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RESEARCH ARTICLE

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The relative influence of geographic and environmental factors on rare plant translocation outcomes

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Abstract

1. Conservation translocations are an established method for reducing the extinction risk of plant species through intentional movement within or outside the indigenous range. Unsuitable environmental conditions at translocation recipient sites and a lack of understanding of species–environment relationships are often identified as critical barriers to translocation success. However, previous syntheses have drawn these inferences from analyses of qualitative feedback rather than quantitative environmental data.
2. In this study, we use a data set of 235 translocations conducted in the US to understand the influences of geographic and environmental factors on three metrics of translocation success: population persistence, next-generation recruitment and next-generation maturity. We use random forest models to quantify the relative importance of geographic and environmental factors that characterize dissimilarity between source and recipient locations, the position of recipient sites relative to species' ranges and niche metrics derived from these ranges. We also compare the importance of these variables with more conventional predictors (e.g. founder population size).

For affiliations refer to page 11.

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3. Our results indicate that geographic and environmental variables can be as insightful as conventional variables for predicting plant translocation outcomes. The climate suitability of recipient sites, estimated using species distribution models, was the strongest relative predictor of whether a population persisted, with populations situated in more suitable climates displaying greater persistence. Next-generation recruitment and maturity were best predicted by niche metrics; species in more biotically limiting environments, including tropical regions and soils with high relative nutrient retention, as well as species with the broadest precipitation niches, were the least likely to attain these next-generation benchmarks.
4. *Synthesis and applications*. Our study is one of the first to quantify the important role of spatial and climatic factors in rare plant translocation outcomes. We provide a novel geographic and environmental perspective on outcomes in plant translocations and demonstrate opportunities to improve translocation success not only by adhering to established best practice guidelines but also by integrating spatial modelling approaches into planning and management processes.

KEYWORDS
climate suitability, conservation translocation, endangered species, population restoration, reintroduction, species distribution model, threatened species

1 | INTRODUCTION

There is an urgent need to halt the loss of biodiversity, as global indicators report widespread and ongoing decline (Díaz et al., 2019). A recent study of vascular plant diversity estimates that approximately 40% of species are at risk of global extinction (Nic Lughadha et al., 2020). Conservation translocation, defined by the IUCN as the intentional movement of a target organism for its conservation benefit (IUCN, 2013), is an established approach for reducing the extinction risk of plants when in situ measures have failed to meet conservation objectives (Maunder, 1992). Thousands of plant translocations have been documented worldwide, allowing insights into management trends and the factors that drive project outcomes (Bellis, Osazuwa-Peters, et al., 2024; Fenu et al., 2023; Liu et al., 2015; Silcock et al., 2019).

Translocation syntheses have consistently confirmed that using a large number of founding plants is one of the best predictors of a positive outcome (Bellis, Osazuwa-Peters, et al., 2024; Godefroid et al., 2011; Silcock et al., 2019). In contrast, environmental attributes of the recipient site (e.g. climate, Godefroid et al., 2011; Silcock et al., 2019), and a lack of understanding of species' relationships with the environment, are often identified as critical barriers to success (Godefroid et al., 2016). However, to date, the role of environmental factors in influencing translocation outcomes has generally been inferred from qualitative feedback from practitioners rather than quantitative environmental data (though see Monks et al., 2023).

Evidence and theories from the restoration and biogeographical literatures point towards several ways in which species-environment relationships may influence translocation outcomes. First, because adaptation to local environments is both taxonomically and geographically widespread in plants (local adaptation detected in 71% of studies, Leimu & Fischer, 2008), shorter environmental distances between source and recipient sites should help to avoid maladaptation of the translocated individuals (Houde et al., 2015). Second, as geographic and environmental gradients operating across species' ranges are associated with variability in the survival and growth of populations (Bontrager et al., 2021; Brown, 1984), placement of plants within environmentally optimal areas of the range may promote long-term viability (Guisan et al., 2013; Maschinski et al., 2012). Third, because the response of introduced plants to site conditions is influenced by properties of the species' environmental niche (Pywell et al., 2003), species with broader niches may respond better to translocation through a wider tolerance of environmental conditions (Vincent et al., 2020).

Some of these concepts have been explored through analyses of transplant experiments and botanical garden collections, where relationships between plant performance and geographic or macroclimatic factors have been quantified (Bontrager et al., 2021; Thomas et al., 2022). For example, analyses of transplant experiments have shown that populations moved to climatically marginal sites (e.g. colder or drier parts of the range) exhibit lower relative performance (Bontrager et al., 2021), whereas analyses of a botanical garden's ex situ collection have demonstrated that individual survival increases

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with greater climate similarity between in situ and ex situ sites (Thomas et al., 2022). However, the goals and ecological settings in which plant material was moved in these studies differs from those of a conservation translocation, where the primary goal is to establish a self-sustaining population in the wild.

Here, we utilize the Center for Plant Conservation Reintroduction Database (Bellis, Albrecht, et al., 2024) to assess the importance of geographic and environmental variables for achieving population persistence, next-generation recruitment and next-generation maturity in conservation translocations. We calculate a suite of predictors that characterize the dissimilarity between source and recipient locations, the position of recipient sites relative to species' ranges and niche metrics derived from these ranges. A prior study used the database to assess the importance of management techniques, qualitative site attributes and biological traits for attaining different metrics of translocation success (Bellis, Osazuwa-Peters, et al., 2024). Here, we use the top-performing variables in that study to understand the relative importance of our novel set of geographic and environmental predictors for influencing translocation outcomes and their potential application in translocation planning and management.

2 | MATERIALS AND METHODS

2.1 | Data collection

We accessed data on 235 translocations of 121 plant taxa from the questionnaire-based Center for Plant Conservation Reintroduction Database (CPCRD) (Center for Plant Conservation, 2022) (see Appendix S1). This subset of the CPCRD included projects with data on at least one metric of success (persistence, recruitment or maturity) as well as data for creating at least one of the categories of geographic and environmental predictors (site dissimilarity, site position or niche metric). We excluded population 'augmentations' or 'reinforcements', as it was unclear whether persistence or the attainment of life-cycle benchmarks in these projects was due to outplanted individuals or naturally occurring plants. Our subset of translocations had been monitored for an average of 8.4 (SD 7.4) years and encompassed diverse biogeographical representation, featuring species with distributions centred in tropical (<25° latitude, *n* projects = 61), subtropical (25–35°, *n* = 71) and temperate regions (>35°, *n* = 87) (species distribution information was unavailable for 16 projects).

