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Review paper

Factors affecting success of conservation translocations of terrestrial vertebrates: A global systematic review☆

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ABSTRACT

Translocation—moving individuals for release in different locations—is among the most important conservation interventions for increasing or re-establishing populations of threatened species. However, translocations often fail. To improve their effectiveness, we need to understand the features that distinguish successful from failed translocations. We assembled and analysed a global database of translocations of terrestrial vertebrates (n = 514) to assess the effects of various design features and extrinsic factors on success. We analysed outcomes using standardised metrics: a categorical success/failure classification; and population growth rate. Probability of categorical success and population growth rate increased with the total number of individuals released but with diminishing returns above about 20–50 individuals. Positive outcomes—categorical success and high population growth—were less likely for translocations in Oceania, possibly because invasive species are a major threat in this region and are difficult to control at translocation sites. Rates of categorical success and population growth were higher in Europe and North America than elsewhere, suggesting the key role of context in positive translocation outcomes. Categorical success has increased throughout the 20th century, but that increase may have plateaued at about 75% since about 1990. Our results suggest there is potential for further increase in the success of conservation translocations. This could be best achieved by greater investment in individual projects, as indicated by total number of animals released, which has not increased over time.

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☆ All data and code used for this analysis can be assessed here https://zenodo.org/record/4755697#.YKNXVVpR2Ul.

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1. Introduction

Humans have been moving animals around the globe for millennia, both accidentally and intentionally for a wide range of economic, religious, and cultural reasons (Simberloff, 2013).

The first documented translocation for conservation purposes (for definition see Table 1) took place in 1895, when kakapo (*Strigops habroptilus*) were released on offshore islands in New Zealand (Lloyd and Powlesland, 1994) to protect surviving individuals and establish insurance populations. Since then, translocations have been responsible for some of conservation’s most celebrated successes, such as the rescue from the brink of extinction of the Arabian oryx (*Oryx leucoryx*) (Price, 1989; Al Jahdhami et al., 2011), Californian condor (*Gymnogyps californianus*) (Walters et al., 2010; Parish and Hunt, 2016) and Lord Howe Island woodhen *(Hypotaenidia sylvestris*) (Frith, 2013).

Despite these success stories, conservation translocations often fail. Previous global reviews of conservation translocations have reported success rates of around 50% or less: 46% (Griffith et al., 1989), 54% (Bubac et al., 2019), 26% (Fischer and Lindenmayer, 2000), and 47% (Resende et al., 2020); the low success rate reported by Fischer and Lindenmayer (2000) may have been an underestimate because the outcome of many reviewed translocations was unknown at the time. For North America (including Central America and the Caribbean), Brichieri-Colombi and Moehrenschlager (2016) noted a success rate of 64%.

To improve success rates of conservation translocations, we need to identify the factors that distinguish successful from failed attempts. Previous reviews have proposed several predictors of success, including the number of animals released, habitat quality at the release site, the centrality of the release location in the species’ original range, the animals being sourced from the wild rather than by captive breeding, the nature of the original threatening process, and whether that threat had been removed at the release site (Griffith et al., 1989; Fischer and Lindenmayer, 2000; Brichieri-Colombi and Moehrenschlager, 2016; Bubac et al., 2019). Griffith et al. (1989) also suggested that success increased with the duration of the release programme and the reproductive potential of the species, but these two factors were refuted in a re-analysis of their data (Wolf et al., 1996, 1998).

Although these previous reviews had the general aim of identifying factors that differentiate successful conservation translocations from failed ones, the scale of this task caused them to differ in their approaches. Griffith et al. (1989) issued a questionnaire to conservation practitioners who carried out the intentional releases of mammals and birds (including game

Table 1
Definitions of terms taken from IUCN/SSC (6). * although this term is not ideal, it was preferred over assisted colonisation due to its negative connotations for First Nations peoples. First Nations peoples have land tenure over 40% of all terrestrial protected areas and intact ecosystems (Garnett et al., 2018) so the avoidance of alienating language and actions should be a priority amongst conservation biologists.

Term	Definition	Synonym
Conservation translocation	Conservation translocation is the intentional movement and release of a living organism where the primary objective is a conservation benefit: this will usually comprise improving the conservation status of the focal species locally or globally, and/or restoring natural ecosystem functions or processes.	–
Reinforcement	Reinforcement is the intentional movement and release of an organism into an existing population of conspecifics.	Augmentation; Supplementation; Re-stocking; Enhancement (plants only)
Reintroduction	Reintroduction is the intentional movement and release of an organism inside its indigenous range from which it has disappeared.	–
Assisted migration*	Assisted migration is the intentional movement and release of an organism outside its indigenous range to avoid extinction of populations of the focal species.	Benign Introduction; Assisted Colonisation; Managed Relocation
Ecological replacement	Ecological replacement is the intentional movement and release of an organism outside its indigenous range to perform a specific ecological function.	Taxon Substitution; Ecological Substitutes/ Proxies/ Surrogates; Subspecific Substitution, Analogue Species

species) in Australia, Canada, Hawaii, New Zealand, and the United States, asking them to identify factors associated with success.

Fischer and Lindenmayer (2000) extracted data from publications in 12 journals published over 20 years, included translocations from all countries and of all animal species, and analysed associations between certain factors and success. Brichieri-Colombi and Moehrenschlager (2016) carried out a systematic review of the North American translocation literature to identify participants for a questionnaire survey. Their aim was to analyse the relationship between success and the project goals, conservation status of the species, risk factors considered, and obstacles encountered. Bubac et al. (2019) systematically reviewed the worldwide translocation literature to quantify the frequency and duration of monitoring post-translocation and to observe any changes in reintroduction trends through time. Resende et al. (2020) aimed to provide an overview of the characteristics of translocation programmes and, specifically, assess the efficiency of release techniques.

There is a broad consensus that for a translocation to be successful it must result in the ultimate establishment of a self-sustaining viable population (Seddon, 2010; IUCN/SSC, 2013). In practice, however, it can be difficult to evaluate whether a particular project has succeeded in this way. Also, the success of translocations can be evaluated in other ways, depending on their specific goals and context. For example, a reinforcement (see Table 1) may be judged successful if it increases the genetic diversity of an inbred group, while for a critically endangered species the establishment of a breeding population in the wild may be considered a sufficient achievement in itself to judge the project a success even before the ultimate viability of the population is known. Several reviews have responded to this variability by accepting authors' evaluations of success as reported in their publications (Brichieri-Colombi and Moehrenschlager, 2016; Bubac et al., 2019; Resende et al., 2020). This approach has the disadvantage that inconsistencies in the definition of success add uncertainty to analysis of extrinsic factors affecting success. Other reviews have defined success as the establishment of a viable population, but Griffith et al. (1989) study was based on a survey, and success was likely judged by the practitioners who responded to the survey rather than being evaluated consistently across all studies. Fischer and Lindenmayer (2000) did not provide the criteria used to evaluate the viability of translocated populations.

