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Bellis, J, Bourke, D, Maschinski, J, Heineman, K and Dalrymple, SE (2020) Climate suitability as a predictor of conservation translocation failure. Conservation Biology, 34 (6). pp. 1473-1481. ISSN 0888-8892

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1	Climate suitability as a predictor of conservation translocation failure
2	Joe Bellis ¹ , David Bourke ¹ , Joyce Maschinski ² , Katie Heineman ² & Sarah E. Dalrymple ¹ ,
3	
4	1. Liverpool John Moores University, UK
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6	
7	Accepted by Conservation Biology, 10 April 2020
8	Abstract
9	
10	The continuing decline and loss of biodiversity has caused an increase in the use of interventionist
11	conservation tools such as translocation. However, many translocation attempts fail to establish
12	viable populations, with poor release site selection often flagged as an inhibitor of success. We used
13	species distribution models (SDMs) to predict the climate suitability of 102 release sites for
14	amphibians, reptiles and terrestrial insects and compared suitability predictions between successful
15	and failed attempts. We then quantified the importance of climate suitability relative to five other
16	variables frequently considered in the literature to be important determinants of translocation
17	success: number of release years, number of individuals released, life stage released, origin of the
18	source population and position of the release site relative to the species' range. We found that the
19	probability of translocation success increased with predicted climate suitability and this effect was
20	the strongest amongst the variables considered in our analysis, accounting for 48.3% of the variation
21	in translocation outcome. These findings should encourage greater consideration of climate
22	suitability when selecting release sites for conservation translocations and we advocate the use of
23	SDMs as an effective way of doing this.
24	

25 Introduction

27	Threatened species management is increasingly involving more interventionist forms of conservation
28	action to secure viable metapopulations and reverse local extinctions (Hobbs et al. 2011).
29	Conservation translocation, defined as the intentional human-mediated movement of organisms
30	from one location to another for conservation purposes (IUCN 2013), represents one such approach.
31	In recent decades, there has been a global proliferation in the number of translocation-related
32	studies (Seddon et al. 2007; Taylor et al. 2017). However, many translocations fail to establish viable
33	populations (Fischer & Lindenmayer 2000; Cochran-Biederman et al. 2015). Attempts to improve
34	translocation practice have identified a number of influential factors, such as the origin of the source
35	population (Cayuela et al. 2019), the length of supplementary feeding (White et al. 2012), the life
36	stage of individuals released (Muths et al. 2014) and the overall habitat suitability of the release site
37	(Cochran-Biederman et al. 2015). Climate constitutes a fundamental component of overall habitat
38	suitability but has received little attention in the literature, with very few translocation projects
39	explicitly citing the use of techniques to estimate climate suitability (but see Brooker et al. 2018).
40	Instead, past attempts have often relied on previous occupancy and the intuition of involved parties
41	to select release sites (Osborne & Seddon 2012).
42	
43	Poor release site selection has been flagged as an impediment to translocation success (Osborne &
44	Seddon 2012). To mitigate the risk of poor release site selection, the updated Guidelines for
45	Reintroductions and Other Conservation Translocations (IUCN 2013) recommend that "the climate
46	requirements of the focal species should be understood and matched to current and/or future
47	climate at the destination site". Species distribution models (SDMs) represent the most widely
48	advocated approach for dealing with the challenge of selecting climatically suitable release sites
49	(Osborne & Seddon, 2012; IUCN, 2013; but see White et al. 2015). SDMs identify statistical

- 50 relationships between species occurrence and environmental descriptors. However, SDMs have
- 51 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).

55

56 Ectothermic species are particularly sensitive to climate (Angilletta et al. 2004). Temperature 57 regulates the metabolism and physiology of ectotherms, which in turn affects the demographic 58 performance of ectothermic populations through controls on their development, growth, 59 reproduction, overwinter survival and behaviour. Precipitation also affects many of these 60 parameters (Saenz et al. 2006), not as directly as temperature, but in some cases with 61 equal/increased severity (Ficetola & Maiorano 2016). The metabolic and physiological controls 62 imposed by temperature and precipitation on ectotherms mean that the performance of 63 translocated populations is strongly influenced by exposure to climatic conditions present at release 64 sites. Therefore, it is unsurprising that for a number of failed translocation projects involving 65 ectotherms, the authors proposed that unfavourable temperature and precipitation regimes 66 impeded population establishment (e.g. Cook in prep; Dempster & Hall 1980; Kuussaari et al. 2015). 67 68 In this paper, we analysed data extracted from the available literature on the outcomes of 69 amphibian, reptile and terrestrial insect translocations from a range of biogeographical regions. We 70 constructed global SDMs for each species to compare the predicted climate suitability between sites 71 of successful and failed translocation projects and then quantified the importance of climate 72 suitability as a predictor of translocation success relative to five other variables commonly reported 73 in the literature. These include how many individuals were released (Germano & Bishop 2009; Bellis 74 et al. 2019), the duration of releases (Griffith et al. 1989), the life stage of individuals released 75 (Muths et al. 2014; Cayuela et al. 2019), whether the source population was captive-bred or wild-76 caught (Rummel et al. 2016) and the position of the release site relative to the species' range 77 (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.