Each data point in the CPCRD represents a unique translocation project defined as the outplanting of plant propagules of a single species over a single or multiple years at the same site, or in multiple locations (<1 km apart) within a single site. If a species was translocated to multiple locations, the CPCRD requires contributors to determine whether they qualified as single or separate projects based on their familiarity and knowledge of the species and translocation sites. To support this decision, the CPCRD also provides two rules of thumb: (1) spatial proximity rule: (i) distinct units that are <1 km apart should be collapsed into a single translocation project, (ii) distinct units that are 1–10 km apart should be considered single or separate projects depending on the species biology, project goals and habitat, (iii) distinct units that are >10 km apart should be considered separate translocation projects and (2) Experimental treatments rule: collapse all experimental treatments (such as competition reduction, herbivore exclusion or water supplementation) at a site into a single translocation project unless they can be considered separate projects based on the spatial proximity rule.

2.2 | Metrics of translocation success

We evaluated translocation success across three metrics: population persistence (extant or extinct), next-generation recruitment (attained or not attained) and next-generation maturity (attained or not attained). Although these binary metrics simplify complex outcomes, they are necessary for standardizing diverse data sets and allow comparability with Bellis, Osazuwa-Peters, et al. (2024) and other relevant syntheses (e.g. Silcock et al., 2019). For population persistence, we grouped all extinct populations with populations containing <50 individuals and a decreasing population trend, based on the minimum viable effective population size rule in which 50 individuals are assumed to represent the absolute minimum number of plants required to prevent inbreeding depression (following the same methodology and justification as in Bellis, Osazuwa-Peters, et al., 2024).

2.3 | Predictor variables

We identified 39 geographic and environmental predictor variables that may influence rare plant translocation outcomes (Table 1). We assigned each of these predictors to one of three categories: site dissimilarity, site position or niche metric. We formulated hypotheses according to long-standing biogeographical theories, work on translocations and transplant experiments and research from the restoration and invasive species literature (Table 1). We considered studies on restoration and invasive species based on the assumption that characteristics that are associated with invasion success for widespread species, or restoration success in common species, would also be associated with translocation success in rare species (Dalrymple et al., 2012; Kaye, 2009).

We also analysed the relative importance of eight 'conventional' predictors of translocation outcomes (Table 1), including management techniques (founder size, monitoring length, number of source populations and number of outplanting subsites), qualitative site attributes (habitat quality pre-outplanting and habitat quality change) and biological traits (clonal reproduction and life span). We selected the top three conventional variables for each success metric in the all-life span models presented in Bellis, Osazuwa-Peters, et al. (2024). As model evaluation was low for the all-life span population persistence model in that study, we selected the top-ranked

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TABLE 1 Predictor variables included in random forest models that may influence population persistence, the attainment of next-generation recruitment and next-generation maturity in US-based rare plant translocations.

Variable(s)	Variable description (units)	Hypothesized relationship	Biogeographical theory/example evidence from previous studies
Site dissimilarity			
Geographical distance	Euclidean distance between source and recipient site (km)	Negative	McKay et al. (2005), but see Maschinski et al. (2013)
Environmental dissimilarity ($n=8$)[a]	Euclidean distance between source and recipient site in environmental space (unit determined by variable)	Negative	Maschinski et al. (2012), Houde et al. (2015), Thomas et al. (2022)
Site position			
Geographic peripherality	Position of recipient site relative to the centre and the edge of the species' range (peripherality ranges from 0 to 1 with larger values indicating greater proximity to range edge)	Negative	'Center–periphery hypothesis' (Brown, 1984)
Latitudinal position	Location of recipient site relative to species' latitudinal extent (normalized for comparability; values range between 0 and 1, low to high)	Bell shape	'Center–periphery hypothesis' (Brown, 1984), but see Angert et al. (2020)
Environmental position ($n=8$)[a]	Location of recipient site within gradient of environment variable encompassed by range polygon (values range between 0 and 1, lowest and highest)	Bell shape	'Center–periphery hypothesis' (Brown, 1984), but see Angert et al. (2020), Bontrager et al. (2021)
Climate suitability	Climatic suitability predicted using species distribution models (normalized for comparability, values range between 0 and 1, low to high)	Positive	Maschinski et al. (2012), Guisan et al. (2013)
Niche metric			
Geographic range size	Area (km^2)	Positive	Goodwin et al. (1999), Pywell et al. (2003)
Latitudinal centre	Central point of species range (decimal degrees)	Variable	Stronger abiotic selection towards poles versus biotic selection towards tropics (Hargreaves et al., 2020; Runquist et al., 2020); Ecological tolerance scales with latitude, 'Rapoport's rule' (Stevens, 1989)
Latitudinal extent	Extent of species range (decimal degrees)	Positive	Goodwin et al. (1999), Pywell et al. (2003)
Environmental niche breadth ($n=8$)[a]	Breadth of environmental conditions observed across the species range (unit determined by variable)	Positive	Goodwin et al. (1999), Pywell et al. (2003), Vincent et al. (2020)
Environmental niche center ($n=8$)[a]	Median of the environmental conditions observed across the species range (unit determined by a variable)	Variable	Louthan et al. (2015), Rajakaruna (2018)
Conventional			
Founder size	Number of individuals across all life stages introduced to recipient site (natural logarithm, ln)	n/a	Bellis, Osazuwa-Peters, et al. (2024)
Life span	Approximate life span of focal species (levels: Annuals|2–10 years|11–50 years|>50 years)	n/a	Bellis, Osazuwa-Peters, et al. (2024)
Clonal reproduction	Clonality of focal species (levels: none, weakly/intermediately clonal, strongly clonal)	n/a	Bellis, Osazuwa-Peters, et al. (2024)
Monitoring length	Number of years between first outplanting and most recent monitoring (square root, sqrt)	n/a	Bellis, Osazuwa-Peters, et al. (2024)
Number of source populations	Number of selected source populations (levels: Single|Multiple)	n/a	Bellis, Osazuwa-Peters, et al. (2024)

