

How well do species distribution models predict occurrences in exotic ranges?

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Abstract

Aim: Species distribution models (SDMs) are widely used predictive tools to forecast potential biological invasions. However, the reliability of SDMs extrapolated to exotic ranges remains understudied, with most analyses restricted to few species and equivocal results. We examine the spatial transferability of SDMs for 647 non-indigenous species extrapolated across 1,867 invaded ranges, and identify what factors may help differentiate predictive success from failure.

Location: Global.

Time period: Current.

Major taxa studied: Six hundred and forty-seven terrestrial species; eight taxonomic classes.

Methods: We performed a large-scale assessment of the transferability of SDMs using two modelling approaches: generalized additive models (GAMs) and MaxEnt. We fitted SDMs on the native ranges of species and extrapolated them to exotic ranges. We examined the influence of general factors and factors related to biological invasions on spatial transferability.

Results: Despite both modelling approaches performing well in the range of the species used for fitting, we observed moderate to low spatial transferability on average (mean area under the receiver operating characteristic curve [AUC] ~ .7) when extrapolating to their invaded ranges. Transferability differed between taxonomic classes and invaded continents and was positively influenced by the performance of the model and environmental generalism in the native range, and the year of first record. Models performed worse with greater environmental coverage in the exotic range, gross domestic product and number of occurrences in the native range, geographic distance between ranges and when extrapolating to islands.

Main conclusions: After controlling for sampling bias, half of SDMs were only weakly predictive, which should affect how SDM-based forecasts are interpreted. Performance differed based on characteristics of the data, species, and ranges, and can suggest when SDMs may be reliable and when we should be most cautious. These considerations touch directly upon the potential use of SDMs for management of biological invasions. We discuss possible mechanisms of these findings.

KEYWORDS

GBIF, global, invasive species, presence-only data, species distribution model, transferability

1 | INTRODUCTION

Predicting species distributions within exotic ranges is critical to manage biological invasions (Elith, 2017) due to their severe effect on biodiversity (Bellard et al., 2016) and economic loss (Bradshaw et al., 2016). Given the increasing availability of large databases, species distribution models (SDMs) have become the tool of choice for prediction (e.g., Lozier & Mills, 2011).

The challenges of developing SDMs as predictive tools have been summarized in recent publications (Sequeira et al., 2018; Werkowska et al., 2017; Yates et al., 2018), noting that the transferability of SDMs is largely unknown, within both spatial and temporal contexts. Our focus is on the former, where most direct analyses of spatial transferability to exotic ranges have been restricted to few species or taxonomic groups [e.g., Beaumont et al. (2009) examined three plant species; Goncalves et al. (2014) examined one plant species; Peterson et al. (2003) examined four plant species; Hill et al. (2017) examined 22 insect species]. Moreover, there has been a lack of consensus on whether SDMs are transferable, as studies have had varying success in extrapolating across time and space (e.g., Beaumont et al., 2009; Goncalves et al., 2014; Morán-Ordóñez et al., 2017; Petitpierre et al., 2012), the latter of which is relevant for the prediction of biological invasions. Recent advances have been made by Liu et al. (2020), using meta-analyses for 235 invasive species, and found poor overall spatial transferability. However, SDMs vary widely in how they are constructed. For example, presence-only records can be heavily affected by non-random sampling, where the majority of studies using such data likely suffer from sampling biases, and rarely control for these concerns (Yackulic et al., 2013). Whether these accurately measure transferability is therefore unclear. Likewise, model building and quality control vary between studies (e.g., criteria for inclusion of data points), making comparability difficult. Thus, building many SDMs with consistent formulations would be useful to provide the most rigorous analysis of transferability possible.

Comparability across SDMs is particularly important when identifying factors that may influence model transferability. Putative factors include: habitat-generalist species, which may lead to poorer transferability as they may not be constrained by the environmental factors considered (Brotos et al., 2007), taxonomic groups given differences in biological traits (Urban et al., 2016; Yates et al., 2018), data quality (Yates et al., 2018), model complexity (Werkowska et al., 2017), statistical approach (Yates et al., 2018), stochasticity given small sample sizes (Yates et al., 2018), and the choice of predictors (Petitpierre et al., 2017).

