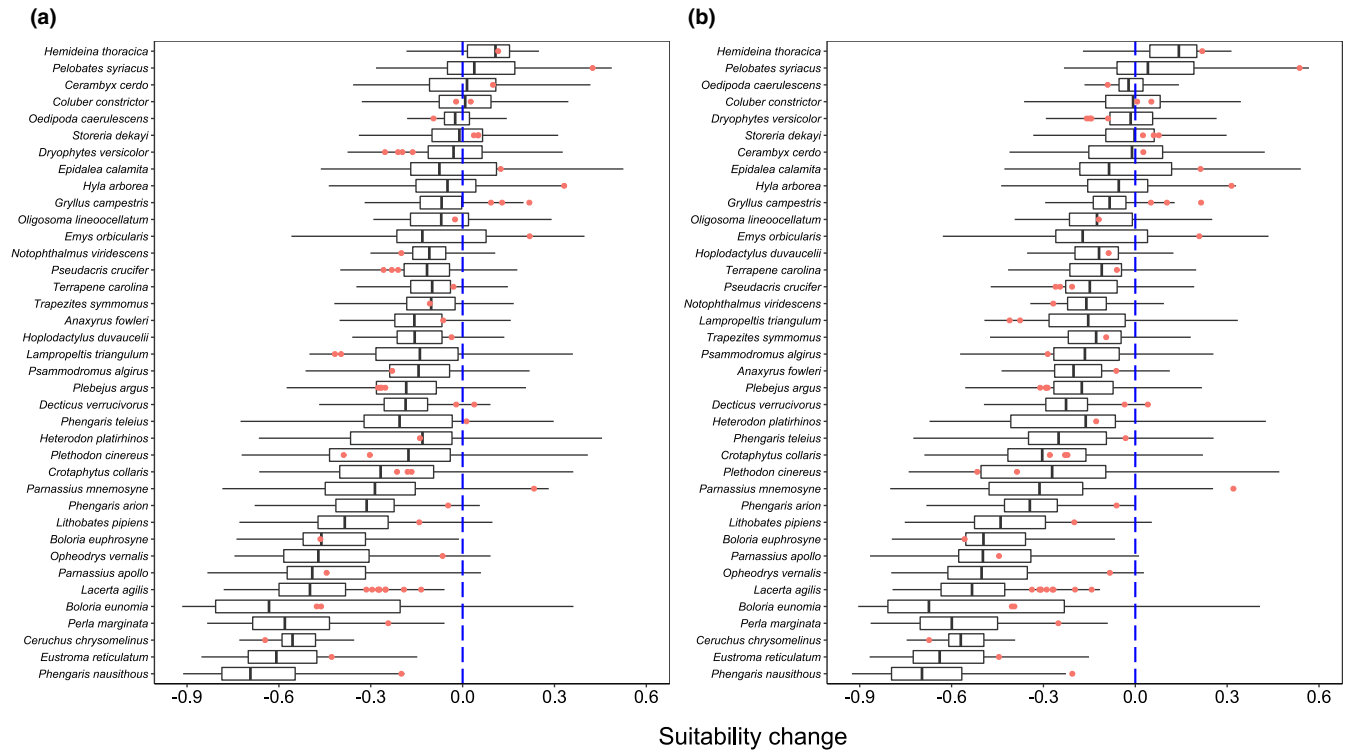


FIGURE 3 Average projected change in suitability across species global ranges by 2041–2060, according to two different climate change scenarios: SSP126 (a) and SSP370 (b). Red dots represent predicted suitability change for translocated populations. Future projections have been averaged across 5 GCMs for each SSP scenario. Outputs for 2021–40 and 2061–2080 are presented in Figure A4.2.