In this review, we systematically compiled data from published reports of conservation translocations of terrestrial vertebrates worldwide and used these data to build models of the factors influencing outcomes of those translocations. We measured translocation outcomes in two ways: a general categorisation of projects as being successful or not, and population growth rate of translocated populations. To achieve consistency in the categorical evaluation of success, we identified the demographic factors associated with explicitly self-reported success and failure of translocations published in the International Union for Conservation of Nature's (IUCN) "Global re-introduction perspectives" reports (Soorae, 2008, 2010, 2011, 2013, 2016, 2018). We then used these same factors to consistently assign ratings of success or failure to a larger set of studies published in the broader literature. For a subsample of all published translocations that provided monitoring data on population size post-translocation, we estimated population growth rate and used that as a quantitative and unambiguous descriptor of the outcomes of those translocations. If a viable population is the ultimate goal of a translocation, then population growth is an "essential pre-requisite" for this (Armstrong and Seddon, 2008).

We analysed three broad categories of factors as predictors of translocation outcomes: (i) design elements of translocation projects; (ii) species-specific factors, such as higher-taxon membership, the nature of threatening processes, and level of threat according to IUCN categories; and (iii) situational factors, such as geographic locations and translocation type. The full list of predictors is provided in Table S1. The design elements included several that are frequently debated in the literature on conservation translocations, such as the best source of animals, from the wild or captivity; the best release method, soft or hard; and others such as the number of animals to release. These factors have large implications for the resourcing of translocation projects. The threatening processes affecting the species were included to assess whether certain threats are more difficult to ameliorate, potentially aiding future resource allocation. Biological traits such as body size and fecundity were not considered, as in some previous reviews (Fischer and Lindenmayer, 2000; Brichieri-Colombi and Moehrenschlager, 2016; Bubac et al., 2019), because these were deemed to be answering a related but different question about the capacity of species to establish new populations (Sol et al., 2012; Capellini et al., 2015; Redding et al., 2019), whereas our primary goal was to identify factors that can be controlled or manipulated by conservation managers and agencies responsible for design and implementation of translocation projects.

2. Methods

We followed the systematic review methodology outlined in Vetter et al. (2013). This has six main steps: (1) definition of a clear question; (2) extensive literature search; (3) formulation of inclusion and exclusion criteria; (4) critical appraisal of papers; (5) statistical synthesis; and (6) interpretation of results. We summarise these below (steps 3 and 4 are combined for brevity and step 6 is reported wholly within the main text).

2.1. Definition of clear question

> "How successful are conservation translocations of terrestrial vertebrates worldwide, and what features distinguish successful from failed translocations?".

2.2. Extensive literature search and inclusion/exclusion criteria

Data were acquired from two sources: (i) the Web of Science (Web of Science, 2019) (hereafter WoS) and (ii) the IUCN's "Global re-introduction perspectives" reports compiled by Pritpal Soorae (Soorae, 2008, 2010, 2011, 2013, 2016, 2018) (hereafter referred to as the IUCN reports). In April 2017, a Boolean string containing the terms "assisted migration", "reintroduction", "reinforcement", and "ecological replacement" and related synonyms was searched in WoS, with results constricted to the fields of conservation and ecology. This returned 1167 results in the initial methodological screening. Fifty papers were randomly (each paper was assigned a number and fifty numbers were randomly generated) assessed for suitability, and as a result of this several specific search terms were excluded. The revised search string yielded 620 publications. This assessment process was repeated for a sample of 20 papers to finalise the exclusion criteria, which omitted such terms as plant*, bacteria*, and geolog*. Both Boolean strings are provided in full in the SI methods. Only results in English were included. This yielded 543 publications. The final Boolean string was used again to update the review in June 2018 bringing the final total of 597 publications.

2.3. Critical appraisal

Following the IUCN/SSC (2013) definition (Table 1) and other publications discussing (Seddon, 2010) conservation translocations, projects were excluded if they were primarily experimental, for hunting purposes, or where the benefit was received only by the individual animal(s) translocated and not a broader population. Translocation events or units were defined as a group of the same species moved from one or more sources to the same general recipient area over a set period of time, because this was broadly how they were treated in the literature. Animals were considered terrestrial if they were listed as such by the IUCN Red List (IUCN, 2019). Of the 597 publications, 154 were deemed to meet all the above criteria, yielding data on 334 translocations. If more than one publication reported a single translocation unit, the most recent was chosen.

The same appraisal method was applied to the IUCN reports, which added information on 226 translocations. If these detailed the same translocation as a WoS publication, they were merged, i.e., information from two or more entries was combined to make one entry, to reveal the most complete data on a translocation. In all, 48 WoS datapoints were merged with 36 IUCN datapoints, resulting in 38 merged datapoints. The lack of overlap justifies the inclusion of the IUCN reports as they were included to reduce publication bias by capturing a portion of the grey literature. The final total number of non-duplicate cases was 514. This will be referred to as the complete dataset: IUCN reports (n = 190), WoS reports (n = 286), and merged (n = 38).

2.4. Definition of "success" and testing of its validity

Authors of the IUCN reports classified the outcomes of their projects using a standard terminology, as follows: failure (n = 9), partially successful (n = 70), successful (n = 67), highly successful (n = 42), for a total of 190 ratings (two were not categorised). However, no standard criteria were provided to place projects in these classes, and authors of IUCN reports chose classes based on their own perception of success. We accepted these classifications after assessing the grounds on which they were made (see below), except that to reduce ambiguity and create a binary success/failure classification we omitted projects judged by their authors to be 'partially successful', and we combined the 'highly successful' and 'successful' projects into a single category.

Publications collected from WoS (n = 286) did not conform to any single scheme for defining success, so the authors' views on whether their projects succeeded or failed were sometimes unclear and may have been inconsistent among studies. We therefore classified success or failure of the WoS-reported translocations using an approach that was consistent with the IUCN reports. To do this, we began by testing what population-level outcomes were associated with choices by authors of the IUCN reports to classify their projects as successes or failures. To guide this process, we first identified a priori a series of demographic indicators (see Table 2) that would indicate a range of outcomes of translocations, from inviable to viable populations. These were ordered following the logic that to achieve a self-sustaining population, released animals must first survive in adequate numbers, then reproduce, and then birth rates must be sustained above death rates such that population growth rate is

Table 2
The categorical definitions of demographic outcomes of conservation translocations.