Beyond these general issues, some factors may be particularly relevant for biological invasions. Species may still be spreading within their introduced range (Václavík & Meentemeyer, 2011), violating the underlying assumption of SDMs that species are in equilibrium (Araújo & Peterson, 2012; Guisan & Thuiller, 2005). As the invasion progresses, species spread to a greater fraction of suitable sites (i.e., 'exposure'). Thus, we predict that older invasions, which should have higher exposure, should be closer to equilibrium and show stronger SDM performance (Leung et al., 2012; Runquist

et al., 2019). Analogously, exposure should increase with propagule pressure (the frequency of introduction events and number of individuals introduced, potentially to multiple locations within an invaded range; Lockwood et al., 2005). Higher trade should transport more organisms to a greater number of locations, allowing greater opportunity to spread within a range. Thus, we predicted a positive relationship between transferability and macro-economic metrics such as gross domestic product (GDP) of native and exotic regions, which have both been shown to jointly determine trade and thus propagule pressure between source and destination countries (Sardain et al., 2019).

Non-analogous environments could also affect transferability, if models fitted on truncated curves fail to predict species responses to new conditions (Yates et al., 2018). This is particularly relevant as invasive species are introduced to disjoint ranges. Thus, we predicted a positive relationship between transferability and environmental similarity between native and exotic ranges. Likewise, we predicted an inverse relationship between spatial transferability and geographic distance, given increasing environmental, biotic, or human differences. Finally, we also hypothesized lower transferability to islands. Islands differ from mainland areas by higher levels of endemism, lower species richness and restricted land areas (Kier et al., 2009), suggesting non-analogous conditions. Moreover, impacts often differ between island and mainland invasions (Spatz et al., 2017), suggesting ecological differences at play. Identifying which locations (e.g., islands or mainlands), types of species (e.g., generalists or specialists) and conditions (e.g., non-analogous environments) where SDMs may be reliable would provide critical information for conservation purposes in invasion biology (Werkowska et al., 2017).

The objectives of this study were to (a) evaluate the capacity of SDMs to predict species distribution when extrapolated to exotic ranges, and (b) identify factors that may influence model transferability. We constructed SDMs on the native range of 647 terrestrial species across 8 taxonomic classes and analysed model transferability to exotic ranges. We provided the most systematic (controlling for issues such as sampling bias and quality control) and extensive analysis of native to exotic range transferability to date (extrapolating to 1,867 exotic ranges), and identified several predictors of transferability, relevant for invasive species management.

2 | METHODS

To assess the transferability of SDMs, we fitted models for species on their native range and extrapolated them to their exotic ranges (Figure 1). Background sites were sampled using the 'target-group background' approach (TGB; Phillips et al., 2009) within ranges to account for biases associated with presence-only data. We assessed the transferability of SDMs to invaded ranges in terms of discriminatory power and examined several potential predictors of model success (Table 1). All analyses were performed in R (R Core Team, 2019). Descriptions of the datasets used are provided in Supporting Information Table S1.