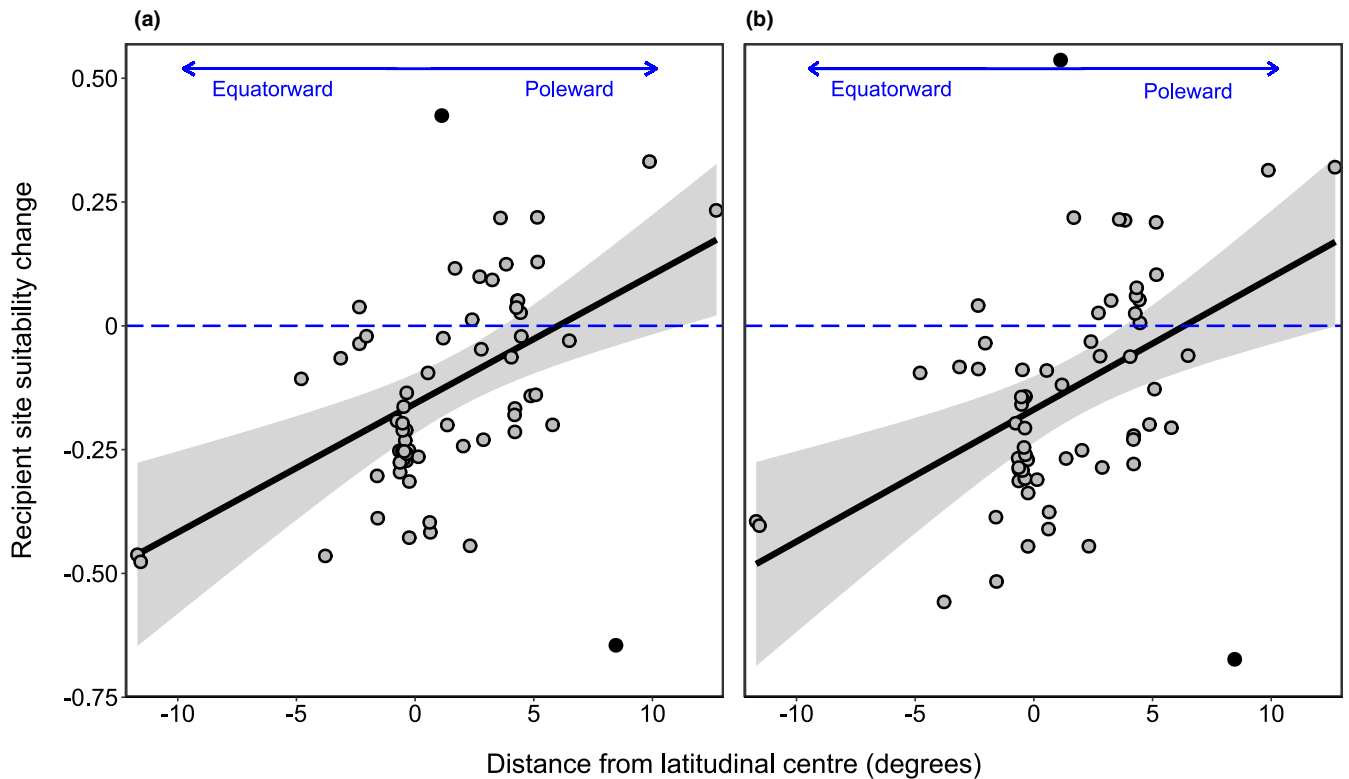


FIGURE 4 Effect of distance from latitudinal centre (decimal degrees) on projected changes in macroclimatic suitability at recipient sites, according to SSP126 (a) and SSP370 (b) for the period 2041–2060. The two black dots (upper = *Pelobates syriacus*; lower = *Ceruchus chrysomelinus*) represent outliers that were omitted from the LMMs. Effect plots for other time horizons are presented in Figure A4.3; standardised effect plots are presented in Figure A4.4.

further supported by a recent meta-analysis concentrating on plant translocations in the Western Palearctic, which concluded that climate change considerations were rarely taken into account when selecting recipient sites and much greater consideration would be necessary moving forward (Diallo et al., 2021). Indeed, most conservation translocations are undertaken over short-distances (Bellis et al., 2019; Diallo et al., 2021; Skikne et al., 2020) to address local threats and satisfy local conservation objectives (Bubac et al., 2019), which may explain why so few appear to factor climate change in to recipient site selection processes.

Due to the overarching influence of latitude on global temperatures, one way to buffer translocated populations from the effects of climate change is to select recipient sites closer to the poles. The latitude of recipient sites relative to the latitudinal mean of distribution (LatDiff) proved to be a useful indicator of SDM-derived climate change vulnerability in our analyses, concordant with previous studies where populations located closer to equatorial range margins were identified as the most vulnerable to climate change (e.g., Araújo et al., 2006; Bell et al., 2014; Cheaib et al., 2012). In the mid-century SSP370 scenario, all but one of the recipient sites situated in the equatorial half of species' distributions were predicted to decline in suitability (Figure 4). Populations located in these warmer portions of species' ranges are typically operating in conditions that are closer to the species' maximum heat tolerance, making them more immediately threatened by rising temperatures (e.g., Lesica & Crone, 2017; Nicastro et al., 2013). Given the high risk of suitability decline, translocation programmes aiming to secure long-term population viability would be sensible to avoid locations in the equatorial portion of species' ranges, unless outputs from spatiotemporal models suggest otherwise.