Outcome	Description
Extinction	the translocated population declined to zero (or quasi-extinction).
High mortality	primarily consisted of translocations in which a large proportion of the animals died, this level of mortality being considered unsustainable given the typical life history and demography of the species in question.
Survival	a large proportion of translocated individuals survived, at a level deemed to be promising for the establishment of the species given its typical history and demography.
Reproduction	assumes the previous category as a baseline, with reproduction being reported. This was deemed as sufficient for inclusion due to the wide range of taxa included and the information available in the publications precluded the use of a fixed percentage.
Population increase	a population was deemed to have increased if stated by the author or the size or density of the translocated population was greater than the number translocated.
Viable population	survival, reproduction, and population growth continue for long enough (generations) that the population is considered likely to persist without further augmentation. This was assumed if stated by the author.

maintained or increased (Sarrazin and Barbault, 1996; Armstrong and Seddon, 2008). We expressed these indicators in general terms that could be matched to data or descriptions provided in various ways on various species by authors.

We reviewed all translocations from both the IUCN reports (n = 118) and the WoS publications (n = 286), and noted which of these outcomes was reported. We then tested the IUCN reports to assess which of the population outcomes was correlated with the practitioner-assigned classifications of 'success' and 'failure'. Translocations reported in the IUCN reports as being successful were primarily made up of cases that resulted in a viable population (24.8%), a growing population (26.6%), and reproduction (29.4%), although some reported only that they had achieved high initial survival (10.1%). Failures were associated with high initial mortality (55.6%) and population extinction (33.3%). These do not sum to 100% as the remainder could not be categorised. We then reviewed the WoS reports (n = 286), and classified them as successes (n = 99), failures (n = 64), or unclear (n = 123), according to whether they reported indicators of success or failure that matched those in projects in the IUCN reports that were considered to have succeeded or failed. WoS successes were primarily translocations that resulted in a viable population (23.2%), a growing population (45.5%), and reproduction (16.2%), a few exhibiting high survival (8.1%), and 6.1% of the 99 successes that could not be categorised on the basis of a population outcome but were considered successful by their authors.

The success and failures from the IUCN reports (109 successes, 9 failures) were combined with those from the WoS (99 successes, 64 failures) and the merged data (24 successes, 3 failures; 11 could not be categorised) to give a total of 232 success and 76 failures. Of these, 49 were omitted because they had non-numeric values for one or more predictor variable (start year of translocation and/or number of individuals translocated), and two were excluded as extreme outliers (the translocation of 6000 bison *Bison bison* in the 1920s and the translocation of 4110 European tree frog *Hyla arborea*). This left 257 translocations, of which 72% were classed as successes and 28% as failures. This is the composition of the categorical success dataset.

To further test whether our interpreted success or failure categorisation for the WoS data matched the evaluations of the authors of those studies, we used data acquired from a questionnaire (see Appendix item S1) emailed to 108 authors between March and May 2018. These 108 authors were the corresponding authors of the data-containing publications collected up until May 2018, for which an email address could be obtained and whose publication contained less than three translocation events. Publications with more than three translocations were excluded to reduce complexity because the original intention of the questionnaire was to gain access to standardized information for all variables of interest rather than having to infer some from the literature. However due to the relatively low response rate (37 responses out of 108), the questionnaire was used instead to test the validity of our interpretation of success and failure against the authors' knowledge. Of these 37 publications, we had to interpret 11 as the others had stated in the text whether they considered their projects to have been successes or failures. One publication was removed (Smeeton and Weagle, 2000), because it treated the translocations as separate in print but as a single translocation in the questionnaire, leaving ten data points. Of these ten, three had been classified correctly by us, in two cases we had been more cautious than the authors (we considered them partially successful while the authors considered them successful), three could not be classified at the time (we considered the outcome uncertain while the authors labelled partially successful or successful), and the final two were misclassified (we considered them successful while the authors considered them as partially successful or too early to tell). Both were populations of amphibians, one had persisted for over twenty years (Gustafson et al., 2016) while the other was stated as having less than 3% chance of extinction in 50 years (Chandler et al., 2015). Although this is ultimately an ad hoc qualitative assessment on a subset of our data, it increased our confidence that our categorisations of success and failure were realistic and conservative.

A subset of studies reported data on population numbers following translocation. We extracted these data for 87 translocations, 72 of which were also in the categorical success dataset. The annual growth rate was then calculated by subtracting the number of individuals translocated from this number of individuals stated at a later date (or publication year if not stated) and dividing the result by the initial number of individuals and the number of years elapsed. As this analysis contained animals of varying life histories, this annual growth rate was re-calibrated by dividing it by the generation length (in years) of the species (see Supporting Information for calculation of generation length). This weighted growth rate will be referred to as population growth rate and the 87 translocations make up the population growth subset. Positive population growth rate (mean 2.28) was associated with categorical success and negative (mean −2.42) with categorical failure (a post-translocation decline). This further supports the meaningfulness of the categorical success criteria.

2.5. Statistical synthesis

Twelve predictor variables (37 variables when formatted as dummy variables, due to some being multi-level factors; see Table S1) were tested for their relationship with success or failure, measured either as a binomial dependent variable in the complete sample of translocations, or as population growth rate in the subsample for which growth-rate data were available. Animal taxa were grouped at the species level, and all names standardised to those in the IUCN Red List (IUCN, 2019). Some species were translocated in several different projects. To prevent the introduction of non-independent errors by several representations of a single species, a random entry for each species was selected, and a sample dataset (with all species represented only once) was created. This dataset sub-sampling was repeated 1000 times. Each sub-sampled categorical success dataset contained 148 entries, detailing the translocation of 155 species, as there were two multi-species translocations, two endemic Hawaiian honeycreepers (Soorae, 2008) and seven species of ungulate in Zimbabwe (Soorae, 2013). Each sub-sampled population growth subset included 40 entries, comprising 40 species. Linear mixed effects models, with species as a random effect, were not used because of the unbalanced nature of the dataset (Harrison et al., 2018) i.e. few species were translocated multiple times while the majority were only translocated once. All numerical predictors were standardized.

To identify the most important variables in determining success, stepwise model simplification (forward and backward), using regression (logistic for categorical success and linear for population growth rate), and random forests (1000 trees) were carried out using the R v3.5 (R Core Team, 2018) package caret (Kuhn et al., 2018). Ten-fold cross-validation was used for both methods and the "best" model (in terms of dimension and variables included) for each dataset was selected by lowest cross-validation predictive error (Area Under the Curve (AUC) for the categorical success dataset and Root Mean Squared Error (RMSE) for population growth subset). The random forests technique —an averaged tree-based machine-learning method for fitting predictive models— was used to detect non-linear effects, via branch splitting, not captured by linear regressions (Breiman, 2001). The problem of overly correlated variables was avoided by setting the number of variables available to each tree to ten. The resultant variables—the ten most commonly selected by the stepwise selections and the ten most important in the random forests (see Table 3)— were combined into revised logistic and linear regressions, with non-linearities incorporated with the package splines (R Core Team, 2018). Polynomials above three degrees were not tested to avoid overfitting. All correlations were calculated using Pearson's r coefficient and controlled for the effect of species.