82

- 83 Methods
- 84
- 85 Literature search

86

87 We applied a range of approaches to find translocation case studies useful for quantifying the 88 relative importance of climate suitability as a predictor of translocation success. As translocation 89 reviews have already been published for herpetofauna (Dodd & Seigel 1991; Germano & Bishop 90 2009) and terrestrial insects (Bellis et al. 2019), we began by capitalizing on the case studies found in 91 these reviews. The herpetofauna reviews only covered literature up until 2006, thus, for relevant 92 literature published post-2006 (until 2018) we performed our own search on the 'Thomson Reuters 93 Web of Science'. We used the following advanced search criteria: TS=((reintro* OR re-intro* OR 94 translocat* OR conservation translocat* OR reinforce* OR re-inforce* OR reenforce* OR re-enforce* 95 OR assisted migration OR assisted colonization OR assisted colonisation OR conservation 96 introduction OR ecological replacement OR augment* OR restor* OR restock* OR re-stock* OR 97 reseed* OR re-seed* OR managed relocation) AND (amphibian OR reptile)). The search retrieved 98 1,419 results. We then imported all of the resulting papers into EndNote referencing software and 99 manually screened each record to verify its relevance to amphibian and reptile translocation (see 100 Supporting Information for full inclusion criteria). We screened the reference sections of each 101 relevant paper to find additional studies of relevance. We also included translocation projects that 102 were found via personal communication with authors. For terrestrial insects, as well as using the 103 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).
- 107

108 **Defining translocation success**

109

110 There is no broadly accepted definition of translocation success (Robert et al. 2015) and this was 111 reflected in the variability of definitions adopted in the translocation projects that we found. For the 112 purposes of this study, we adopted our own standardized definition of translocation success, but 113 note that alternative metrics such as a translocated population's finite rate of increase (growth rate 114 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) \geq 10 years 115 116 had elapsed between the time of most recent release and most recent monitoring, ii) the period 117 between the most recent release and most recent monitoring exceeded the generation time of the 118 species, and iii) the results of the most recent monitoring indicated individuals were still present. We 119 applied a 10-year minimum threshold in order to reduce the potential for abnormally favourable 120 conditions following release to have temporarily benefitted the translocated species. Enforcing 121 criterion ii led to the omission of seven translocations, all of which involved turtle or tortoise species 122 with generation times exceeding 15 years. A translocation project was only considered to have failed 123 if monitoring indicated that the species was no longer present at the site. Translocation projects that 124 could not be categorized as a success or failure were not considered for analysis. In total, 102 125 translocation projects covering 50 different species were eligible for statistical analysis (see 126 Supporting Information for full eligibility criteria).

127

128 Species distribution models

132 We downloaded species occurrence data from the Global Biodiversity Information Facility (GBIF). As 133 occurrences were very limited for endemic New Zealand species, we supplemented the GBIF data 134 with records from the New Zealand Department of Conservation. For all species, we considered their 135 global range in order to model the full extent of their climatic niche (Barbet-Massin et al. 2010; Raes 136 2012). We quality control checked each species occurrence dataset and reduced spatial bias caused 137 by unequal sampling (Supporting Information). We downloaded current climate data from the 138 WorldClim Database at a 30 arc-second resolution (Fick & Hijmans 2017) for eight standard 139 bioclimate predictors known/presumed to be important in structuring the distributions of 140 ectotherms (Wiens et al. 2006; Kozak & Wiens 2007; Clusella-Trullas et al. 2011), describing annual 141 averages, seasonality and highest/lowest monthly values of temperature and precipitation. Based on 142 recommendations made in Barbet-Massin et al. (2012), pseudo-absences were sampled at random 143 from the background extent for each species, weighted to reach an equal prevalence with presence 144 records (see Supporting Information for more details).

145

146 Modeling approach

147

148 We used an ensemble of species distribution model algorithms in order to minimise the uncertainty 149 associated with single modeling techniques (Buisson et al. 2010). Our ensemble consisted of 150 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 151 152 model performance using the receiver operating characteristic to determine an area under the curve 153 (AUC) (Supporting Information). In order to make SDM predictions comparable across species, we 154 standardized the predicted climate suitability values to range between 0 and 1 with the following 155 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).