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TABLE 1 (Continued)

Variable(s)	Variable description (units)	Hypothesized relationship	Biogeographical theory/example evidence from previous studies
Number of subsites	The number of subsites at which outplanting took place (levels: Single|Multiple)	n/a	Bellis, Osazuwa-Peters, et al. (2024)
Habitat quality (pre-planting)	The quality of the recipient site at the time of outplanting as perceived by practitioners (levels: Poor or fair|Good|Excellent)	n/a	Bellis, Osazuwa-Peters, et al. (2024)
Habitat quality change	The change in site quality between the time of outplanting and most recent monitoring (levels: Negative|No change|Positive)	n/a	Bellis, Osazuwa-Peters, et al. (2024)

[a] Eight environmental variables were used to characterize environmental dissimilarity, environmental position, environmental niche breadth and environmental niche centre: elevation (m), mean annual temperature (°C) (bio1), annual precipitation (mm) (bio12), climatic moisture index (mm), sand fraction (%), clay fraction (%), soil pH and soil cation exchange capacity (cmol(c)/kg).

predictors from the model fit on species with medium relative life spans (2–10 and 11–50 years).

2.4 | Environmental data

We created mean annual temperature (°C) (bio1), annual precipitation (mm) (bio12) and climatic moisture index (mm) (CMI) variables with climate data downloaded for the period 1984–2018 from the CHELSA climate data set (v2.1) at a 30 arc-second resolution (Karger et al., 2017). Soil physicochemical properties were derived from the SoilGrids global resource (v2.0), which was produced at a 250 m resolution (Poggio et al., 2021). These included two measures of soil texture (sand fraction and clay fraction, %), soil pH and cation exchange capacity at pH 7 (cmol(c)/kg). All values represent means from soil sampled from a depth of 5–15 cm. Elevation data were derived from the Space Shuttle Radar Topography Mission 30 m digital elevation model. We resampled the soil and elevation layers to match the climate data resolution using bilinear interpolation, as this method ensures smooth transitions between pixels, yielding more realistic estimates at the resampled resolution.

2.5 | Species distribution data

We used species' range polygons to calculate two geographic predictors: geographic peripherality and range size. We also used environmental data from areas encompassed by these range polygons to calculate the environmental position, environmental niche breadth and environmental niche centre variables (Table 1; Figure 1). Where available, we used expert-drawn range maps from the US Fish and Wildlife Service (USFWS) Environmental Conservation Online System (US Fish and Wildlife Service, 2023) (see Table A2.1). We downloaded expert-drawn range maps at the species level (Sillero et al., 2021). In practice, this meant including the entire distribution of the species within our North American study region (defined by the coverage of the Ecoregions of North America created by Wiken et al., 2011, in addition to Hawaii) rather than restricting our analyses to infraspecific taxon levels.

For the remaining species, we constructed our own range polygons using occurrence data from the Global Biodiversity Information Facility (GBIF) and natural heritage programs (Appendix S2) in the following five states: California (http://www.dfg.ca.gov/biogeodata/cnddb/), Florida (https://www.fnai.org/publications/gis-data), North Carolina (www.ncnhp.org), Oregon (https://inr.oregonstate.edu/orbic) and Tennessee (https://www.tn.gov/environment/program-areas/na-natural-areas/na-natural-heritage-inventory-program.html) (see Data Availability Statement for full data set reference and access details). Although our focal species were also distributed in other states, these five covered a disproportionately large number of translocations (49% of the sample) and species' distributions within their boundaries.

We carefully cleaned occurrence data sets and checked whether records were within known ranges according to scientific publications, state-level atlases, NatureServe and other available sources (full data cleaning protocol presented in Appendix S2). For species with adequate spatial coverage, we constructed alpha hulls to approximate their ranges, as this method reduces overestimation of range extents compared to the minimum convex polygon method when there are disjunctions or discontinuities in the distribution (see Appendix S2 for further details).

2.6 | Creating geographic and environmental predictors

Site dissimilarity predictors included geographic distance and eight environmental dissimilarity variables (Figure 1; Table 1). Before conducting geographic measurements, we reprojected spatial data to the North America Equidistant Conic projection.

Site position predictors included geographic peripherality, latitudinal position, eight environmental position variables andclimate suitability (Figure 1; Table 1). We characterized the environmental position of recipient sites relative to species' ranges by calculating their rank within the empirical cumulative frequency distribution of the climatic, soil or elevational space encompassed by the range polygon (Figure 1). To characterize the climate suitability of recipient sites, we constructed presence-only species distribution models (SDMs) for sites in the continental US (no Hawaiian species had sufficient

