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

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9 10 Abstract

11
12 Translocation is increasingly used as a management strategy to mitigate the effects of human
13 activity on biodiversity. Based on the current literature, we summarised trends in terrestrial insect
14 translocations and identified factors associated with success and failure. As the authors' definitions
15 of success and failure varied according to the individual sets of goals and objectives in each project,
16 we adopted a standardised species-specific definition of success. We applied generalised linear
17 models and information-theoretic model selection to identify the most important factors associated
18 with translocation success. We found literature documenting the translocation of 74 terrestrial
19 insect species to 134 release sites. Of the translocations motivated by conservation, 52% were
20 considered successful, 31% were considered to have failed and 17% were undetermined. Our results
21 indicate that the number of individuals released at a translocation site was the most important
22 factor associated with translocation success, despite this being a relatively infrequent perceived
23 cause of failure as reported by authors. Factors relating to weather and climate and habitat quality
24 were the most commonly perceived causes of translocation failure by authors. Consideration of
25 these factors by managers during the planning process may increase the chance of success in future
26 translocation attempts of terrestrial insects.

27 28 Introduction

29
30 Translocation represents a valuable tool for wildlife conservation (Fischer and Lindenmayer, 2000;
31 Germano and Bishop, 2009). There has been substantial growth in translocation practice during the
32 past three decades (Seddon *et al.*, 2007; Taylor *et al.*, 2017), resulting in a taxonomically diverse
33 assemblage of translocation case studies. In response to the growing use of translocation as a
34 management tool, the International Union for the Conservation of Nature (IUCN) published a set of
35 broad guidelines in 2013 for conservation-based translocations (IUCN, 2013). These guidelines offer
36 a detailed framework for all phases of a translocation, generalised for all organisms and have likely
37 contributed to the successful recovery of threatened species. In addition to the IUCN guidelines,
38 there have been a number of global reviews, covering amphibians and reptiles (e.g. Dodd and Seigel,
39 1991; Germano and Bishop, 2009), birds and mammals (Griffith *et al.*, 1989; Wolf *et al.*, 1996), plants
40 (Dalrymple *et al.*, 2012), freshwater fish (Cochran-Biederman *et al.*, 2015) and freshwater
41 macroinvertebrates (Jourdan *et al.*, 2018). The majority of these reviews also aim to improve the
42 success rate of translocations for their focal taxa, by identifying specific factors associated with
43 success. Terrestrial insects represent one of the major taxonomic classes that is yet to be the focus
44 of a global review. Terrestrial insects are defined as insect species with lifecycles that are partly or
45 fully dependent on habitats existing in the terrestrial environment.

46
47 The Class Insecta has the highest abundance, biomass and diversity in the animal kingdom (Wilson,
48 1987; Kim, 1993). Insects occupy almost every type of terrestrial habitat and they provide numerous

49 ecosystem services (Losey and Vaughan, 2006). The value of their ecosystem services has been
50 conservatively estimated at US\$57 billion per year in the United States alone (Losey and Vaughan,
51 2006). Despite their enormous contribution, insects are often neglected in conservation strategies,
52 which typically focus on more iconic vertebrate species (Seddon *et al.*, 2005). The lack of attention
53 given to insects is reflected by the paucity of policies that protect them, for example, legislation in
54 Europe protects only 0.12% of the region's insect species (Leandro *et al.*, 2017). This figure is
55 concerning, particularly given recent research revealing a dramatic global decline in insect
56 populations that could lead to the extinction of over 40% of the world's insect species during the
57 next few decades (Sánchez-Bayo and Wyckhuys, 2019). The growing recognition of the global decline
58 in insect populations (e.g. Hallmann *et al.*, 2017; Vogel 2017; Taylor *et al.*, 2018) is likely to increase
59 the demand for methods and approaches, such as translocation, to restore lost species and
60 functions.