158

159 Statistical analysis

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161 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 162 163 predictor variables commonly considered in comparative analyses of translocation outcomes (see 164 Table 1 and Supporting Information). These five variables were treated as fixed effects in the GLMM. 165 As the three continuous variables (climate suitability, number of release years and number of 166 individuals released) were on very different scales, we standardized them for easier interpretation of 167 model outputs. To account for evolutionary differences between the three taxonomic groups when 168 submitted to a translocation, we included Class as a random effect in the model. We tested for 169 multicollinearity amongst the predictor variables using the Variation Inflation Factor (VIF), 170 implemented in R with the package car (v. 3.0-2) (Fox et al. 2019). Each predictor variable had a VIF 171 of <2, indicating minimal correlation between the predictors (Quinn & Keough 2002). The global 172 model, including all five predictor variables and taxonomic Class, was implemented in R with the 173 package *lme4* (v. 1.1-19) (Bates et al. 2019).

174

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

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.

tests were executed in R with the package hier.part (v. 1.0-4) (Walsh & Mac Nally 2013).

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194

probability of conservation translocation success (Figure 1; Table 2). The average climate suitability was higher at sites where conservation translocations were successful (mean \pm S.E. = 0.576 \pm 0.030) compared to sites where translocations failed (0.365 \pm 0.037). This was consistent across amphibians (successful = 0.741 \pm 0.048; failed = 0.433 \pm 0.092), reptiles (successful = 0.538 \pm 0.048; failed = 0.356 \pm 0.123) and terrestrial insects (successful = 0.533 \pm 0.045; failed = 0.329 \pm 0.034).

There was a positive relationship between the SDM-based predicted climate suitability and the

201 When comparing the variation in translocation outcome explained by each of the variables, climate 202 suitability came out on top (48.3%) (Figure 2). Life stage released and number of release years 203 accounted for the second (21.3%) and third (15.3%) most variation, respectively (Figure 2). The 204 independent effect of each of these three variables was significant (P < 0.05) but this was not the 205 case for origin, number of individuals released or the position of the release site. For the life stage 206 released variable, releasing a mixture of life stages proved to be the most successful approach 207 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).

210

211 Discussion

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213 Climate suitability predicted from SDMs was higher at sites of successful translocation. When 214 comparing the strength of this effect against five other variables commonly considered in 215 comparative analyses of translocation outcomes, climate suitability explained the most variation in 216 translocation outcome. Using real-life case studies with known outcomes, our findings provide the 217 first evidence-based support for the use of SDMs to select suitable release sites (as recommended in 218 Osborne & Seddon 2012; IUCN 2013). These findings both highlight the importance of climate as a 219 key influencer of translocation outcome, as well as validating the usefulness of SDMs as a tool to aid 220 release site selection.

221

222 <u>Climate-driven translocation failure</u>

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224 Explicit consideration of release site climate suitability is rarely reported in the translocation 225 literature (though see Brooker et al. 2018), but our results indicate that it is important to the 226 outcome of conservation translocations. This supports the findings of a recent review of terrestrial 227 insect translocations, where weather and climate related factors were the most frequently reported 228 causes of failure (Bellis et al. 2019). We suspect that most managers do not explicitly consider the 229 climate suitability of release sites because the majority of translocation projects involve the release 230 of organisms into their indigenous range (definition as per IUCN 2013), i.e. reintroduction (97% of 231 our sample were reintroductions). The failure to assess climate suitability might be excusable given 232 the constraints facing conservation workers on the ground, however, the frequent concordance 233 between predicted climate suitability and translocation outcome observed in our study shows that

234 climate warrants consideration.

235

236 Climate change offers one potential explanation for why areas within the indigenous range fail to 237 support the establishment of translocated populations, as areas that once met the climatic niche 238 requirements of species may no longer be able to support viable populations (Wiens 2016). Some 239 reintroductions in our sample took place many decades after the species' initial extirpation (e.g. 240 Knisley et al. 2006; Fred & Brommer 2015) potentially allowing for considerable climate alteration at 241 their release sites. The longer the time between initial extirpation and the planned release, the less 242 likely the site will have retained its climatic suitability (Dalrymple & Broome 2010) and the greater 243 the need to apply tools such as SDMs to assess the current suitability (Osborne & Seddon 2012). 244 245 An interactive effect of climate with other limiting factors not considered in our analysis offers 246 another potential cause of climate-driven translocation failure. A substantial proportion of the 247 release sites in our sample received climate suitability predictions of between 0.3 and 0.5 (Figure 1) 248 and there was a relatively even mixture of successes (n = 16) and failures (n = 14) within this range. 249 When examining the authors' perceived causes of failure, sub-optimal climate conditions in addition 250 to other factors such as predation, competition and disease were frequently reported to have 251 constrained population establishment (e.g. Harvey et al. 2014; Fred & Brommer 2015; Kuussaari et 252 al. 2015). Behavioural alterations in response to sub-optimal climates (e.g. altered activity patterns) 253 may diminish the effectiveness of an organism's anti-predator strategy (Mori & Burghardt 2004) or 254 its ability to forage (Traniello et al. 1984), thus reducing its fitness. This suggests that sites with low-255 intermediate climate suitability (0.3 - 0.5) may require more detailed assessments of other 256 potentially limiting factors (e.g. density of predators) before they are designated for translocation. 257