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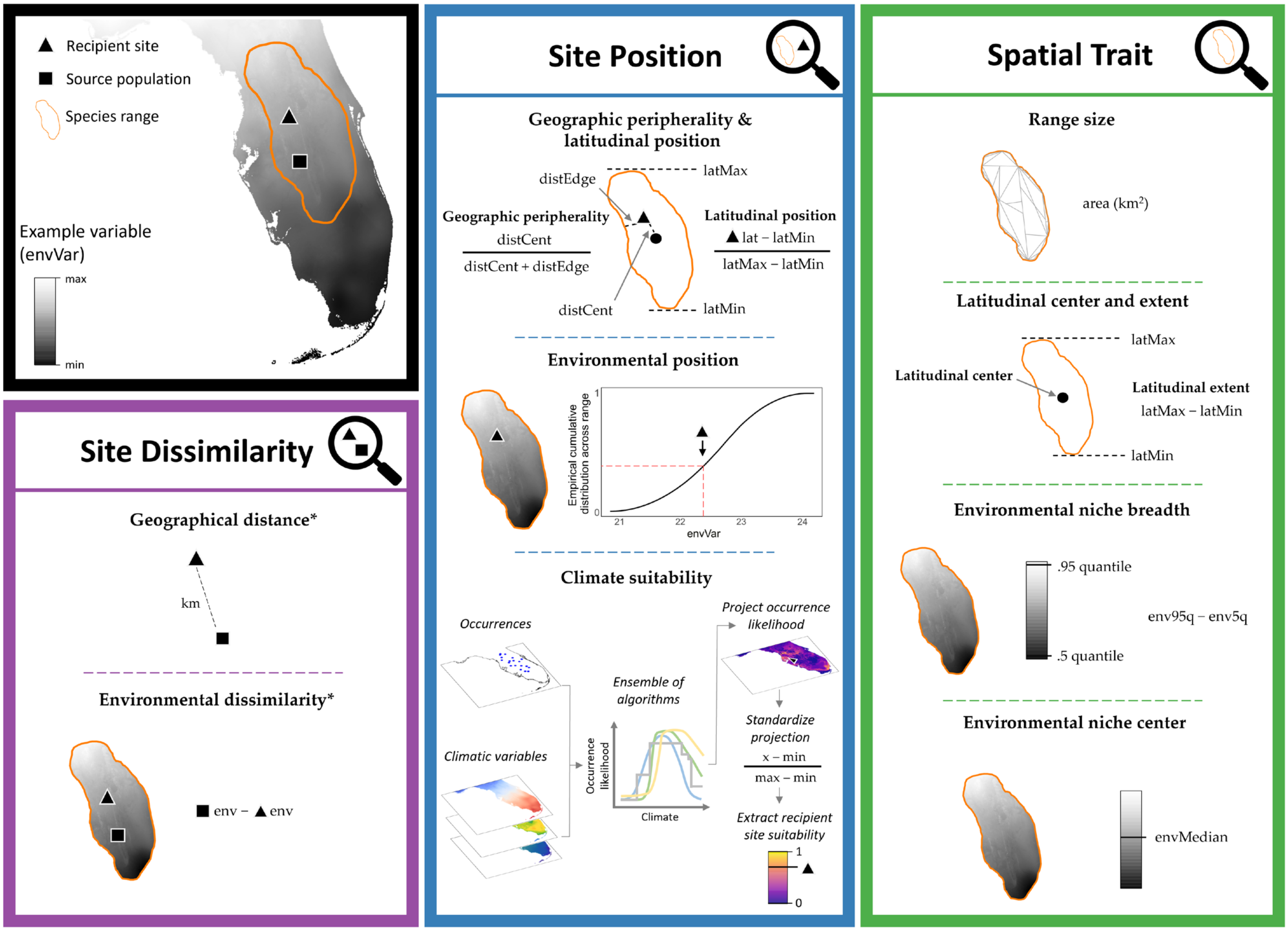

FIGURE 1 Schematic of methodology for calculating geographic and environmental predictor variables considered for analysis in the present study. The methodologies presented for environmental dissimilarity, environmental position, environmental niche breadth and environmental niche were applied to eight climate, soil and elevation variables (see Table 1 for a full list of variables). *If multiple source populations were selected, the average distance or dissimilarity between sources and the recipient site was calculated.

occurrences to build a model, i.e. ≥10) using up to eight climatic variables and multiple ensemble modelling frameworks in R (v4.3.1) (R Core Team, 2023). As true absences are difficult to obtain and verify, we drew up to 10,000 pseudo-absence points (or background points) at random from each species' modelling extent for use in the SDMs (see Appendix S3 for the full SDM methodology). To ensure that our SDM work was transparent and reproducible, we complied with the Overview, Data, Model, Assessment and Prediction protocol (ODMAP; Zurell et al., 2020). This meta-data summary provides a detailed key to the steps of our SDM-based analyses (Appendix S3).

Niche metric predictors included geographic range size, latitudinal extent, latitudinal centre, eight environmental niche breadth variables and eight environmental niche centre variables (Figure 1; Table 1). Because of the tendency for overestimation of species occupancy when using expert-drawn range polygons and polygons derived from alpha-hull methods (Hurlbert & Jetz, 2007), we calculated niche breadth as the difference between the 5th and 95th quantiles of the environmental data encompassed by the species' range polygons (Figure 1). The polygon approach enabled us to calculate niche metric variables for significantly more species ($n=107$) than if we had relied on occurrence points because much fewer occurrence data sets had sufficient spatial coverage to be ecologically meaningful ($n=52$). We validated this decision by comparing variable estimates from polygons and points for the 52 species with sufficient occurrence data and found strong correlations in variable estimates (e.g. temperature niche breadth, Spearman's rank correlation = 0.84).

We also computed a principal component analysis of the 19 BIOCLIM variables (Nix, 1986), CMI and CMI seasonality, masked to our North American study region, in order to generate multivariate climate predictors (the first three principal components) of site dissimilarity, position, niche breadth and niche centre. However, these multivariate predictors did not outperform the three raw climate variables (Table 1) in preliminary analyses and were more difficult to interpret, so we excluded them from further analyses.

2.7 | Statistical analyses

We quantified the relative importance of predictor variables (Table 1) for each metric of translocation success using the random forest (RF)

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algorithm. RFs are a robust method for evaluating data sets with large numbers of missing values and a low ratio between the number of observations and predictor variables (Strobl et al., 2009). These characteristics of RF models made them suitable for our data set and study objectives, as the CPCRD contains numerous missing values in some data fields (e.g. source site coordinates), and our exploratory goals necessitated an approach adaptable to the low observation:predictor ratio. For comparability, we adopted the same modelling approach and model parameters as described in Bellis, Osazuwa-Peters, et al. (2024) by implementing unbiased conditional inference trees drawn without replacement. We quantified the importance of each predictor using the *party* package (v1.3-10) (Hothorn et al., 2022) in R by comparing model prediction accuracy before and after permutation (Strobl et al., 2008); larger decreases in model accuracy indicate greater variable importance. We adopted a variable screening approach to identify and address any pairwise statistical relationships between predictors in each RF model prior to modelling (see Appendix S4). Models were evaluated using the area under the curve (AUC) of the receiver operating characteristic (Hanley & McNeil, 1982).