61
62 Despite having not featured as frequently in translocation projects as vertebrate groups such as
63 birds and mammals (Seddon *et al.*, 2005), the life-history attributes of insects would suggest they are
64 potentially ideal candidates for translocation. The small body size and short generation time of
65 insects makes them comparatively low cost and quick to propagate in preparation for a translocation
66 (Balmford *et al.*, 1996). They also require smaller habitat patches to support viable populations
67 compared to most vertebrate species (e.g. Baur *et al.*, 2017), meaning pre- and post-release habitat
68 management costs are more economical. Indeed, many managers already recognise the candidacy
69 of insects for translocation, which has led to the instigation of insect translocation projects for a
70 variety of motivations including conservation (e.g. Baur *et al.*, 2017), mitigation (e.g. Simon *et al.*,
71 2016), research (e.g. Forsman *et al.*, 2012) and biological control (e.g. Kapranas *et al.*, 2014).
72

73 In this paper, we begin by exploring the global trends in terrestrial insect translocations. This
74 includes regional trends, taxonomic trends and their respective biases. We will then focus more
75 specifically on conservation translocations with the objective of identifying the general mechanisms
76 that explain past successes and failures. Knowledge of such mechanisms has the potential to inform
77 future management decisions, and encourage further investigation into how these and other factors
78 influence translocation outcome for terrestrial insects.
79

80 **Methodology**

81

82 Data Collection

83 We performed a literature search to find examples of terrestrial insect translocations from across
84 the globe. We used the search engines 'Thomson Reuters Web of Science' and 'Directory of Open
85 Access Journals', and the 'Conservation Evidence Individual Studies repository' to retrieve relevant
86 papers published at the earliest possible date up until 08/10/2018 (for further detail on the search
87 methodology and search terms used on each platform, see Supplementary Material 1). Once we had
88 performed the search, we imported all of the resulting papers into EndNote referencing software
89 and manually screened each record to verify its relevance to insect translocation. Articles were not
90 included in the study if they were irrelevant to insect translocation based on their title and abstract
91 or upon further scrutiny of the paper. We also screened the bibliographies of each relevant
92 publication identified during our search to find additional studies of relevance. Using the methods
93 outlined above, we found two national cross-taxonomic translocation reviews, one for the United
94 Kingdom (Carter *et al.*, 2017) and one for New Zealand (Sherley *et al.*, 2010), which led to the
95 addition of eighteen translocation projects that were not found individually through our search

96 methodology. In every case, this was because these translocations were restricted to the grey
97 literature or unpublished reports and accounts.

98

99 Once our literature search was complete, we categorised each translocation project based on its
100 primary motivation. We identified five types of translocation motive from the dataset: conservation,
101 mitigation, research, functional restoration and biological control. We could often infer the
102 motivation of the translocation based on the article's stated aims or objectives and these were
103 recorded accordingly. However, this was not possible for every article, in which case authors were
104 contacted to corroborate. We categorised translocations as research-motivated if they aimed to
105 further the field of conservation translocations through the release of insects in more experimental
106 circumstances. For example, Willis *et al.* (2009) translocated two common butterfly species ~35 and
107 ~65 km beyond their current ranges in the United Kingdom to test the use of species distribution
108 models for identifying potential assisted colonisation release sites. In this study, the aim was to test
109 the principle of the approach, rather than to establish populations of the two species for
110 conservation purposes. We made the decision to remove biological control-related articles from the
111 dataset, as this is an extensive discipline with core objectives that diverge significantly from the ones
112 typical of the other motives. As one of the primary goals of our study is to identify the key
113 determinants of success in insect translocations, we split the dataset based on motivation. Every
114 translocation, irrespective of motivation (except biological control), was used to identify general
115 trends in insect translocations, such as regional and taxonomic biases, i.e. descriptive statistics.
116 However, in order to identify the key determinants of success using statistical analyses, we
117 incorporated only translocations where the primary motivation was conservation. This decision was
118 made because conservation translocations principally aim to establish a viable population (IUCN,
119 2013), whereas translocations motivated by other factors often do not (e.g. Willis *et al.*, 2009; Pratt
120 and Emmel, 2010; Forsman *et al.*, 2012).

121

122 Data Extraction and Refinement

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

144

145 Defining Translocation Success

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

159

160 Statistical Analyses

161 We used a generalised linear model (GLM) with a logit link and binomial random component that
162 can be used with mixed data categories to identify variables associated with successful
163 translocations (see Table 1 for list of predictor variables). The binary response variable was success
164 or failure. We refer to this statistical approach herein as logistic regression. As our statistical
165 analyses were of a more exploratory than confirmatory nature, we included all single-variable
166 models and models with two-way interactions that represent potentially meaningful ecological
167 relationships between variables and are not in breach of the assumptions of logistic regression
168 analysis.