The elevation of recipient sites relative to the wider species range had little effect on predicted suitability change when modelled using LMMs. However, there was a lack of higher elevation translocations in our sample, with just one release, of *Pelobates syriacus*, above 1000m. 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 relative to baseline conditions (e.g., Figure 2). Temperature changes rapidly with rising elevation; a simple altitude-for-latitude model estimates that a fall in temperature of 1°C that occurs with an increase of 167m altitude is equivalent to a 145 km change in latitude (Jump et al., 2009). Consequently, mountains may represent an opportunity for conservation managers to translocate species over shorter geographical distances, which tends to result in higher post-release survival (Skikne et al., 2020), while gaining the level of climate stability equivalent to a translocation of hundreds of kilometres in latitude.

The diversity of LatDiff values in our dataset demonstrates the macroclimatic stability and gains obtainable through longer distance poleward translocations (Figure 4). As conservation translocations often focus on species with small geographic ranges, the distances required to move them into areas of stable suitability could equate

to translocations beyond their indigenous range, i.e., an assisted colonisation (IUCN, 2013). Despite the well-documented risks and uncertainties (Butt et al., 2020; Chauvenet et al., 2013; Ricciardi & Simberloff, 2021), there appears to be a growing recognition that assisted colonisation may be the only option for safeguarding some species (Prober et al., 2019), with SDMs often promoted as a tool that can support the identification of candidate species and recipient sites for these types of projects. Our sample of translocations consisted of two assisted colonisation projects (involving *Boloria eunomia*). Importantly, both of these projects were located in cells that were flagged by our MESS analyses for extrapolation into novel climate space. Assisted colonisation projects could frequently encounter this issue because climatically secure recipient sites may be located in conditions that are not represented in species' current geographical ranges. Consequently, we highly recommend integrating a measure of extrapolation between the conditions used for model calibration and transfer in assisted colonisation projects, so that model uncertainties can be quantified and incorporated into decision making (Yates et al., 2018).

By focusing only on climatic variables when modelling suitability change at recipient sites and across species' ranges, we disregard other processes that may determine the future persistence and distribution of species. In addition to climate, biotic interactions, dispersal, demography, adaptive potential, land-cover and land-use, and other abiotic factors (e.g., geology, soil, hydrology and topography) determine where a species can and will be able to survive (Sexton et al., 2009). Current data for most abiotic factors are available on public repositories (e.g., Amatulli et al., 2020; Lehner et al., 2008; Poggio et al., 2021) and can be added as additional predictor variables in SDMs. While data on future projections of these variables at conservation-relevant scales are more limited, progress has been made on the development of land-cover and land-use change projections (e.g., Li et al., 2017). Although the classification system of these projections is coarse (limited to six categories), this information may be helpful for establishing which regions to avoid in a translocation project due to, for example, projected expansion of urban or agricultural land.

As an alternative to the correlative SDMs computed in the present study, process-based modelling frameworks such as RangeShifter (Bocedi et al., 2021) and poems (Fordham et al., 2021) allow the integration of information on dispersal and population dynamics for modelling future suitability. Careful construction of process-based models can result in more insightful and reliable predictions about where to translocate species for future viability. However, these models require precise parameterisation and a large amount of data to function effectively, limiting their use for most species due to data deficiencies (Sequeira et al., 2018). Consequently, for translocation practitioners considering using spatial modelling techniques to identify recipient sites with long-term viability (which we would encourage), they must strike a balance between a model's predictive power and the availability of biotic and abiotic data.

Calls for a more proactive approach to conservation management (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 declining populations, properties that are not typically associated with a capacity to adapt. 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 recipient sites that are projected 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.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

DOIs for the occurrence data downloads used in the SDM-based analyses of the paper are uploaded as Data S1. The climate data that support this study are available from the WorldClim website (<https://www.worldclim.org/>). Where available, range maps were downloaded from the IUCN Spatial Data Download page (<https://www.iucnredlist.org/resources/spatial-data-download>) or, in the case of reptiles, from the Global Assessment of Reptile Distributions (<http://www.gardinitiative.org/>).

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BIOSKETCH

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SUPPORTING INFORMATION

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

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