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

260 environmental disturbances) in addition to the global macroclimate influence the overall habitat 261 suitability of individual sites (Louthan et al. 2015). If local interactions dominate species distributions 262 in suitable climates then the population dynamics of translocated populations may be decoupled 263 from macroclimatic suitability. For example, in areas of high predicted climate suitability, 264 populations might perform poorly due to intense competition, or in response to a temporary period 265 of unfavourable weather (Fancourt et al. 2015; Louthan et al. 2015). The same counterintuitive trend 266 may be observed in areas of low predicted climate suitability, with populations performing well 267 through confinement to suitable microclimates (Dullinger et al. 2012; Dahlberg et al. 2014). 268 However, local-scale processes may also be influenced by the global macroclimate (Louthan et al. 269 2015) and our results suggest that generalizations about habitat suitability can be made with global 270 SDMs. 271 272 Using SDMs for release site selection 273 274 Several authors have examined potential links between climate suitability estimated from SDMs and 275 measures of demographic performance (Thuiller et al. 2014; Lee-Yaw et al. 2016; Csergő et al. 2017). 276 Lee-Yaw et al. (2016) used SDMs and transplant experiments to uncover the positive relationship 277 between predicted climate suitability and the short-term individual fitness of plant and invertebrate 278 species. The frequent concordance between climate suitability and the translocation outcome of the 279 three ectothermic groups considered in our study provides fresh support for the use of SDMs to 280 infer measures of demographic performance. 281 282 Our results indicate that the decision to select release sites based on SDM predictions of climate 283 suitability influences translocation outcome more than other decisions frequently identified as 284 important in the literature, such as how many individuals should be released (Germano & Bishop 285 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 wildcaught 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.

293

294 The limited uptake of SDMs to guide conservation management decisions was noted by Guisan et al. 295 (2013). Based on personal experiences with managers involved in translocation projects, we believe 296 the lack of uptake may partly be resulting from a general assumption that parameterising and 297 running SDMs requires advanced statistical and coding expertise. Although we chose an ensemble 298 modeling approach that requires the use of coding software, one of the individual modeling 299 techniques that contributed to our ensemble, MaxEnt, can be run through a standalone software 300 package with a graphical user interface (Phillips et al. 2006). MaxEnt represents one of the most 301 popular SDM techniques and can achieve high levels of predictive performance (Elith & Graham 302 2009; Merow et al. 2013). Our model evaluation results support this (Area Under the Curve; mean ± 303 S.E. = 0.849 ± 0.007), as do the climate suitability predictions, which also indicate an overall contrast 304 between successful (0.579 \pm 0.033) and failed (0.398 \pm 0.040) translocations. Moreover, these 305 outputs were generated with MaxEnt's default configurations (though see Merow et al. 2013 for 306 potential shortfalls of retaining the default configurations). These results should encourage wider 307 uptake of SDMs by the translocation community, irrespective of statistical and coding expertise. 308

309 Limitations

310

311 Although there was frequent concordance between predicted climate suitability and translocation

312 failure, it should be noted that failures were not always equally represented in the dataset. 313 Specifically, due to a skewed success:failure ratio (26:5) of reptile translocations, our findings 314 potentially carry less relevance for this group. The paucity of failed reptile translocations is not 315 necessarily indicative of a high success rate, but instead may be explained by the greater likelihood 316 of reporting a successful project (see Miller et al. 2014 for a review of publication rates according to 317 translocation outcome). The large number of successful reptile translocations also provides an 318 explanation for the unexpected negative effect of number of individuals released on translocation 319 outcome (Table 2), which contrasts with findings from previous reviews of insect and herpetofauna 320 translocations (Germano & Bishop 2009; Bellis et al. 2019). In our dataset, reptile translocations 321 contributed the greatest number of successes but on average released far fewer individuals than 322 projects involving amphibians or insects. This likely results from the fewer offspring per annum that 323 are produced by reptiles, thus constraining the number of individuals available for release. As our 324 sample was of an insufficient size to split by taxonomic Class, the number of individuals released 325 variable may have been less informative than in the previous review papers.

326

327 Using correlative SDMs fitted with macroclimatic data to estimate the suitability of potential release 328 sites may be hindered by their known weaknesses. A source of uncertainty may arise from not 329 incorporating physiologically meaningful climate variables for all species or meaningful interactions 330 between variables (Mod et al. 2016). AUC represents one of the most widely used evaluation metrics 331 for SDMs, but has been criticized for its ability to assess the biological significance of models based 332 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 333 334 known/presumed to be important in structuring the distributions of ectotherms (Wiens et al. 2006; 335 Kozak & Wiens 2007; Clusella-Trullas et al. 2011), thereby conferring biological realism to the 336 models. However, when planning for a translocation, it is advisable to adopt a more detailed 337 species-specific variable selection protocol according to the known eco-physiology of the species of

interest (Austin & Van Niel 2011).