169

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

179

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

187

188 **Results**

189

190 We found literature documenting the translocation of 74 terrestrial insect species to 134 release
191 sites. A total of seven different taxonomic orders received translocations (Figure 1). Lepidoptera was

192 the most frequently translocated Order with 52 translocations (39%) involving this group, while
193 Orthoptera was second with 39 translocations (29%) (see the Supplementary Material 2 for a list of
194 species translocated). Translocations of insect species were most commonly conducted on the
195 European continent ($n=74$), with the Oceania ($n=35$) and North America ($n=19$) carrying out the
196 second and third most translocations respectively (Figure 2). There were a very limited number of
197 terrestrial insect translocations in Africa, Asia and South America.

198
199 There were some notable regional biases in the orders targeted for translocation projects
200 (Supplementary Material 2). For example, Orthoptera, the second most frequently translocated
201 order globally, were not the subjects of any translocation projects in North America, but comprised
202 the majority of projects in Oceania (71%). In Europe and North America, the taxonomic bias was
203 skewed more towards Lepidoptera species, with 54% and 58% of translocation projects comprising
204 this group, respectively. Just one project focused on the translocation of a Lepidoptera species in
205 Oceania.

206
207 Conservation was the most commonly identified motivation behind terrestrial insect translocation
208 projects, with a total of 107 translocations being conducted for this purpose. Research was a
209 relatively frequent motivation ($n=20$), whereas translocations for mitigation ($n=4$) or functional
210 restoration ($n=3$) were uncommon.

211
212 Based on our success criteria, 56 conservation translocation projects were successful (52%), 33 failed
213 (31%) and 18 were undetermined (17%). Based on a subset of these translocations that were eligible
214 for statistical analysis, the information-theoretic model selection resulted in the highest ranked
215 logistic regression model consisting of the number of individuals released (NumRel) as a single
216 predictor variable (Table 2). The second and third highest ranked models also featured the NumRel
217 variable, with Origin and LifeHistory as additive terms, respectively. When Origin and LifeHistory
218 were taken individually the models had considerably less support, suggesting that NumRel was more
219 influential than these two variables. A proportion of support was given to every model considered in
220 the analysis, with the three highest performing models accounting for 40% of the Akaike weights,
221 which we acknowledge as being relatively low. However, the consistent presence of NumRel
222 amongst the top performing models suggests that this variable was the most important determinant
223 of success for terrestrial insect translocations.

224
225 Successful translocation projects released more individuals than failed projects - successful projects
226 released a mean average of 2030 ± 706 individuals, while failed projects released a mean average of
227 667 ± 166 individuals. Most terrestrial insect translocation projects sourced their stock from wild
228 populations, with 66% of translocation projects opting to release wild-caught individuals. Success
229 rate was 67% when using wild stock, which was marginally higher than the 59% success rate
230 achieved by translocation projects that used captive-bred stock. The average distance between
231 source population and release site was 110.9 ± 28.9 km. However, there was no statistically
232 significant difference in the distance separating source population and release site between
233 successful and failed translocation projects ($p=0.714$).

234
235 Habitat quality, as well as weather and climate, were the most frequently cited causes of
236 translocation failure according to those involved with terrestrial insect translocation projects (Figure
237 3). Of the 33 insect translocations that resulted in failure, over a third were believed to have failed
238 due to poor habitat quality or the effects of weather and climate at the release site. After these two
239 factors, the main reported causes of translocation failure were predation pressure and pollution.

240 Factors relating to the technique of a translocation were rarely considered as potential causes of
241 failure. Similarly, an insufficient number of individuals released was rarely considered as a potential
242 cause of failure ($n=2$), despite successful translocation projects releasing an average of around three
243 times as many individuals compared to those that failed.

244

245 Discussion

246

247 The state of terrestrial insect translocations

248 The terrestrial insect translocation literature is regionally and taxonomically diverse, and contains a
249 wealth of case studies possessing the potential to inform future translocation management
250 decisions. Of the translocation projects summarised here, around half were defined as successful.
251 This figure is slightly higher than the success rates reported for other animal groups (e.g. Griffith *et al.*,
252 1989; Germano and Bishop, 2009), suggesting that insects respond comparatively well to
253 translocation. Although more translocations were defined as successful (52%), the proportion of
254 undetermined (17%) and failed translocations (31%) suggests that there is room for improvement in
255 terms of planning and conducting terrestrial insect translocations, as well as post-release monitoring
256 and the reporting of results.

