Climate suitability as a predictor of conservation translocation failure

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Accepted by *Conservation Biology*, 10 April 2020

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 five other variables frequently considered in the literature to be 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. We found that the probability of translocation success increased with predicted climate suitability and this effect was the strongest amongst the variables considered in our analysis, 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 of doing this.

Introduction

Threatened species management is increasingly involving more interventionist forms of conservation action 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 the origin of the source population (Cayuela et al. 2019), the length of supplementary feeding (White et al. 2012), the life stage of individuals released (Muths et al. 2014) and the 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, with very few translocation projects explicitly citing 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). SDMs identify statistical relationships between species occurrence and environmental descriptors. However, SDMs have recognized 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; 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/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. Cook in prep; Dempster & Hall 1980; Kuussaari et al. 2015).

In this paper, we analysed data extracted from the available 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), the duration of releases (Griffith et al. 1989), the 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). Our study represents the first global comparative analysis on 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.

Methods

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. As 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 found in these reviews. The herpetofauna reviews only covered literature up until 2006, thus, for relevant literature published post-2006 (until 2018) we performed our own search on the 'Thomson Reuters 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 colonization OR assisted colonisation 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 Supporting Information 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 1; Supporting Information).

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 standardized definition of translocation success, but note that alternative metrics such as a translocated population's finite rate of increase (growth rate predicted when the sex and age distribution stabilizes) have been used (Armstrong & Reynolds 2012). We defined translocations as successful if they met the following three criteria: i) ≥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. We applied a 10-year minimum threshold in order to reduce the potential for abnormally favourable conditions following release to have temporarily benefitted the translocated species. Enforcing criterion ii led to the omission of seven translocations, all of which involved turtle or tortoise species with generation times exceeding 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 (see Supporting Information for full eligibility criteria).

Species distribution models

Species and climate data

We downloaded species occurrence data from the Global Biodiversity Information Facility (GBIF). As 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 in order to model the full extent of their climatic niche (Barbet-Massin et al. 2010; Raes 2012). We quality control checked each species occurrence dataset and reduced spatial bias caused by unequal sampling (Supporting Information). We downloaded current climate data from the WorldClim Database at a 30 arc-second resolution (Fick & Hijmans 2017) for 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), describing annual averages, seasonality and highest/lowest monthly values of temperature and precipitation. Based on recommendations made in Barbet-Massin et al. (2012), pseudo-absences were sampled at random from the background extent for each species, weighted to reach an equal prevalence with presence records (see Supporting Information for more details).

Modeling approach

We used an ensemble of species distribution model algorithms in order to minimise the uncertainty associated with single modeling 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 (v. 3.3-7) (Thuiller et al. 2016) in R v. 3.5.1 (R Core Team 2018). We evaluated model performance using the receiver operating characteristic to determine an area under the curve (AUC) (Supporting Information). In order to make SDM predictions comparable across species, we standardized the predicted climate suitability values to range between 0 and 1 with the following formula: (x - min) / (max - min). Using the standardized outputs, we extracted the climate suitability values for the 1 x 1 km grid cell(s) corresponding to the location of each translocated population (Supporting Information).

Statistical analysis

We fitted a binomial multivariate generalized linear model with mixed effects (GLMM) to test how translocation outcome (binary success/failure) depends on climate suitability and five other predictor variables commonly considered in comparative analyses of translocation outcomes (see Table 1 and Supporting Information). These five variables were treated as fixed effects in the GLMM. As 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 Class as a random effect in the model. We tested for multicollinearity amongst the predictor variables using the Variation Inflation Factor (VIF), implemented in R with the package *car* (v. 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 taxonomic Class, was implemented in R with the package *lme4* (v. 1.1-19) (Bates et al. 2019).

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 using 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 randomization approach with 1000 iterations and a significance level of 0.05 (Mac Nally 2002). Hierarchical partitioning and associated randomization tests were executed in R with the package *hier.part* (v. 1.0-4) (Walsh & Mac Nally 2013).

Results

The definition of translocation success adopted for this study resulted in the categorization of 61 successful translocations and 41 failures. The majority of translocation projects were carried out on the European (61%) and North American continents (35%), with a limited number of projects originating from Oceania (3%) and a single project from Asia.

The SDMs of the final species set were generally of high quality (Area Under the Curve; mean ± S.E. = 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 1; Table 2). The average climate suitability was higher at sites where conservation translocations were successful (mean ± S.E. = 0.576 ± 0.030) compared to 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 2). Life stage released and number of release years accounted for the second (21.3%) and third (15.3%) most variation, respectively (Figure 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 the position of the release site. For the life stage released variable, releasing a mixture of life stages proved to be the most successful approach among the three categories considered (Table 2; Supporting Information). When considering the number of years to release individuals at a site, the probability of success increased with the number of release years (Table 2; Supporting Information).