We estimated the partial effects of the most important predictors in each model. This approach examines the effects of a variable on the predicted response when all other predictors are held constant at their average values. We determined the most important predictors that warranted interpretation by visually assessing the size of the descending steps in the variable importance plots (Bellis, Osazuwa-Peters, et al., 2024).

2.8 | Sensitivity tests

We tested the sensitivity of the estimated partial effects of the most important predictors in each RF model to the inclusion of projects involving species with annual or >50 year life spans. These two classes represent the extreme ends of the life span continuum in our sample, and success metrics may be more sensitive to the evaluation timeframe in projects involving these species (Albrecht et al., 2019). In each sensitivity test, we used the same RF methodology described in the 'Statistical analyses' section but excluded cases involving one extreme life span class (annuals or >50 years). We then computed partial effects to assess potential confounding effects of life span on fitted relationships (Appendix S5).

3 | RESULTS

3.1 | Population persistence

Among the 199 projects with available information on population persistence, 64% remained extant with a stable or increasing population of >50 individuals at the time of most recent monitoring. Variables associated with attributes of the recipient site generally had the largest relative influence on persistence

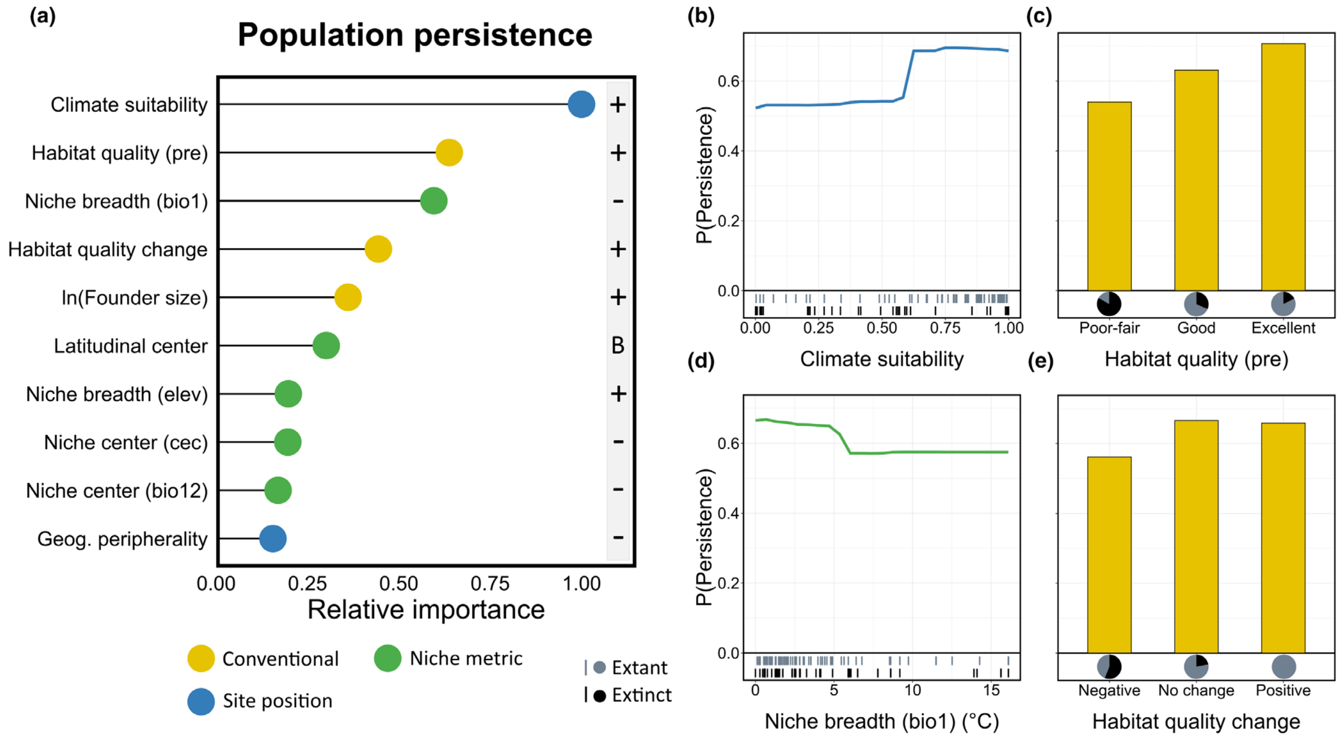

FIGURE 2 Relative importance of the 10 most influential predictors for population persistence (a) according to a random forest (RF) model (area under the curve = 0.77). Three categories are represented in the top 10 predictors: conventional, site position and niche metric (see Table 1). The symbols next to each relative importance bar indicate the direction of effect: +, positive; −, negative; B, bell-shaped. (b–e) Partial effects of the most influential variables in the RF model. The rug plots or pie charts below the *x*-axis of (b–e) display the distribution (b, d), or proportion if categorical (c, e), of the predictor across the two response classes of extant and extinct. bio1, mean annual temperature; bio12, total annual precipitation; cec, cation exchange capacity; elev, elevation.

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(Figure 2a). Climate suitability, estimated using SDMs, was the best predictor of persistence (Figure 2b), followed by practitioner-reported habitat quality (pre-planting) (Figure 2c), temperature niche breadth (Figure 2d), and practitioner-reported habitat quality change (Figure 2e). The probability of persistence began to increase sharply at sites with a predicted climate suitability of >0.54 (Figure 2b), levelling off at sites with a suitability of ≥0.63. Temperature niche breadth (mean annual temperature, bio1) negatively influenced persistence, with the non-linear relationship stabilizing at breadths of ≥6°C, where data became more scarce (Figure 2d).

3.2 | Next-generation recruitment

Of the 185 translocations with available information on next-generation recruitment, 62% had attained this benchmark. The latitudinal centre of a species' range had a similar relative influence as two conventional predictors, founder size and life span, for attaining next-generation recruitment (Figure 3a–d). The probability of recruitment increased non-linearly with latitudinal centre, levelling off at temperate latitudes, above 36.4° (roughly the latitude of Nashville, Tennessee, USA).