257

258 Unlike for other animal taxa (Fischer and Lindenmayer, 2000; Seddon *et al.*, 2014), the majority of
259 insect translocation projects originated from Europe, rather than Oceania or North America. This
260 places Europe as a global leader in insect translocations, a position that has generally been filled by
261 Oceania with respect to vertebrate translocations due to the large number of translocations that
262 have been undertaken there (Fischer and Lindenmayer, 2000; Seddon *et al.*, 2014). It is possible that
263 some regional biases were introduced to the dataset through our decision to include national
264 translocation reviews (e.g. Sherley *et al.*, 2010; Carter *et al.*, 2017). However, the omission of these
265 reviews would have had little effect on the regional trends that were detected via our search
266 methodology (Figure 1 and Figure 2) and their inclusion provided valuable additional case studies for
267 analysis.

268

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

285

286 There are many motivations behind animal translocations (Seddon *et al.*, 2012) with conservation
287 the most frequently identified motivation in the present study due to our search focus. However,

288 translocations motivated by biological control, which were beyond the scope of this study, are
289 frequently conducted with insects as the control agent species. Biological control has been used
290 extensively around the world: 6,158 documented insect introductions were conducted prior to 2010
291 for this purpose (Cock *et al.*, 2016), of which 32.6% resulted in the establishment of the control
292 agent species. This level of establishment is high given that such a large proportion of biological
293 control releases are far outside the species indigenous range (e.g. Dahlsten *et al.*, 1998; Chauzat *et al.*,
294 2002; Quacchia *et al.*, 2007). Although the field of biological control is ecologically, economically
295 and socially divergent from that of conservation translocations, there remains scope for practical
296 skill exchange. Biological control programmes often involve highly skilled entomologists that use
297 increasingly sophisticated technologies and protocols to maximise the population viability and
298 chances of establishment for their captive-bred stock (e.g. Duan *et al.*, 2013; van Lenteren *et al.*,
299 2018). Conservation translocation programmes with a captive-breeding component, which remain
300 less common than wild to wild translocations for insects, can incorporate many of the pathogen
301 screening, animal husbandry and genetic management procedures used in successful biological
302 control programmes to develop their own existing and future programmes.

303

304 Characteristics of translocation success

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

315

316 The definition of translocation success adopted for this research is similar to that for reviews of
317 other animal taxa (e.g. Germano and Bishop, 2009; White *et al.*, 2012; Cochran-Biederman *et al.*,
318 2015). This definition ensures that the focal species has completed all phases of its lifecycle at the
319 release site, which is widely regarded as a fundamental indicator of translocation success (McCoy *et al.*,
320 2014; Robert *et al.*, 2015). The potential drawback of defining success in this way is that it may
321 allow for more translocations that only achieved short-term success to be defined as successful (e.g.
322 translocated population still present after one lifecycle duration of a univoltine species). However,
323 the conservation translocations analysed during this study generally established long-term
324 populations, with 80% reporting the persistence of the translocated population for >5 years after the
325 most recent release and 46% for >10 years (see Supplementary Material 2).

326

327 Our results indicate that terrestrial insect translocation success is influenced most by the number of
328 individuals released – translocations are more likely to be successful when releasing more
329 individuals. Our findings are unsurprising – with a greater number of founder individuals, a
330 translocated population is less vulnerable to the effects of demographic stochasticity, loss of genetic
331 diversity by drift, and inbreeding depression, which are more prevalent in smaller populations.
332 Therefore, we suggest that managers should aim to maximise the number of individuals released.
333 Population models can be a useful tool for predicting the optimal number of individuals for release
334 (e.g. Wagner *et al.*, 2005; Unger *et al.*, 2013; Heikkinen *et al.*, 2015), but their outputs are less
335 valuable for species with inadequate population and life-history data. The optimal number of

336 individuals for release will vary depending on their life stage due to fluctuating mortality rates
337 between adult, juvenile and egg phases (Price *et al.*, 2011). With a large enough sample size, we
338 would have split the number of individuals released variable based on the life stage released variable
339 and compared differences in translocation outcome for each life stage category, but this was
340 impractical with the number of cases that were available.