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; 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 (though see Brooker et al. 2018), but our results indicate that 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), i.e. reintroduction (97% of our sample were reintroductions). The failure to assess climate suitability might be excusable given the constraints facing conservation workers on the ground, however, the frequent concordance between predicted climate suitability and translocation outcome observed in our study 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, as 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 analysis offers another potential cause of climate-driven translocation failure. A substantial proportion of the release sites in our sample received climate suitability predictions of between 0.3 and 0.5 (Figure 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, sub-optimal 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 anti-predator strategy (Mori & Burghardt 2004) or its ability to forage (Traniello et al. 1984), thus reducing its fitness. This suggests that sites with low-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 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 the population dynamics of translocated populations may be decoupled from macroclimatic suitability. For example, in areas of high predicted climate suitability, populations might 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, with populations performing 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 generalizations 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 considered in our study provides fresh support for the use of SDMs to infer measures of demographic performance.

Our results indicate 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), the duration of releases (Griffith et al. 1989), the 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 the 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 on the optimum site for release.

The limited uptake of SDMs to guide conservation management decisions was noted by Guisan et al. (2013). 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 modeling approach that requires the use of coding software, one of the individual modeling 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 (Area Under the Curve; mean ± S.E. = 0.849 ± 0.007), as do the climate suitability predictions, which also indicate 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 (though 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, it should be noted that failures were not always equally represented in the dataset. 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 2), which contrasts with findings from previous reviews of insect and herpetofauna translocations (Germano & Bishop 2009; Bellis et al. 2019). In our dataset, reptile translocations contributed the greatest number of successes but on average released far fewer individuals than projects involving amphibians or insects. This likely results from the fewer offspring per annum that are produced by reptiles, thus constraining the number of individuals available for release. As our sample was of an insufficient size to split by taxonomic Class, the number of individuals released variable may have been less informative than in the previous review papers.

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). AUC represents one of the most widely used evaluation metrics for SDMs, but has been criticized 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 standardized approach to predict the suitability of translocation release sites by selecting eight climate variables known/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 according to the known eco-physiology 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 fewer than 30 spatially distinct occurrences as accuracy has been shown 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.

Conclusions

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 to 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, as they represent a useful predictive tool capable of reducing uncertainty in the planning and implementation of future translocation projects.

Supporting Information

Inclusion criteria and predictor variable data extraction (Appendix S1), species and climate data (Appendix S2), modeling and climate suitability extraction approach (Appendix S3), data summary (Appendix S4) and results with all failures included (Appendix S5). The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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Table 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)

Table 2. Generalized Linear Mixed Model results used to assess the effect of each parameter on translocation outcome for amphibians, reptiles and terrestrial insects. Variable abbreviations are described in Table 1.

Parameter	**β**	**β SE**
(Intercept)	1.008	0.852
ClimSuit	1.161 ***	0.337
NRelYears	0.764 *	0.419
NumRel	-0.083	0.383
LifeStageRel (Immature)[a]	-0.892	0.719
LifeStageRel (Mixed)[b]	-0.267	0.876
Origin (Captive)[c]	-0.940	0.631
Position(Edge)[d]	0.827	0.585