340	Correlative macroclimatic SDMs may also be less informative for species with few occurrence
341	records, such as rare or data-deficient species. For rare species, the geographical range limit may be
342	controlled by other factors such as dispersal capacity and biotic interactions (Svenning & Sandel
343	2013), whereas data-deficiency is often an artefact of reporting mechanisms and therefore strongly
344	dependent on the location of the species (e.g. species in the tropics, Feeley & Silman 2011). We
345	excluded species with fewer than 30 spatially distinct occurrences as accuracy has been shown to
346	decline severely beyond this threshold (Wisz et al. 2008). However, rare species are often the focus
347	of translocation projects and for managers considering the movement of these species, alternative
348	SDM methods such as the calibration of an ensemble of bivariate models (Breiner et al. 2015) or the
349	construction of more complex mechanistic models (Kearney & Porter 2009) could be explored.
350	
351	Conclusions
352	
352 353	The effects of management decisions in conservation translocations are inherently uncertain and the
	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
353	
353 354	fundamental step of selecting the release site is no exception (Osborne & Seddon 2012). By
353 354 355	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
353 354 355 356	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
353 354 355 356 357	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
353 354 355 356 357 358	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
353 354 355 356 357 358 359	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
353 354 355 356 357 358 359 360	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

	364	Sup	porting	Inform	nation
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366	Inclusion criteria and predictor variable data extraction (Appendix S1), species and climate data
367	(Appendix S2), modeling and climate suitability extraction approach (Appendix S3), data summary
368	(Appendix S4) and results with all failures included (Appendix S5). The authors are solely responsible
369	for the content and functionality of these materials. Queries (other than absence of the material)
370	should be directed to the corresponding author.
371	
372	Literature Cited
373	
374	Angilletta MJ, Steury TD, Sears MW. 2004. Temperature, growth rate, and body Size in ectotherms:
375	fitting pieces of a life-history puzzle. Integrative and Comparative Biology 44 :498–509.
376	
377	Armstrong DP and, Reynolds MH. 2012. Modelling Reintroduced Populations: The State of the Art
378	and Future Directions. In Ewen JG, Armstrong DP, Parker KA, Seddon PJ, editors. Reintroduction
379	Biology: Integrating Science and Management. Wiley-Blackwell, Oxford, UK.
380	
381	Austin MP, Van Niel KP. 2011. Improving species distribution models for climate change studies:
382	Variable selection and scale. Journal of Biogeography 38 :1–8.
383	
384	Barbet-Massin M, Jiguet F, Albert CH, Thuiller W. 2012a. Selecting pseudo-absences for species
385	distribution models: How, where and how many? Methods in Ecology and Evolution 3 :327–338.
386	
387	Barbet-Massin M, Thuiller W, Jiguet F. 2010. How much do we overestimate future local extinction
388	rates when restricting the range of occurrence data in climate suitability models? Ecography 33 :878–

389	886.
390	
391	Bates D et al. 2019. Ime4: Linear Mixed-Effects Models using "Eigen" and S4. R package version 1.1-
392	19.
393	
394	Bellis J, Bourke D, Williams C, Dalrymple S. 2019. Identifying factors associated with the success and
395	failure of terrestrial insect translocations. Biological Conservation 236 :29–36.
396	
397	Breiner FT, Guisan A, Bergamini A, Nobis MP. 2015. Overcoming limitations of modelling rare species
398	by using ensembles of small models. Methods in Ecology and Evolution 6 :1210–1218.
399	
400	Brooker RW, Brewer MJ, Britton AJ, Eastwood A, Ellis C, Gimona A, Poggio L, Genney DR. 2018. Tiny
401	niches and translocations: The challenge of identifying suitable recipient sites for small and immobile
402	species. Journal of Applied Ecology 55 :621–630.
403	
404	Buisson L, Thuiller W, Casajus N, Lek S, Grenouillet G. 2010. Uncertainty in ensemble forecasting of
405	species distribution. Global Change Biology 16 :1145–1157.
406	
407	Cayuela H, Gillet L, Laudelout A, Besnard A, Bonnaire E, Levionnois P, Muths E, Dufrêne M, Kinet T.
408	2019. Survival cost to relocation does not reduce population self-sustainability in an amphibian.
409	
	Ecological Applications:e01909.
410	Ecological Applications:e01909.
410 411	Ecological Applications:e01909. Chevan A, Sutherland M. 1991. Hierarchical Partitioning. The American Statistician 45 :90–96.
411	