341

342 Reviews of vertebrate translocations suggest that wild source populations are generally associated
343 with greater translocation success than captive-bred source populations (e.g. Griffith *et al.*, 1989;
344 Rummel *et al.*, 2016), and concerns have been raised over the behavioural, morphological,
345 demographic and genetic changes resulting from captive-breeding programmes (Lewis and Thomas,
346 2001; Williams and Hoffman, 2009). Our results suggest that insect translocations are also more
347 successful when individuals are sourced from wild populations, though the magnitude of this
348 difference is marginal (<10%), and is much less than that found for vertebrate taxa (e.g. 37% for
349 birds and mammals, Griffith *et al.*, 1989). It may not always be feasible to acquire large numbers of
350 wild individuals for translocation as remaining wild populations may have declined in abundance and
351 extent-of-occurrence to the point where they are too fragile to withstand the loss of a sufficiently
352 large number of source individuals (Dimond and Armstrong, 2007). Under these circumstances,
353 captive-breeding programmes provide a possible alternative for the acquisition of large numbers of
354 individuals whilst minimising loss of viability of wild populations.

355

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

366

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

378

379 Examining translocation failure

380 The effects of weather and climate were one of the most frequently reported causes of translocation
381 failure. Insect life-cycles and abundance are influenced strongly by temperature (Danks, 1987) and
382 precipitation (Roy *et al.*, 2008; Liberal *et al.*, 2011). Mismatches in climate conditions between
383 source populations and release sites, and extreme weather (e.g. drought or high rainfall) can be

384 detrimental to translocated insect populations (e.g. Dempster and Hall, 1980; Daniels, 2009) and
385 difficult to avoid or manage. However, there are preventative steps prior to translocation that can
386 be taken. For example, estimating the climate suitability of potential release sites under current and
387 future environmental conditions can minimise the risk of selecting sub-optimal release sites or sites
388 that will become unsuitable under future climate change (Guisan *et al.*, 2013). This is possible with
389 the use of species distribution models (SDMs), which in their most widely used form, correlatively
390 identify suitable environmental conditions for a species based on the conditions present at sites
391 supporting extant populations.

392
393 The use of SDMs during the translocation planning process is highly advised when contemplating the
394 movement of a species beyond its indigenous range (i.e. assisted colonisation) (Chauvenet *et al.*,
395 2013). However, SDMs are also useful for reintroduction planning (see Osborne and Seddon, 2012
396 for potential applications and issues of using SDMs for reintroductions), especially if the focal species
397 became extinct at the proposed reintroduction site some time ago. It is risky to use historic site
398 occupancy as a prerequisite for site suitability; climate change during the intervening period
399 between the initial extinction and time of release could have rendered the site unsuitable. For
400 example, the Apollo Butterfly (*Parnassius apollo* Linnaeus, 1758) went extinct in southern Finland in
401 the 1950s and reintroductions were attempted to a number of islands between 2009 and 2011 (Fred
402 and Brommer, 2015; J. Brommer pers. comm.). The reintroduction failed, and the authors
403 hypothesise that climatic factors, such as unfavourable winter conditions and the timing of spring,
404 may have played a role in the failure of the species to persist on the islands.

405
406 To our knowledge, no attempt has been made within the peer-reviewed literature to assess the
407 extent to which climate conditions at release sites may have influenced the outcome of past
408 translocation attempts. The frequent attribution of translocation failure to unsuitable weather and
409 climate conditions by those involved with insect translocations suggests there is a necessity to
410 investigate this factor further. A statistical modelling approach similar to the one applied in Csergő *et al.*
411 (2017), in which predicted climate suitability values generated from SDMs were related to the
412 demographic performance of plant populations, could be applied to detect potential correlations
413 between release site climate suitability and the outcome of insect translocations.