[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 0.001 level

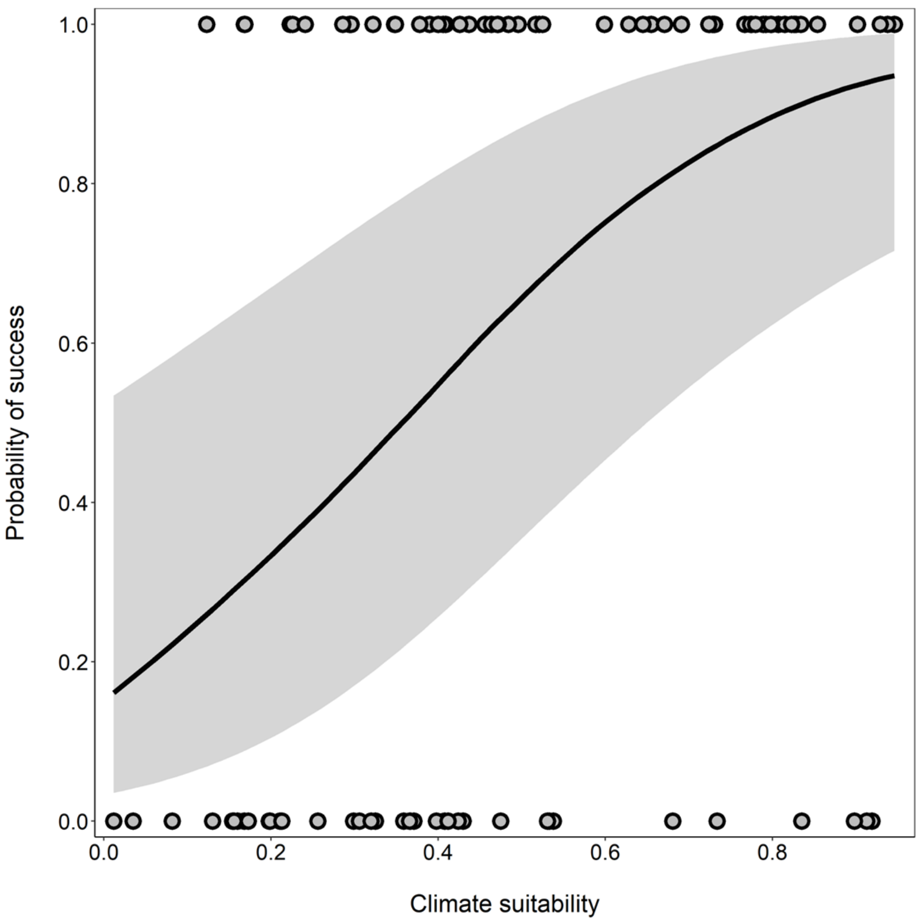

Figure 1. Effect of predicted climate suitability on model-based probabilities of translocation success for amphibians, reptiles and terrestrial insects. The shaded area indicates 95% confidence intervals.

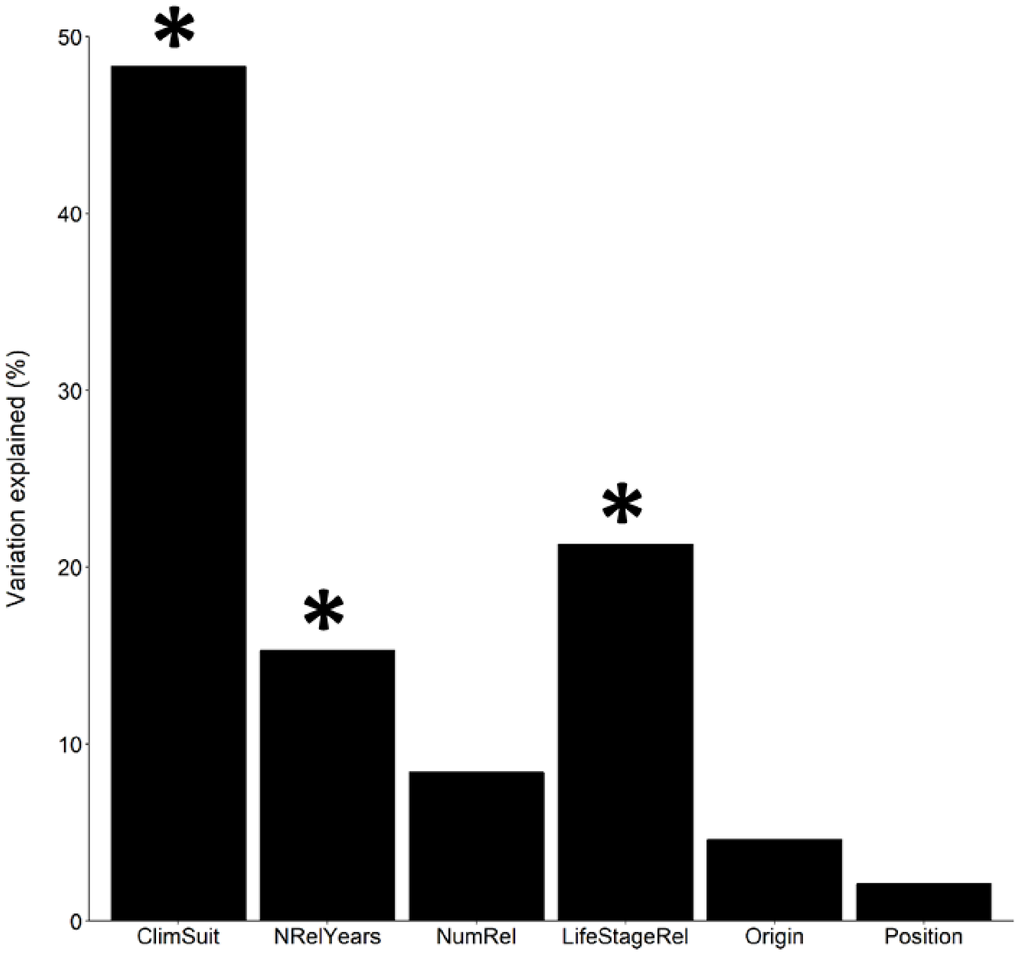

Figure 2. The percentage independent contribution of each predictor variable derived by hierarchical partitioning to translocation outcome for amphibians, reptiles and terrestrial insects. Predictor variables with significant ($P < 0.05$) independent contributions to translocation outcome are denoted with an asterisk. Variable abbreviations are described in Table 1.

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