415 177 :738–751.	
--------------------------	--

417	Cochran-Biederman JL, Wyman KE, French WE, Loppnow GL. 2015. Identifying correlates of success
418	and failure of native freshwater fish reintroductions. Conservation Biology 29 :175–186.
419	
420	Cook RP. (in prep). Amphibians and Reptiles of Gateway NRA: Impacts of Urbanization and
421	Restoration. Cape Cod National Seashore, United States.
422	
423	Csergő AM et al. 2017. Less favourable climates constrain demographic strategies in plants. Ecology
424	Letters 20 : 969-980.
425	
426	Dahlberg CJ, Ehrlén J, Hylander K. 2014. Performance of forest bryophytes with different
427	geographical distributions transplanted across a topographically heterogeneous landscape. PLoS
428	ONE 9 .
429	
430	Dalrymple SE, Broome A. 2010. The importance of donor population identity and habitat type when
431	creating new populations of small Melampyrum sylvaticum from seed in Perthshire, Scotland.
432	Conservation Evidence 7:1–8.
433	
434	Dempster JP, Hall ML. 1980. An attempt at re-establishing the swallowtail butterfly at Wicken Fen.
435	Ecological Entomology 5:327–334.
436	
437	Dodd KC, Seigel RA. 1991. Relocation , Repatriation , and Translocation of Amphibians and Reptiles:
438	Are they Conservation Strategies that work? Herpetologica 47 :336–350.
439	

440	Dullinger S et al. 2012. Extinction debt of high-mountain plants under twenty-first-century climate
441	change. Nature Climate Change 2 :619–622.
442	
443	Elith J, Graham CH. 2009. Do they? How do they? WHY do they differ? On finding reasons for
444	differing performances of species distribution models. Ecography 32 :66–77.
445	
446	Fancourt BA, Bateman BL, Vanderwal J, Nicol SC, Hawkins CE, Jones ME, Johnson CN. 2015. Testing
447	the role of climate change in species decline: Is the eastern quoll a victim of a change in the
448	weather? PLoS ONE 10 :1–15.
449	
450	Feeley KJ, Silman MR. 2011. The data void in modeling current and future distributions of tropical
451	species. Global Change Biology 17 :626–630.
452	
453	Ficetola GF, Maiorano L. 2016. Contrasting effects of temperature and precipitation change on
454	amphibian phenology, abundance and performance. Oecologia 181 :683–693.
455	
456	Fick SE, Hijmans RJ. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land
457	areas. International Journal of Climatology 37 :4302–4315.
458	
459	Fischer J, Lindenmayer DB. 2000. An assessment of the published results of animal relocations.
460	Biological Conservation 96:1–11.
461	
462	Fourcade Y, Besnard AG, Secondi J. 2018. Paintings predict the distribution of species, or the
463	challenge of selecting environmental predictors and evaluation statistics. Global Ecology and
464	Biogeography 27 :245–256.
465	

466	Fox J et al. 2019. Companion to Applied Regression "car". R package version 3.0-3.
467	
468	Fred MS, Brommer JE. 2015. Translocation of the endangered apollo butterfly parnassius apollo in
469	southern Finland. Conservation Evidence 12 :8–13.
470	
471	Germano JM, Bishop PJ. 2009. Suitability of amphibians and reptiles for translocation. Conservation
472	Biology 23 : 7-15.
473	
474	Griffith B, Scott JM, Carpenter JW, Reed C. 1989. Translocation as a species conservation tool: Status
475	and strategy. Science 245 :477–480.
476	
477	Guisan A et al. 2013. Predicting species distributions for conservation decisions. Ecology letters
478	16 :1424–35.
479	
480	Harvey DS, Lentini AM, Cedar K, Weatherhead PJ. 2014. Moving Massasaugas: Insight into
481	Rattlesnake relocation using Sistrurus c. catenatus. Herpetological Conservation and Biology 9:67–
482	75.
483	
484	Heikkinen RK, Pöyry J, Virkkala R, Bocedi G, Kuussaari M, Schweiger O, Settele J, Travis JMJ. 2015.
485	Modelling potential success of conservation translocations of a specialist grassland butterfly.
486	Biological Conservation 192 :200–206.
487	
488	Hobbs RJ, Hallett LM, Ehrlich PR, Mooney HA. 2011. Intervention Ecology: Applying Ecological
489	Science in the Twenty-first Century. BioScience 61 :442–450.
490	

491 IUCN. 2013. Guidelines for Reintroductions and Other Conservation Translocations. Version 1.0.

492 Gland, Switzerland.

493

Kearney M, Porter W. 2009. Mechanistic niche modelling: Combining physiological and spatial data
to predict species' ranges. Ecology Letters 12:334–350.

496

497 Knisley CB, Hill JM, Scherer AM. 2006. Translocation of Threatened Tiger Beetle Cicindela dorsalis

dorsalis (Coleoptera: Cicindelidae) to Sandy Hook, New Jersey. Annals of the Entomological Society
of America **98**:552–557.