414
415 The quality of release site habitat has been identified as an important factor for translocation
416 success in previous animal translocation reviews (e.g. Dodd and Seigel, 1991; White *et al.*, 2012). We
417 were unable to assess habitat quality for the projects that we reviewed, but habitat quality was one
418 of the most frequently reported causes of translocation failure by authors. The importance of
419 habitat quality for population viability has repeatedly been shown across a diverse range of insect
420 taxa (Baur *et al.*, 2002; Franzén and Nilsson, 2010; Pasinelli *et al.*, 2013) and consequently, defining
421 the crucial habitat requirements prior to reintroduction is required. Habitat descriptions of the focal
422 species at sites supporting healthy populations, preferably including the candidate source
423 population(s), should be conducted to ensure the proposed translocation site is suitable prior to
424 release (IUCN, 2013). Furthermore, assurances of long-term active management should be obtained
425 prior to translocation to safeguard habitat quality under future pressures. Changes to land tenure
426 and discontinuation of habitat management activities have been responsible for the failure of insect
427 translocations in the past (e.g. *Deinacrida mahoenui* Gibbs, 1999 C. Watts pers. comm; *Cicindela*
428 *dorsalis* Say, 1817 M. Brust pers. comm.).

429
430 Based on our method of data collection, we were unable to obtain data on the habitat quality of
431 release sites for insects. This type of data would be obtainable through the circulation of a survey to

432 translocation practitioners, as demonstrated in a review of mammal and bird translocations in which
 433 respondents ranked habitat quality as “excellent”, “good” or “fair or poor” (Griffith *et al.*, 1989).
 434 However, it can be particularly challenging to gauge habitat quality for insects, as highlighted in
 435 Williams *et al.*, (2014), in which conservation professionals often ranked habitat quality for carabid
 436 beetles as both “good” and “bad” in areas where there was maximal diversity. The subjectivity of
 437 habitat quality assessment suggests that, although this variable is of importance, the method by
 438 which this data is collected requires careful consideration of how to maximise objectivity.

439

440 Recommendations for improving standardisation and dissemination

441 Many of the translocations reviewed during this research were poorly documented either
 442 methodologically and/or in terms of long-term results. This presents a challenge to managers who
 443 wish to learn from the successful and the unsuccessful aspects of previous translocations in order to
 444 make evidence-based decisions regarding their own projects. For vertebrates, there is a growing
 445 body of literature encouraging the standardisation of documenting and monitoring the methods and
 446 outcomes associated with translocations (e.g. Fischer and Lindenmayer, 2000; Sutherland *et al.*,
 447 2010; Ewen *et al.*, 2012). Recently, similar standardisation-based recommendations have also been
 448 published for lepidopteran translocations (Daniels *et al.*, 2018). Complementary to improved
 449 standardisation, we also advise the dissemination of information, ideally through a centralised
 450 international database that facilitates the dispersion of information to an audience beyond academic
 451 circles (e.g. TRANSLOC, a translocation database for the Western Palearctic region, link:
 452 <http://translocations.in2p3.fr/>). In comparison to translocation reviews of other taxonomic groups
 453 (e.g. Griffith *et al.*, 1989; Cochran-Biederman *et al.*, 2015) the body of literature surrounding
 454 terrestrial insect translocations is limited; thus it is all the more important that platforms exist on
 455 which successful and unsuccessful projects can be shared and accessed effectively.

456

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Table 1. Predictor variables used in generalised linear models to identify factors relating to terrestrial insect translocation success.