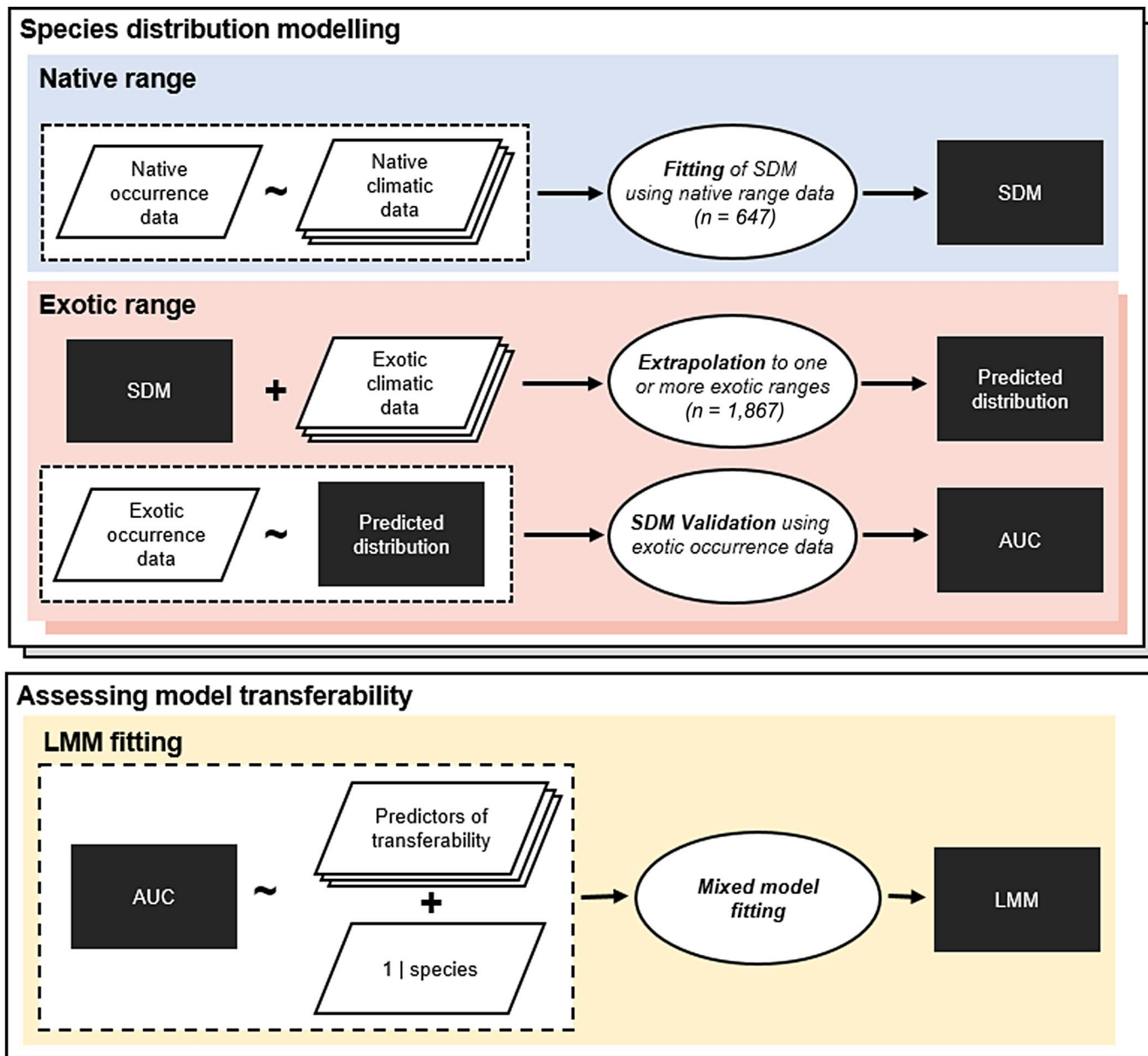


FIGURE 1 Flow chart outlining the analyses performed in the study. AUC, area under the receiver operating characteristic curve; LMM, linear mixed-effects model; SDM, species distribution model

2.1 | Environmental data

We included environmental predictors that are available globally and frequently used in SDM literature. We used bioclimatic variables from WorldClim version 2 at 2.5-arcmin resolution (~ 5-km grid size; Fick & Hijmans, 2017). We included three variables in addition to the bioclimatic predictors: elevation and terrain ruggedness index (TRI; Riley et al., 1999) at 2.5-arcmin resolution, and maximum annual normalized difference vegetation index (NDVI) at 3-arcmin resolution. Elevation and topography have been shown to drive many ecological processes affecting species distributions (Wang et al., 2017). TRI is a measure of topographic heterogeneity calculated as the mean elevation difference between neighbouring cells within the gridded data (using the 'terrain' function in the 'raster'

package; Hijmans et al., 2015), which may reflect the number of available habitats as they vary across elevations (Riley et al., 1999). NDVI is an index of vegetation cover ('greenness') that has been used as surrogate for habitat quality (Pettorelli et al., 2011) and land cover changes (Lunetta et al., 2006). We calculated NDVI as the maximum values across months within a year for a given cell, averaged across all available years (2000 to 2020). Topographic and vegetation predictors are globally available and have been widely used in SDMs (Morán-Ordóñez et al., 2017; Wen et al., 2015). Elevation data were downloaded from WorldClim (Fick & Hijmans, 2017), and Moderate Resolution Imaging Spectroradiometer (MODIS) NDVI data were downloaded through National Aeronautics and Space Administration (NASA) Land Processes Distributed Active Archive Center (Didan, 2015).