3. Results

We collated data on 514 published translocations (complete dataset) of 293 terrestrial vertebrate species undertaken between 1895 and 2017. Translocations were documented on every continent except Antarctica, and numbers of translocations have increased through time (Fig. 1). For summary statistics of the complete dataset see Table S2, Figs. S1–S10.

3.1. Identification of important predictor variables

Table 3 shows the important predictor variables identified from modelling in the categorical success dataset and population growth subset (for summary statistics of the categorical success dataset see Table S3, Figs. S11–S19 and for the population growth subset see Table S4, Figs. S20–S22). The effect of the fifteen variables deemed important for predicting categorical success are shown in Fig. 2(a). Six of these variables—the translocation taking place in Oceania, in North America, in Europe, the species being classified as Endangered by the IUCN, the number of individuals released, and the Corruption Perception Index (CPI) of the country where the translocation took place—were also selected in the population growth subset. The final two variables were modelled as non-linear effects with a 2-degree spline as these variables were deemed important by the random forests analysis. The number of individuals released and the threat classification of Endangered had positive effects on success, the translocation taking place in North America or Europe had no or minimal effect, while the translocation taking place in Oceania or in a country with a high CPI score (i.e. low corruption) negatively affected success. The results for the population growth subset (Fig. 2(b)) were similar but with a slightly positive effect for translocations taking place in North America and a reduction in the negative effect of the second spline of the CPI.

Boxplots and response curves for the six variables selected in the analysis of both response variables are shown in Fig. 3. The negative effect of a translocation taking place in Oceania is more pronounced in the probability of categorical success compared to the population growth rate, while the positive effect of North America is more evident in the population growth rate. The effect of the translocation taking place in Europe is positive for both metrics while the species being Endangered had little effect on either metric. The effect of total numbers released was complex: success increased up to about 20–50 individuals and declined slightly above a few hundred individuals (although the evidence of this decline is weak because of few datapoints). The corruption index of each country–-included as a proxy for the ability to enforce conservation-related legislation (e.g. effectively prohibit hunting and/or land clearing)—displayed even greater non-linearity. Both categorical success and population growth were high for countries with low CPI scores (high corruption) and surprisingly low for countries with values close to 80 and 90 (low corruption); this last effect was mainly due to Australia and New Zealand.

3.2. Correlation between variables

The highest correlation exhibited in the categorical success dataset was between Europe and "IUCN threat 9: Pollution" (Pearson's $r = 0.60$) and North America and "IUCN classification: Least Concern" ($r = 0.60$). The population growth subset exhibited the same correlation between Europe and Pollution ($r = 0.60$) and CPI. Oceania was correlated with CPI ($r = 0.50$ in both) and "IUCN threat 8: Invasive & other problematic species, genes & diseases" ($r = 0.30$ categorical success and $r = 0.40$ population growth rate) in the dataset and subset. Invasive species were the dominant component of this IUCN threat, making up approximately 80% of cases in the dataset and subset.

3.3. Temporal trends

The variable 'start-year' was indicated as the most important variable in both statistical methods for the categorical success dataset: success has increased through time (Fig. 4). We tested each of our original predictor variables for a trend with time, to identify any that might explain the effect attributed to start-year. This found three temporal trends in characteristics of translocation: (i) a rising proportion of translocations that were reintroductions versus other types (Pearson's $r = 0.29$) (see Table 1 for definitions); (ii) a declining proportion that were assisted migrations versus other types ($r = -0.44$); and (iii) a rising