3.3 | Next-generation maturity

Among the 91 translocations with available information on next-generation maturity, 70% attained this benchmark. Niche metrics were the most important factors for determining next-generation maturity (Figure 4a), with the best predictors being the niche centre of cation exchange capacity and precipitation niche breadth. The probability of next-generation maturity was highest in species with distributions centred on soils with the lowest capacity for nutrient retention (Figure 4b) and among species with the narrowest precipitation niches (Figure 4c).

4 | DISCUSSION

Our results show that geographic and environmental factors, quantified at the macroscale, can be as insightful as management techniques, biological traits and on-ground habitat quality assessments for understanding plant translocation outcomes. Our analysis of 235 translocation projects revealed that climate suitability, estimated using SDMs, is the strongest relative predictor of whether a population persists following translocation, while niche metrics derived from species' distributions offer novel geographic and environmental

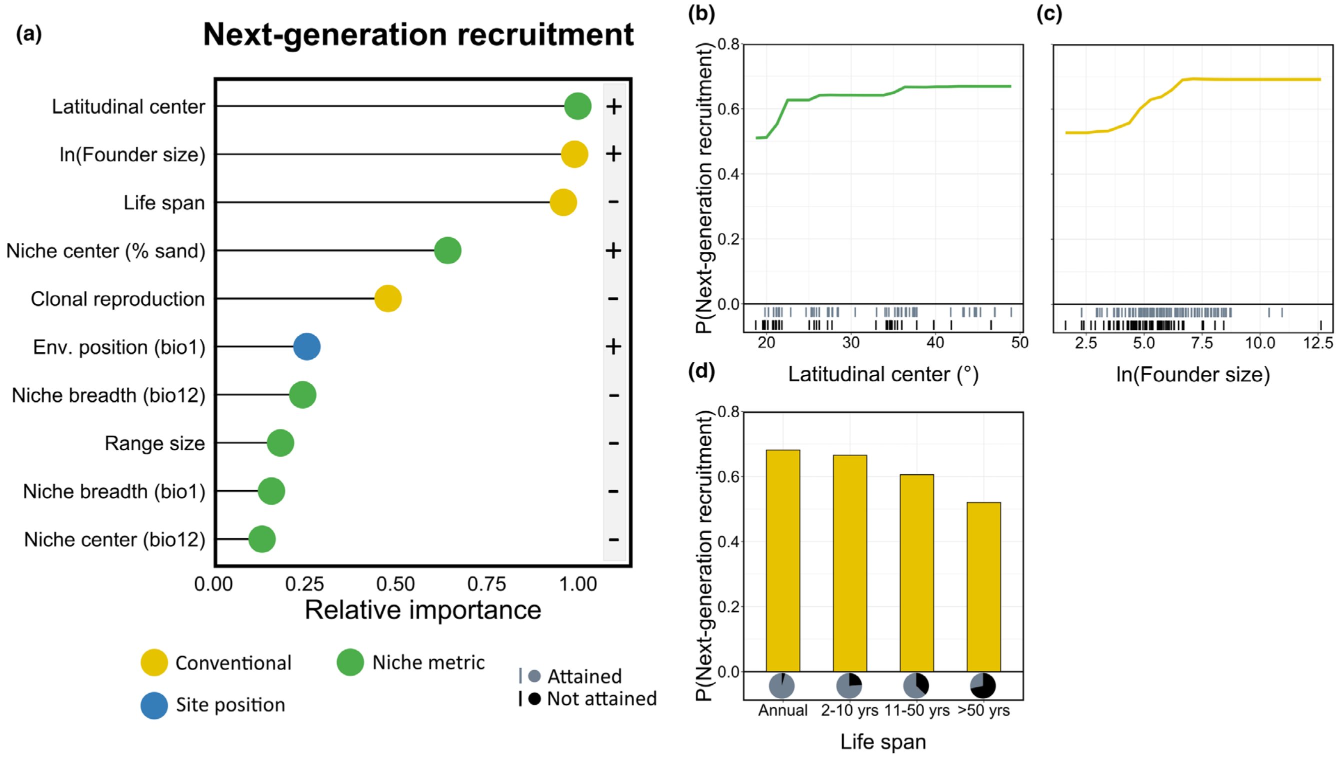

FIGURE 3 Relative importance of the 10 most influential predictors for next-generation recruitment (a) according to a random forest (RF) model (area under the curve = 0.78). Three categories are represented in the top 10 predictors: conventional, site position and niche metric (see Table 1). The symbols next to each relative importance bar indicate the direction of effect: +, positive; −, negative. (b–d) partial effects of the most influential variables in the RF model. The rug plots or pie charts below the *x*-axis of b-d display the distribution (b, c), or proportion if categorical (d), of the predictor across the two response classes of attained and not attained. bio1, mean annual temperature; bio12, total annual precipitation; % sand, soil sand fraction.