500

501 Kozak KH, Wiens JJ. 2007. Climatic zonation drives latitudinal variation in speciation mechanisms.

502 Proceedings of the Royal Society B: Biological Sciences **274**:2995–3003.

503

504 Kuussaari M, Heikkinen R, Heliölä J, Luoto M, Mayer M, Rytteri S, von Bagh P. 2015. Pikkuapollon

siirtoistutukset Uudellemaalle ja Lounais-Suomeen. Baptria **3**:80–94.

506

507 Lee-Yaw JA, Kharouba HM, Bontrager M, Mahony C, Csergo AM, Noreen AME, Li Q, Schuster R,

508 Angert AL. 2016. A synthesis of transplant experiments and ecological niche models suggests that

range limits are often niche limits. Ecology Letters **19**:710–722.

510

511 Louthan AM, Doak DF, Angert AL. 2015. Where and When do Species Interactions Set Range Limits?

512 Trends in Ecology and Evolution **30**:780–792.

513

514 Mac Nally R. 2002. Multiple regression and inference in ecology and conservation biology: further

515 comments on identifying important predictor variables. Biodiversity and Conservation 11:1397–

16 1401	
16 1401	

518	Maes D et al. 2019. The potential of species distribution modelling for reintroduction projects: the
519	case study of the Chequered Skipper in England. Journal of Insect Conservation 23 :419–431.
520	
521	Merow C, Smith MJ, Silander JA. 2013. A practical guide to MaxEnt for modeling species'
522	distributions: What it does, and why inputs and settings matter. Ecography 36 :1058–1069.
523	
524	Miller KA, Bell TP, Germano JM. 2014. Understanding publication bias in reintroduction biology by
525	assessing translocations of New Zealand's Herpetofauna. Conservation Biology 28:1045–1056.
526	
527	Mod HK, Scherrer D, Luoto M, Guisan A. 2016. What we use is not what we know: environmental
528	predictors in plant distribution models. Journal of Vegetation Science 27 :1308–1322.
529	
530	Mori A, Burghardt GM. 2004. Thermal effects on the antipredator behaviour of snakes: a review and
531	proposed terminology. Herpetological Journal 14 :79–87.
532	
533	Muths E, Bailey LL, Watry MK. 2014. Animal reintroductions: An innovative assessment of survival.
534	Biological Conservation 172 :200–208.
535	
536	Osborne PE, Seddon PJ. 2012. Selecting Suitable Habitats for Reintroductions: Variation, Change and
537	the Role of Species Distribution Modelling. In Ewen JG, Armstrong DP, Parker, KA, Seddon PJ editors.
538	Reintroduction Biology: Integrating Science and Management. Wiley-Blackwell, Oxford, UK.
539	

540	Phillips SJ, Anderson RP, Schapire RE. 2006. Maximum entropy modeling of species geographic
541	distributions. Ecological Modelling 190 :231–259.
542	
543	Quinn GP, Keough MJ. 2002. Experimental design and data analysis for biologists. Cambridge
544	University Press., Cambridge, UK.
545	
546	R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for
547	Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.
548	
549	Raes N. 2012. Partial versus full species distribution models. Natureza a Conservacao 10 :127–138.
550	
551	Rummel L, Martínez–Abraín A, Mayol J, Ruiz–Olmo J, Mañas F, Jiménez J, Gómez JA, Oro D. 2016.
552	Use of wild-caught individuals as a key factor for success in vertebrate translocations. Animal
553	Biodiversity and Conservation 39 :207–219.
554	
555	Saenz D, Fitzgerald LA, Baum KA, Conner RN. 2006. Abiotic Correlates of Anuran Calling Phenology :
556	The Importance of Rain , Temperature , and Season. Herpetological Monographs 20 :64–82.
557	
558	Seddon PJ, Armstrong DP, Maloney RF. 2007. Developing the science of reintroduction biology.
559	Conservation Biology 21 :303–312.
560	
561	Svenning JC, Sandel B. 2013. Disequilibrium vegetation dynamics under future climate change.
562	American Journal of Botany 100 :1266–1286.