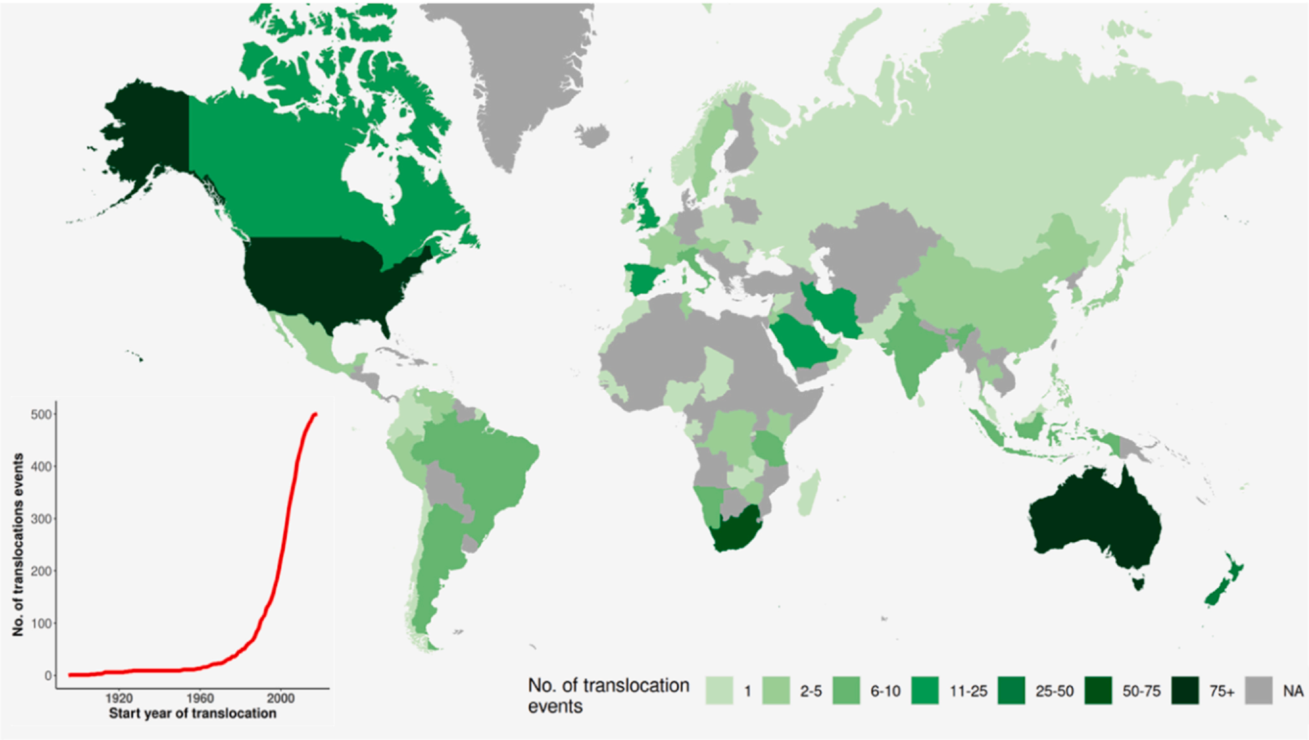
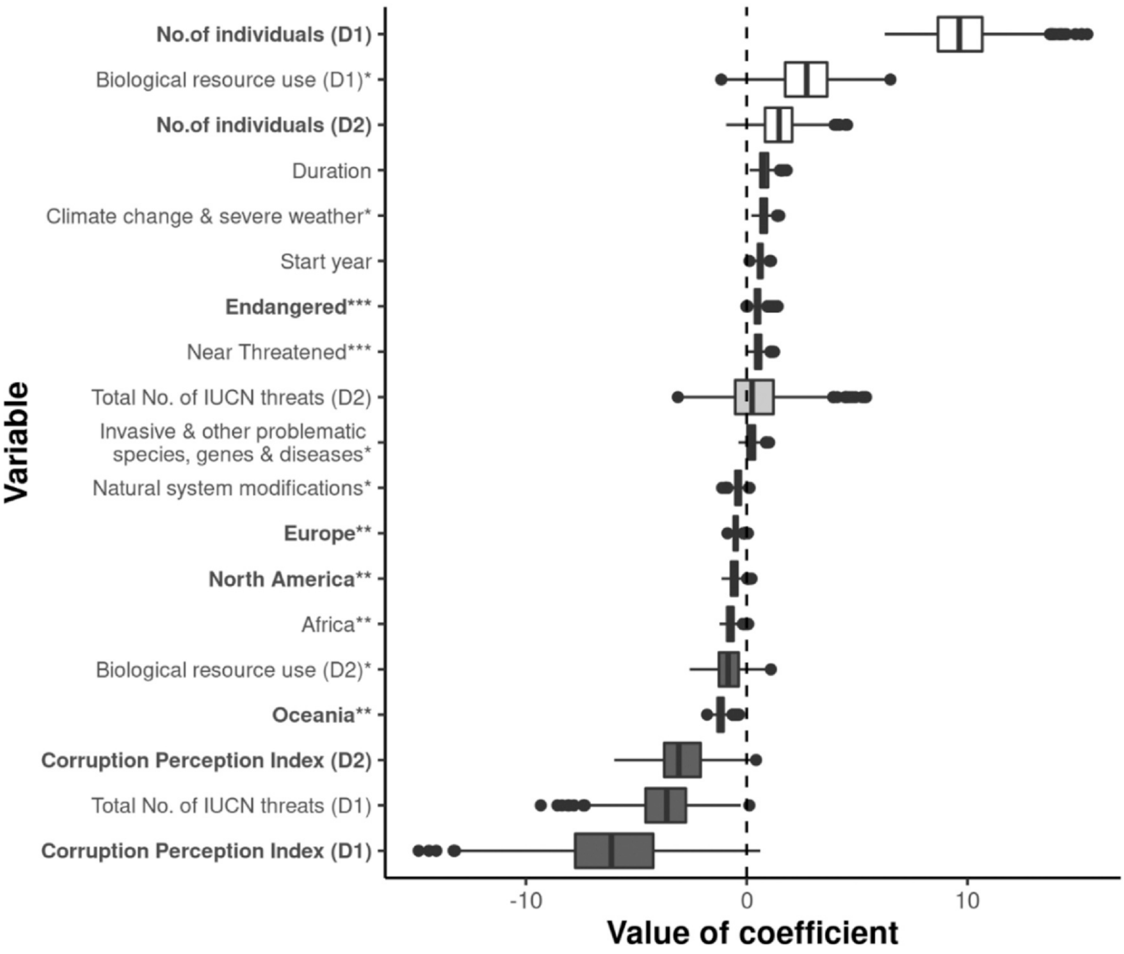


Fig. 1. The spatial and temporal spread of conservation translocations of terrestrial vertebrates. (a) The number of translocations that have taken place in countries worldwide ($n = 514$). (b) The cumulative increase of translocations through time ($n = 500$, 14 had no definitive start year). The apparent recent slow-down may be caused by the lag (median 9 years, mean 13.67, SD 16.03) between the start of the translocation programme and publication.

Table 3
The Top 10 most important variables selected by the stepwise logistic or linear regression method and random forests for the categorical success dataset and population growth subset, as detailed in the main text. The six variables common between both are in italics.

	Categorical success dataset		Population growth subset	
	Logistic regression	Random forests	Linear regression	Random forests
1	The start year of translocation	The start year of translocation	IUCN classification: Least Concern	Animals sourced from captivity
2	IUCN threat 7: Natural system modifications	*The number of individuals translocated*	Animals sourced from captivity	*The number of individuals translocated*
3	IUCN threat 11: Climate change & severe weather	IUCN threat 11: Climate change & severe weather	*Continent: North America*	Animals sourced from wild
4	*Continent: Oceania*	Duration	*The number of individuals translocated*	IUCN classification: Least Concern
5	*IUCN classification: Endangered*	*Continent: Oceania*	Soft release	*Continent: North America*
6	IUCN classification: Near Threatened	IUCN threat 8: Invasive & other problematic species, genes & diseases	*Continent: Europe*	Soft release
7	Duration	Number of IUCN threats experienced by species	*Continent: Oceania*	*Continent: Oceania*
8	Continent: Africa	*Corruption Perception Index of country*	*IUCN classification: Endangered*	Species was a mammal
9	*Continent: North America*	IUCN threat 7: Natural system modifications	Animals sourced from wild	IUCN threat 1: Residential & commercial development
10	*Continent: Europe*	IUCN threat 5: Biological resource use	Translocation was a reintroduction	*Corruption Perception Index of country*