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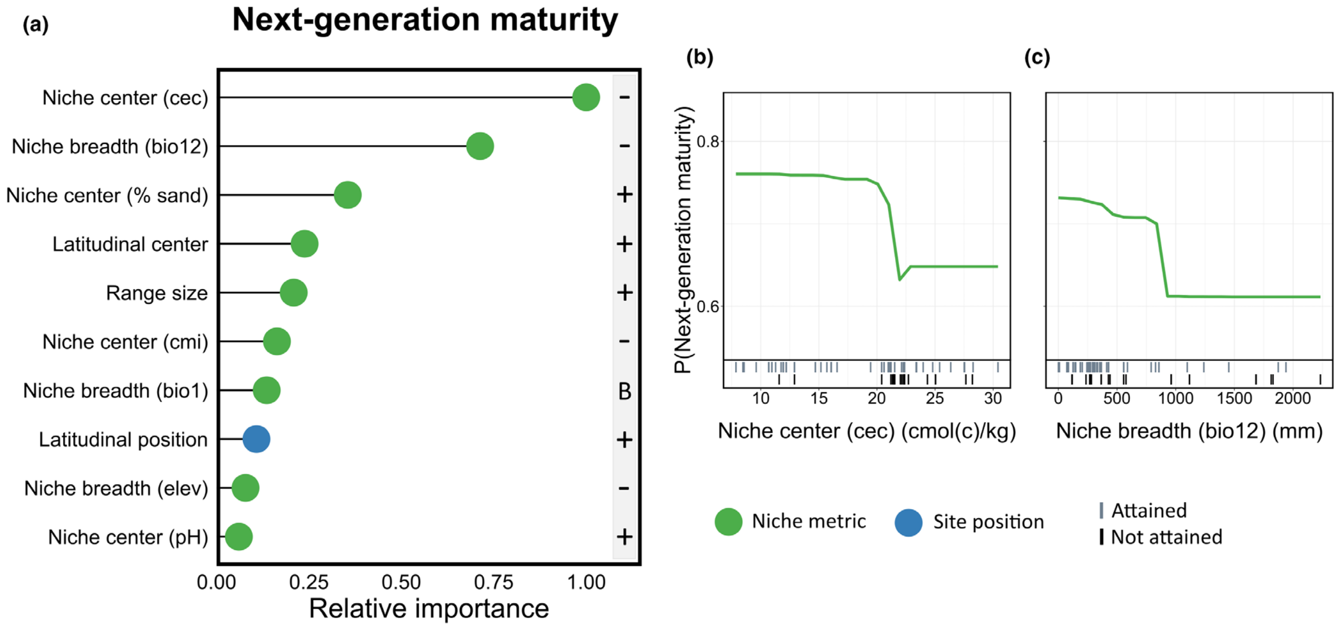

FIGURE 4 Relative importance of the 10 most influential predictors for next-generation maturity (a) according to a random forest (RF) model (area under the curve = 0.74), (b, c) partial effects of the most influential variables in the RF model. Two categories are represented in the top 10 predictors: Site position and niche metric (see Table 1). The symbols next to each relative importance bar indicate the direction of effect: +, positive; −, negative; B, bell-shaped. The rug plots below the *x*-axis of (b) and (c) display the distribution of the predictor across the two response classes of attained and not attained. bio1, mean annual temperature; bio12, total annual precipitation; cec, cation exchange capacity; cmi, climatic moisture index; elev, elevation; pH, soil pH; % sand, soil sand fraction.

insights on where next-generation recruitment and maturity could be improved. These findings present a fresh perspective on plant translocation outcomes and identify opportunities to improve translocation success not only by adhering to best practice recommendations such as maximizing founder population sizes but also by integrating spatial modelling approaches into translocation planning and management.

4.1 | Climate suitability as a predictor of population persistence

The survival of translocated plants appears to be strongly influenced by attributes of the recipient site (Dalrymple et al., 2012; Godefroid et al., 2011). While previous syntheses have drawn this inference from practitioners' qualitative assessments of habitat quality (Bellis, Osazuwa-Peters, et al., 2024) or from perceptions of why a project succeeded or failed (Godefroid et al., 2011; Silcock et al., 2019), our results mark one of the first instances of support derived from a quantitative metric of the recipient environment—macroscale climate suitability (but see Monks et al., 2023 for importance of rainfall in Mediterranean-type ecosystems). Our sample included translocations to sites with low SDM-derived suitability, possibly due to criteria that is often prioritized during recipient site selection: proximity to the source material's origin and historical presence of the species (Osborne & Seddon, 2012). These criteria overlook climatic factors that influence spatiotemporal variability in plant population persistence, such as climate heterogeneity within species' ranges or climate change-induced deterioration in site suitability. Consequently, translocations may have proceeded at sites that met a species fine-scale habitat requirements but had suboptimal temperature and precipitation regimes.

While our results demonstrate the potential of SDMs to inform recipient site selection, it may not be possible to accurately predict suitability for some species (e.g. rare or data-deficient species, Sillero et al., 2021). For example, we were unable to create reliable models for species in Hawaii as all had fewer occurrences than our minimum threshold of 10 (see Appendix S3). Additionally, several factors may cause disequilibrium between range and niche, such as dispersal limitation, source–sink dynamics and/or time-lagged local extinction (Maschinski et al., 2012; Pagel et al., 2020; Pulliam, 2000). Local conditions, biotic interactions or other processes independent of the macroclimate (e.g. edaphic conditions) may also dominate population survival across the species' range (Louthan et al., 2015). These potential sources of bias and uncertainty in SDMs must be carefully considered before any management actions are taken.

Given the potential pitfalls when building SDMs and their sensitivity to different modelling decisions (Sillero et al., 2021), rigorously defined calibration and validation methodologies are necessary to maximize their reliability for use in translocation decision-making (e.g. Finn et al., 2024). Our results suggest that macroclimatic suitability can be useful as a first filter for distinguishing between high- and low-priority candidate sites and should be considered alongside other factors associated with promoting persistence, such as habitat

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quality and founder size. High-priority sites should be surveyed in the field to determine the availability of suitable microsites, the suitability of edaphic conditions, the presence of appropriate pollinators and the identification of, and if necessary management of, potential threats (Maschinski et al., 2012). Potential future climate change impacts should also be incorporated into SDM-based site assessments to prioritize sites conducive to long-term persistence (e.g. Bellis et al., 2021).

4.2 | Niche metrics provide insight into translocation outcomes

Our findings indicate that plant species from more biotically limiting environments, such as in subtropical and tropical regions of the US, or in soils with high relative nutrient retention capacity, are the least likely to reach next-generation recruitment and maturity following translocation. Recent meta-analyses have shown that biotic interactions are stronger at lower latitudes and abiotic selection is greater at higher latitudes (Hargreaves et al., 2020; Runquist et al., 2020); as subtropical and tropical regions are more climatically benign and productive, they host a higher diversity and abundance of enemies (e.g. herbivores, competitors, pathogens). Similarly, more edaphically stressful habitats, such as those with limited capacity for nutrient and water retention (e.g. soils with high sand content), may offer an escape from competitive exclusion and herbivory found in more favourable soils (Sianta & Kay, 2019). These habitats often support rare endemic plants with highly specialized physiological and morphological adaptations that allow them to thrive under nutrient-deprived conditions (Rajakaruna, 2018).