564	Taylor G, Canessa S, Clarke RH, Ingwersen D, Armstrong DP, Seddon PJ, Ewen JG. 2017. Is
565	Reintroduction Biology an Effective Applied Science? Trends in Ecology and Evolution 32 :873–880.
566	
567	Thuiller W et al. 2014. Does probability of occurrence relate to population dynamics? Ecography
568	37 :1155–1166.
569	
570	Thuiller W, Georges D, Engler R, Breiner F. 2016. biomod2: Ensemble Platform for Species
571	Distribution Modeling. R package version 3.3-7.
572	
573	Tocher MD, Fletcher D, Bishop PJ. 2006. A modelling approach to determine a translocation scenario
574	for the endangered New Zealand frog Leiopelma Hamiltoni. Herpetological Journal 16 :97–106.
575	
576	Todd BD, Winne CT. 2006. Ontogenetic and interspecific variation in timing of movement and
577	responses to climatic factors during migrations by pond-breeding amphibians. Canadian Journal of
578	Zoology 84 :715–722.
579	
580	Traniello JFA, Fujita MS, Bowen R V. 1984. Ant foraging behavior: ambient temperature influences
581	prey selection. Behavioral Ecology and Sociobiology 15 :65–68.
582	
583	Unger SD, Sutton TM, Williams RN. 2013. Projected population persistence of eastern hellbenders
584	(Cryptobranchus alleganiensis alleganiensis) using a stage-structured life-history model and
585	population viability analysis. Journal for Nature Conservation 21 :423–432.
586	
587	Wagner G, Köhler G, Berger U, Davis AJ. 2005. An experiment to re-establish the red-winged
588	grasshopper, Oedipoda germanica (Latr.) (Caelifera: Acrididae), threatened with extinction in

	589	Germany. Jo	ournal for	Nature	Conservation	13 :257–266.
--	-----	-------------	------------	--------	--------------	---------------------

591 Walsh C, Mac Nally R. 2013. hier. part: Hierarchical Partitioning. R package version 1.0-4.

592

- 593 White TH, Collar NJ, Moorhouse RJ, Sanz V, Stolen ED, Brightsmith DJ. 2012. Psittacine
- reintroductions: Common denominators of success. Biological Conservation **148**:106–115.

595

- 596 White TH, de Melo Barros Y, Develey PF, Llerandi-Román IC, Monsegur-Rivera OA, Trujillo-Pinto AM.
- 597 2015. Improving reintroduction planning and implementation through quantitative SWOT analysis.
- 598 Journal for Nature Conservation **28**:149–159.

599

Wiens JJ. 2016. Climate-Related Local Extinctions Are Already Widespread among Plant and Animal
Species. PLoS Biology 14:1–18.

602

- 603 Wiens JJ, Graham CH, Moen DS, Smith SA, Reeder TW. 2006. Evolutionary and ecological causes of
- the latitudinal diversity gradient in hylid frogs: Treefrog trees unearth the roots of high tropical
- 605 diversity. American Naturalist **168**:579–596.

606

- 607 Wisz MS et al. 2008. Effects of sample size on the performance of species distribution models.
- 608 Diversity and Distributions **14**:763–773.

609

- 610
- 611
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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 NumRel LifeStageRel	Total number of release years Total number of individuals released Life stage released (Adults, Immatures or Mixed)
	•	Origin of source population (Wild or Captive-bred)
	Origin	
	Position	Position of release site relative to the species' range (Core or Edge)
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	Table 2. Generalized Li	near Mixed Model results used to assess the effect of each

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 LifeStageBel – Immature versus Adult		

^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

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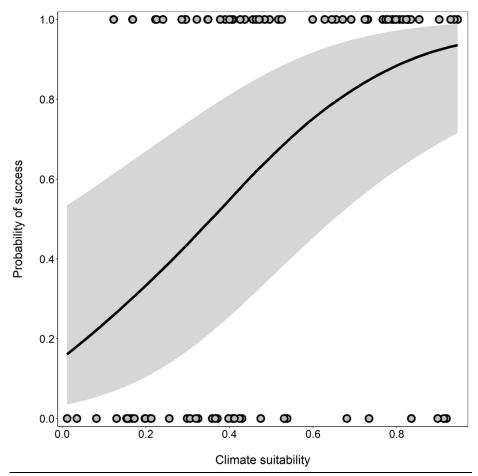


Figure 1. Effect of predicted climate suitability on model-based probabilities of translocation success for amphibians, reptiles and terrestrial insects. The shaded area indicates 95% confidence intervals.

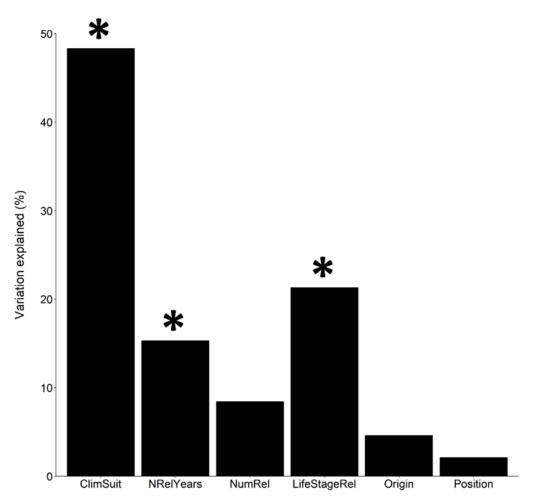


Figure 2. The percentage independent contribution of each predictor variable derived by hierarchical partitioning to translocation outcome for amphibians, reptiles and terrestrial insects. Predictor variables with significant (P < 0.05) independent contributions to translocation outcome are denoted with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