(a) Categorical success



(b) Weighted population growth

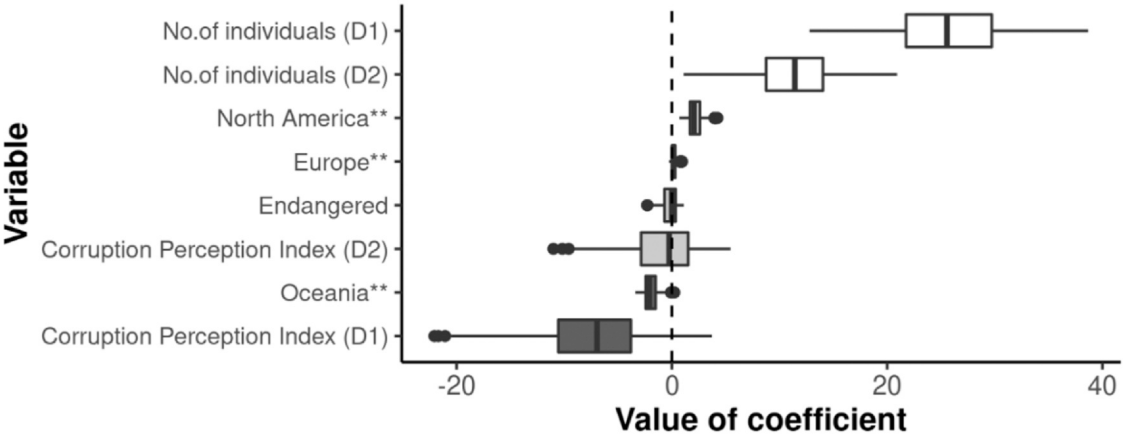


Fig. 2. The standardized coefficient values (i.e., relative effect sizes) from (a) the logistic regression performed on the categorical success dataset ($n = 257$) and (b) the linear regression performed on the population growth subset ($n = 87$). White indicate positive effects where the boxplot whiskers do not overlap zero; light grey overlaps zero; and dark grey indicates a statistically discernible negative effect. Box widths show the interquartile range, the mean is represented as a bold vertical line within each box, and whiskers denote the 2.5–97.5th percentiles. Overlapping zero does not indicate no statistically discernible effect of that variable: as these coefficients are taken from 1000 subsets of the data (see Methods) this only indicates that the species translocated had varying results, e.g., on six occasions the coefficients for the "Corruption Perception Index (D1)" in the categorical success dataset (a) were positive. Variables in bold in (a) are also in the (b). D1 and D2 state the 1st and 2nd degree splines, respectively, of the non-linear variables. *, **, and *** indicate that the variables belong to the IUCN threats, Continent, and IUCN classification variables shown in Table S1.

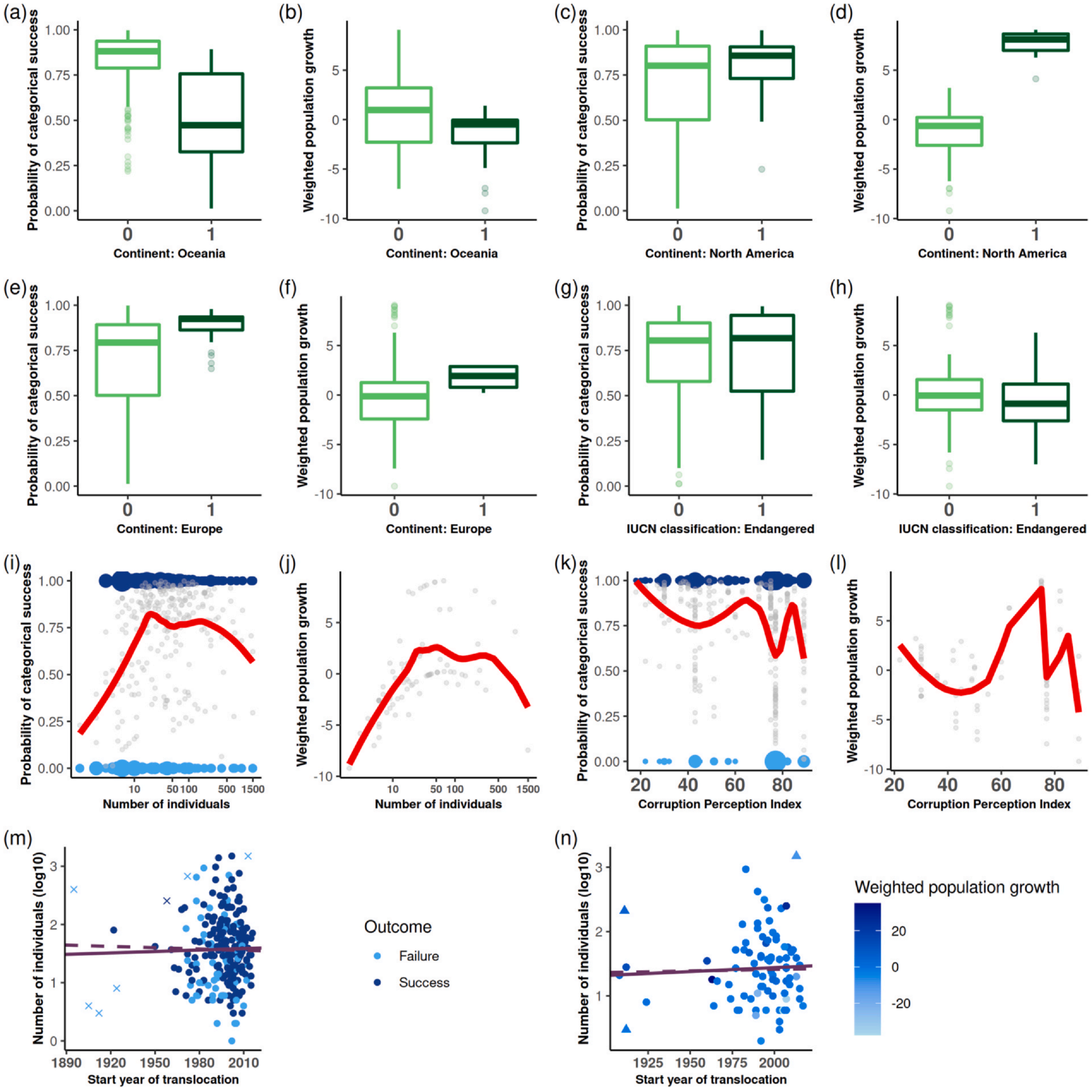


Fig. 3. The effect of Oceania (a–b), North America (c–d), Europe (e–f), the IUCN classification Endangered (g–h), the number of individuals (i–j), the Corruption Perception Index (k–l) in the categorical success dataset and population growth subsets; relationship of start year with number of individuals (m–n). a–h, the features for the boxplots are as in Fig. 2 but only showing the six variables deemed important by both metrics. One and zero on the axes of a–h indicate the presence or absence of the stated predictor, i, Predicted probabilities for success (grey dots) for number of individuals from the logistic regression models (detailed in text). Smoothing (red line, Local Polynomial regression (LOESS) with a span of 50%) indicating the trend. Size of dots are scaled to number of translocations. j, Predicted probabilities for population growth rate (grey dots) for number of individuals from the linear regression models (detailed in text). Smoothing line as in i. k–l as i–j but with Corruption Perception Index. m, Relationship between start year and number of individuals in the categorical success dataset, solid line is linear model trend line ($\beta = 0.0008$, $p = 0.71$), dashed line is linear model ($\beta = -0.0007$, $p = 0.80$) with the most leveraged points (indicated by x's and calculated as four times the mean Cook's Distance) omitted. n, as m but in the population growth subset and triangles used in place of x's. Linear model ($\beta = 0.0012$, $p = 0.65$), linear model without leveraged points ($\beta = 0.0005$, $p = 0.87$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