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

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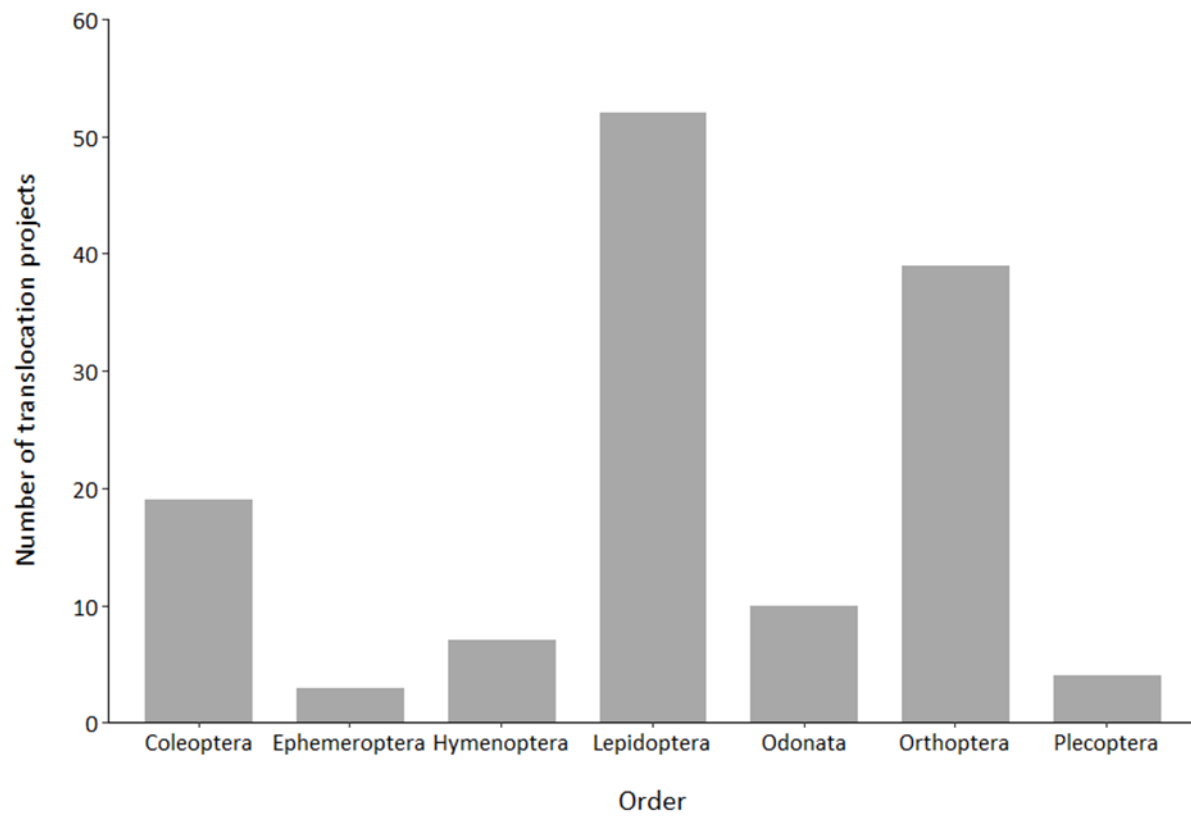


Figure 1. Number of terrestrial insect translocations reviewed for each insect Order ($n=134$).

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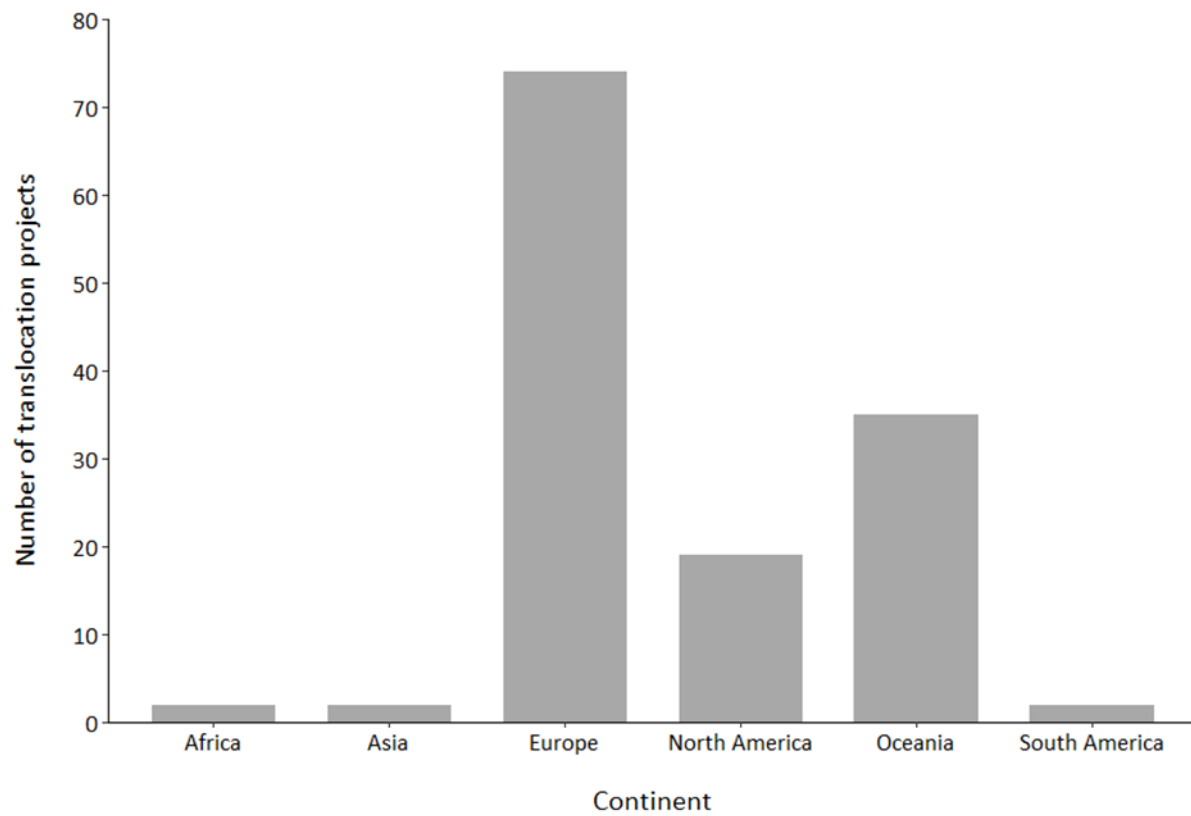