The limiting effects of biotic interactions on plant translocation outcomes have been observed in several studies (Maschinski & Albrecht, 2023). Herbivores can suppress seedling recruitment, while competition for nutrients, light, water and other key resources can inhibit transplant growth (Menges, 2008). In Hawaii, where plants are also exposed to the highest diversity and density of invasive weeds and herbivores in the US (Simpson & Eyler, 2018), the rate of next-generation recruitment was much lower (40%) than on the continent (73%). Life history differences may partly explain the relationship between latitudinal centre and recruitment. Hawaiian translocations included fewer fast-recruiting annuals (2% vs. 17% in the continental US) and more long-lived species with delayed recruitment (18% vs. 9%) (Albrecht et al., 2019). However, next-generation recruitment models run without annuals and long-lived species both produced partial effects consistent with the full data set model (Appendix S5), suggesting that potential confounding effects of life span are limited.

The increasing frequency of recruitment with latitudinal centre may also be explained by Rapoport's rule, an ecological principle stating that range size and environmental tolerance scale with latitude (Stevens, 1989). Species with broader tolerances, which are typically found at higher latitudes where climate variability is greater, may be more likely to attain next-generation recruitment because they can germinate and grow under a wider range of environmental conditions (Canham & Murphy, 2016). However, this advantage appears to be limited to the recruitment niche and may not be associated with climatic attributes of the adult niche, as species with the broadest temperature and precipitation niches experienced the lowest rates of persistence and next-generation maturity in our sample. Interestingly, this result, which did not conform to expectations (Table 1), is concordant with the results of a global plant translocation synthesis where mortality rates were lowest for species with the narrowest geographical distributions (Dalrymple et al., 2012). Species with broad macroclimatic niche estimates may occupy microclimates that represent only a subset of the estimated niche, potentially making it more challenging to distinguish conditions that align with sink populations compared to narrow-ranged species.

5 | CONCLUSIONS

Our synthesis provides quantitative support to widely held perceptions around the influences of species–environment relationships on rare plant translocation outcomes. While no single variable represents the 'silver-bullet' for securing project success, we show that the macroclimatic suitability of recipient sites is as important to population persistence as other more extensively studied variables (e.g. habitat quality and founder size). Encouragingly, this result was obtained using a generalized species distribution modelling approach. When applied in a translocation project, model reliability could be enhanced by leveraging the practitioner's knowledge of the focal species and region to fit models with more proximal variables and refined occurrence data. Our synthesis also identifies particular niche attributes, such as a broad temperature or precipitation niche, that are associated with less successful translocations. For translocation projects involving species with these attributes, outcomes may be improved by incorporating multi-scaled habitat assessments, including fine-scale surveys to ensure critical niche requirements are not overlooked (Maschinski et al., 2012). More broadly, considering estimates of current and future macroclimatic suitability when selecting recipient sites represents a valuable approach for securing the long-term persistence of translocated plant populations.

AUTHOR CONTRIBUTIONS

Joe Bellis and Katherine D. Heineman conceived the ideas and designed the methodology. Joe Bellis, Katherine D. Heineman, Matthew A. Albrecht and Joyce Maschinski gathered the data. Joe Bellis performed the analyses. Joe Bellis led the writing of the manuscript. Joe Bellis, Matthew A. Albrecht, Joyce Maschinski, Sarah E. Dalrymple, Matthew J. Keir, Timothy Chambers, Jennifer Possley, Edith D. Adkins, Elliott W. Parsons, Michael Kunz, Carrie Radcliffe, Emily Coffey, Thomas N. Kaye, Cheryl L. Peterson, Aaron S. David, Sterling A. Herron, Eric S. Menges, Timothy Bell, Michelle Coppoletta, Caitlin Elam, Kathryn McEachern, Paula S. Williamson, Deanna Boensch, Megan Bontrager, Cooper Breeden, Noah Frade, Doria R. Gordon,

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Environmental data used to support this study are available from the following sources: CHELSA (https://chelsa-climate.org/), SoilGrids (https://www.isric.org/explore/soilgrids) and USGS EarthExplorer (https://earthexplorer.usgs.gov/). Publicly available species occurrence data from the global biodiversity information facility are available at the following DOIs: https://doi.org/10.15468/dl.nv86d5 (GBIF.org, 2022), https://doi.org/10.15468/dl.x8kegx (GBIF.org, 2023). Species range polygons from the USFWS can be accessed directly through the Environmental Conservation Online System (https://ecos.fws.gov/ecp/). Occurrences from natural heritage programs are not publicly shareable because they were shared under licence and are not permitted for redistribution. Full citations and access details: California Department of Fish and Wildlife. 2021. California Natural Diversity Database. Biogeographic Data Branch, CDFW, Sacramento, CA. (Accessed: 23-11-2021); Florida Natural Areas Inventory. 2022. Element Occurrence Polygon Data Layer. FNAI, Tallahassee, FL (accessed 23 August 2022); North Carolina Natural Heritage Program, 2022. GIS Data. NCDNCR, Raleigh, NC (accessed 25 July 2022); Oregon Biodiversity Information Center, 2022. Biotics Rare Species Database, Institute for Natural Resources—Portland, Portland State University, Portland, OR (accessed 16 August 2022); Tennessee Division of Natural Areas, 2022, Tennessee Division of Natural Areas Element Occurrence Records, Tennessee Department of Environment and Conservation, Nashville, TN. (accessed 17 August 2022). Data from the questionnaire-based Center for Plant Conservation Reintroduction Database is not publicly shareable, as it was provided under the condition that access would be restricted to vetted individuals with database permissions. These data are sensitive as it relates to endangered species or protected locations that are vulnerable to disturbance and poaching.

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SUPPORTING INFORMATION

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

Appendix S1. Center for plant conservation reintroduction database submission form details.

Appendix S2. Species distribution data cleaning and processing.

Appendix S3. Species distribution modeling methodology.

Appendix S4. Exclusion of statistically associated predictors.

Appendix S5. Results of sensitivity tests.

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