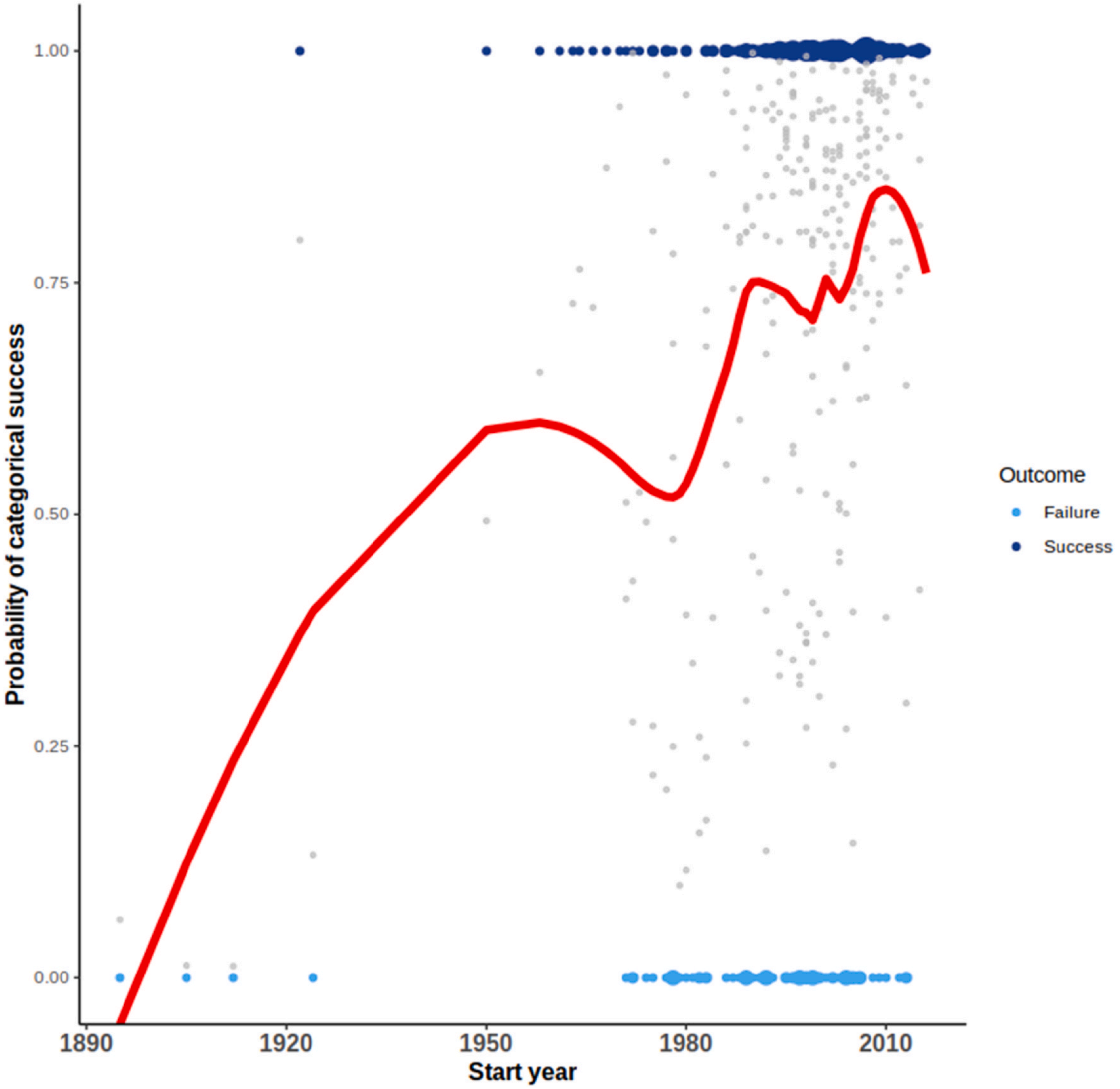


Fig. 4. The effect of start year on the probability of categorical success. Details are as in Fig. 3. Controls for the effect of all variables in Fig. 2(a).

proportion of translocations that used soft versus hard release protocols ($r = 0.27$). Start year was not deemed an important variable when using the population growth rate and, in fact, exhibited a negative trend.

3.4. Design elements of translocation and success

Although wild animals were more likely to be used in translocation projects in the categorical success dataset (Fig. S11), they did not result in higher success rates (wild 70.2%, captive 76.0%). However, translocations using wild animals resulted in higher population growth rates than translocations of captive-bred animals (wild +2.2, sd 5.7; captive −2.8, sd 12.2; mixture −0.1, sd: 2.7, unsure 0.0, sd:0.4) and translocation of wild animals was deemed important by both statistical methods (Table 3). Soft releases were more common in both the categorical success dataset (Fig. S11) and population growth subset (Fig. S20). There was little evidence for a difference in categorical success for soft versus hard releases (soft 79.8%, hard 75.0%). However, hard releases resulted in higher mean population growth rates (hard +5.6, sd 9.8; soft −1.3, sd 6.9). We found similar categorical success rates for amphibians, birds, and mammals, all between 67% and 74%, while categorical success for reptiles was higher at 85%. Mammals had the highest mean population growth rate (amphibians −4.0 (sd: NA), birds −3.8 (sd: 12.4), mammals +0.8 (6.4), reptiles −0.12 (sd: 22.3)).

4. Discussion

The factor that had the strongest influence on the success of translocations was the number of individuals released. This suggests that a crucial determinant of success is sufficient resourcing to enable the release of at least 20–50 individuals. However, there has been no trend for an increase in the number of animals released over the last century (Fig. 3). This suggests that there is further scope for improvement in the success of translocations by increasing investment in individual translocation projects (Berger-Tal et al., 2020). Otherwise, our analysis demonstrates a strong effect of geography on outcomes of translocations. Translocations in Europe and North America were marginally more successful than elsewhere, while translocations that took place in Oceania were more likely to fail. These trends are probably the result of differences in the dominant threats in each region, specifically the prevalence of harmful invasive species in Oceania.

The importance of the number of individuals released in promoting success of translocations is consistent with previous analyses (Griffith et al., 1989; Wolf et al., 1996; Fischer and Lindenmayer, 2000; Germano and Bishop, 2009; Brichieri-Colombi and Moehrenschlager, 2016). Invasion biology also supports a relationship between releasing more individuals and increased likelihood of establishment (Brook, 2004), as does the theory of population viability (Soulé, 1987; Frankham et al., 2014). Small populations are more susceptible to extinction due to stochastic environmental, genetic, and demographic variations (Caughley, 1994). The positive effect of number of individuals is most pronounced at lower numbers, as each additional individual makes a greater contribution to the population escaping the region of high extinction risk when that population is small (Soulé, 1987). There was a plateau in success above approximately 20–50 individuals, and possibly a decline at much larger numbers; this surprising result could be due to cases where invasive predators were still present and able to threaten even quite large founder populations (Short et al., 1992; Lloyd and Powlesland, 1994; Bannister et al., 2016) or where habitat quality was low (Garson et al., 1992; Martinez-Abrain et al., 2011). This is not to say that 20–50 animals is an optimal number to release, because each translocation is affected by context-specific factors (Armstrong and Seddon, 2008), such as the life history of the species, carrying capacity, and others that we could not investigate.