Figure 2. Number of terrestrial insect translocations reviewed by continent ($n=134$).

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Table 2. Information-theoretic model selection results for models relating predictor variables with the probability of successful translocation of terrestrial insect species. Number of estimable parameters (k), the second order Akaike Information Criterion (AICc), the Akaike differences (Δ_i) and the Akaike weights (w_i) are presented.

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

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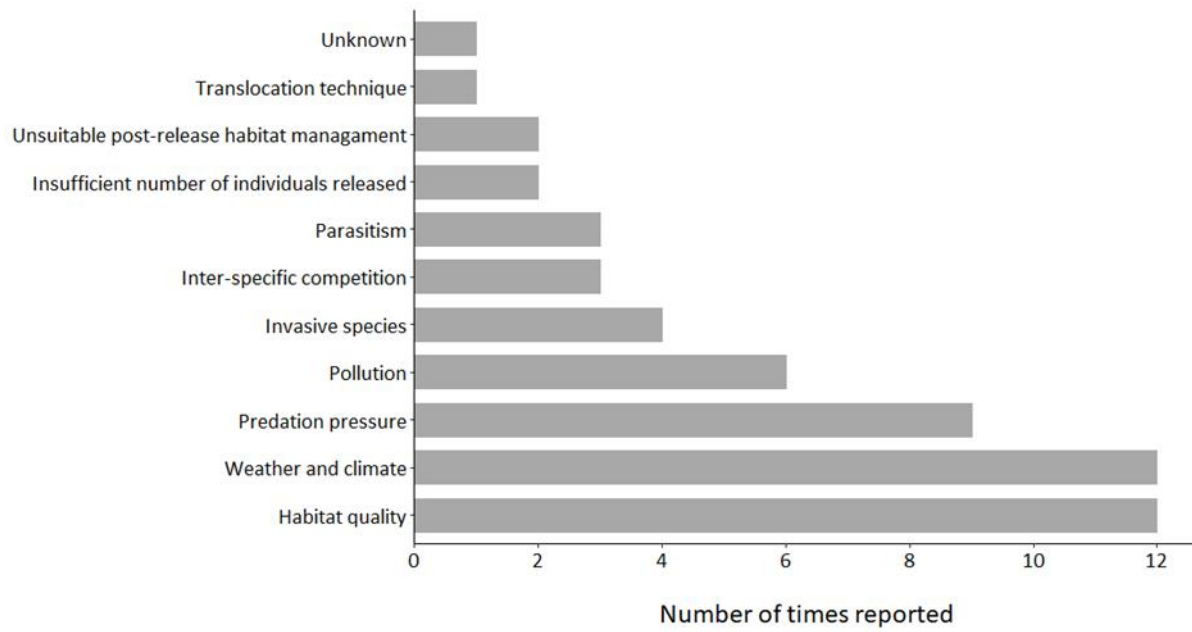


Figure 3. Factors reported as influencing the failure of terrestrial insect translocations ($n=33$). Several influential factors may have been reported for a single translocation project.

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