Correlations between geography and other variables suggest some possible causes of the apparent effect of geography on translocation success. A high proportion of species translocated in Europe were threatened by pollution, suggesting more localised threatening factors than in other continents, such as Oceania. If threats are localised, translocations are more likely to be able to separate threatened species from them. On the other hand, the pervasiveness of the threat of invasive species in Australia (Woinarski et al., 2015) and New Zealand (Holdaway, 1999) is likely a key factor in the low success found in those countries. Historically, species in Oceania have been protected from introduced predators by establishing them in areas surrounded by predator-proof fences or on offshore islands that they had not previously inhabited (Short et al., 1992; Lloyd and Powlesland, 1994). The prevalence of translocating species of Least Concern—and which are therefore abundant in the wild with ample research opportunities—in North America may contribute to the high success rates recorded there. Brichieri-Colombi and Moehrenschlager (2016) also found that many translocations undertaken in the United States of America—which contribute 81% of the North American translocations in this subset—are species that are not globally threatened but only possibly locally at-risk.

The categorical success of conservation translocations has improved through most of the twentieth century, such that while in the early 1980's only around 50% of attempt translocations succeeded, the success rate is now around 75% (Fig. 4). We were unable to identify any single change in features of translocation projects that could explain this rise in categorical success through time. We suggest two potential hypotheses to account for the apparent improvement: that one or more additional unmeasured variable(s) must be responsible; or that authors have become less stringent in their evaluation of success, and that this has influenced our results in spite of our attempts to categorise success consistently. The unknown variable could be a composite factor such as increased skill in the implementation of translocations, or avoidance of cases that previous experience shows to be high-risk (Seddon et al., 2007). A more risk-averse approach is implied by the fact that there has been a decline in releases outside the known range of the species in question (i.e., assisted migrations), which are likely to be more difficult due to the unproven suitability of the recipient area (McLachlan et al., 2007; Seddon et al., 2009). Assisted migrations were a common method employed historically to protect species in Oceania, but even though they have been predicted to increase in the future due to climate change (Hunter, 2007; McLachlan et al., 2007; Hoegh-Guldberg et al., 2008; Seddon et al., 2014; Gallagher et al., 2015) our analysis suggests their use has decreased through time. The decline in riskiness of translocations is also supported by the observation that releases of wild-sourced rather than captive animals have tended to decline, and by an increasing trend for releases into fenced rather than open reserves (see Figs. S16–S18).

Although categorical success of translocations increased through time, we found no corresponding temporal trend in the population growth rate of translocated populations. This could imply that authors have indeed become more generous in labelling translocations as successful. However, it is also possible that the population growth rate metric is inherently biased against more recent translocations in two ways. First, recently translocated populations have had less time to settle and reproduce, so they are less likely to achieve high population growth rates; and second, our weighting of population growth rate may have meant that recently translocated populations of long-lived species would have needed inordinately high fecundity to achieve growth rate.

Our analysis revealed an effect of duration of translocation projects on success: projects involving successive releases that were spread over longer periods were more likely to be categorised as successful. This factor was not deemed important as a predictor of population growth, possibly because only short-lived species could achieve high rates of population growth in projects of short duration. However, 79% (38/48) of translocations with negative population growth rate had a duration of two years or less. The release of animals over longer time periods might improve ultimate success, by providing compensation for short-term fluctuations in survival due to demographic or environmental stochasticity that could otherwise cause the failure of short-term projects (Hardy et al., 2018). This effect would be similar to that of repeated introductions increasing the probability of establishment of invasive species (Redding et al., 2019).

Our observations of temporal trends in success rates of translocations could possibly also be influenced by publication bias against failures. Due to scarcity of conservation funding, translocation projects may simply avoid or delay announcing their failures. This could potentially account for the low failure rate (8%) seen in the IUCN reports. The only attempt to quantify publication bias in studies of translocations, on herpetofauna in New Zealand (Miller et al., 2014), found that it was minimal for failures and high for uncertain outcomes, leading to an overestimation of success rates.

The threat classification ‘Endangered’ was an important predictor of success in our models, but the direction of this effect was unclear and minimal. Arguments could be made for either a positive or negative effect on success of translocating Endangered species. Endangered species may be seen as high priority, and so translocations of Endangered species may be allocated more resources and therefore be more likely to succeed; or such translocations could be more failure-prone because of lack of available habitat or source populations. Soft-release methods, such as the provision of pens and/or supplemental food at release sites, are thought to aid acclimation and promote site-fidelity in some species (Moseby et al., 2014; Tetzlaff et al., 2019), while proponents of hard releases argue that it reduces costs (de Milliano et al., 2016). We found no evidence of a relationship between success and release method, similar to findings of past reviews (Griffith et al., 1989; Wolf et al., 1996, 1998; Fischer and Lindenmayer, 2000; Short, 2009). We did find that the population growth rate for hard releases was substantially higher than that of soft releases, although it may be difficult for reviews to detect such differences (Moseby et al., 2014). Unlike previous studies, we found no evidence for categorical success of translocation of wild-sourced versus captive-bred stock (Fischer and Lindenmayer, 2000; Jule et al., 2008; Resende et al., 2020), nor that translocations of birds were more successful than of mammals (Wolf et al., 1996). However, we did find that the population growth rates were higher for wild-sourced than captive stock, and for mammals rather than birds. Whether translocated animals were sourced from the wild was one of the most important factors in predicting population growth rate (Table 3). Translocations of captive-bred stock were more likely to exhibit negative population growth rates, possibly an outcome of reduced antipredator responses due to captivity involving high levels of human contact (Zidon et al., 2009). The absence of this negative effect in the categorical success dataset may reflect biases of practitioners who have already invested so much in captive breeding programmes and so may be more lenient with success criteria than other practitioners.

5. Conclusions

This comprehensive review of the determinants of success or failure in vertebrate translocations has demonstrated that the level of investment in translocation projects, represented by the number of individuals released and the duration of release programs, has a strong effect on the ultimate success of those translocations. There remains considerable scope for improvement in translocation success, based on the lessons of over a century of trial, error, and refinement in the science of conservation biology. Our analysis suggests that the key to improving success is to increase investment in individual projects. Our use of two different metrics counteracted the drawbacks of each method and increased the robustness of this study but in some cases the two metrics provided inconsistent results. This highlights the need to develop a set of agreed and defined reporting criteria for translocations programs that would allow more thorough and informative global comparisons in the future, echoing calls by Seddon et al. (2007) over a decade ago. This would reduce problems of interpreting success or failure and promote improvements in the practice of translocations, leading to higher rates of success in the future.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at (https://zenodo.org/record/4755697) doi:10.1016/j.gecco.2021.e01630.

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