TABLE 1 Full list of variables and acronyms used to predict the transferability of species distribution models (SDMs), with a description of how the factors were generated. Rationale for why each factor may influence SDM transferability is provided for each factor, with sources. Variables marked with an asterisk (*) denote factors generated for both the native and exotic ranges

Variable (acronym)	Description	Rationale
AUC, native (NAUC)	Performance of the SDM on its own range measured as AUC, using 10-fold cross-validation. Logit-transformed	Models that fail to characterize their own range are likely to fail when extrapolating to new environments (Morán-Ordóñez et al., 2017)
Number of occurrences, native (NOCC) and exotic (EOCC)*	Number of occurrences used to fit or validate the model. Multiple occurrences found in a single cell were counted as a single occurrence. Log-transformed	Ranges with small sample sizes may fail to capture complex ecological relationships and be prone to stochasticity, leading to increased parameter uncertainty and unstable results (Wisz et al., 2008; Yates et al., 2018)
Continent (CONT)	Nominal variable of the invaded continent. Multi-continental invasions were treated as their own level	Generalities in environmental conditions and biotic composition within large regional areas, as well as differences in quality of invasive species records and biodiversity information (Pyšek et al., 2008) may affect SDM transferability.
Taxonomic class (CLASS)	Nominal variable of the species' taxonomic class	SDM transferability may differ between groups of species, or their habitat, which may share similar characteristics (Regos et al., 2019)
Environmental breadth, native (NEB)	Convex hull area of occurrence points projected into environmental principal component analysis (PCA) space. Log-transformed	Generalist species may not be restricted by the environmental factors considered in the SDM, resulting in poor transferability (Brotons et al., 2004; Zhang et al., 2015)
Environmental coverage, native (NEC) and exotic (EEC)*	Proportion of total environmental space of the background sites and occurrences occupied by only the occurrences	A large environmental coverage may lead to SDMs being unable to distinguish between presences and their background environment (Brotons et al., 2004; Zhang et al., 2015)
Gross domestic product, native (NGDP)	Sum of the GDP of all defined regions in the range. Log-transformed	Increased propagule pressure (e.g., through trade) may lead to increased dispersal to all suitable locations for a given range ('exposure'), resulting in species closer to equilibrium with their environment (Leung et al., 2012; Lockwood et al., 2005)
Year of first record (YEAR)	Earliest recorded occurrence of the species within the defined invaded range	Newer invaders may still be spreading, and not yet reached all suitable habitats, violating assumptions of equilibrium (Runquist et al., 2019)
Geographic distance between ranges (DIST)	Haversine distance (in km) between the centroids of the native and exotic ranges, including background environment	Species may experience new environmental conditions or community compositions outside of the range in the fitting data leading to unpredictable responses (Werkowska et al., 2017; Yates et al., 2018)
Environmental similarity between ranges (ESIM)	Proportion of negative multivariate environmental similarity (MES) values in the exotic range with the native range as reference sites	
Island, native (NISL) and exotic (EISL)*	Binary predictor on whether all occurrences were found on an island (1) or not (0). Native and exotic	Ecological characteristics of islands differ significantly from the mainland—higher endemism, lower species richness and restricted distributions—and may greatly affect species distribution (Kier et al., 2009)

Abbreviation: AUC, area under the receiver operating characteristic curve.

Prior to model fitting, we accounted for collinearity by removing highly correlated variables across all cells globally using a threshold pairwise correlation coefficient value of $|r| > .7$. After excluding collinear variables, the reduced set was used in all SDMs: annual mean temperature (bio1), mean diurnal range (mean of monthly maximum

and minimum temperatures; bio2), temperature annual range (bio7), mean annual precipitation (bio12), precipitation seasonality (coefficient of variation; bio15), elevation, TRI and maximum annual NDVI. All variables were standardized to a mean of zero and standard deviation of one.

2.2 | Species data

We obtained occurrence records from the Global Biodiversity Information Facility (GBIF, 2020; Supporting Information Text S1), and gridded them to the environmental data (at 2.5-arcmin resolution). We removed all records without associated environmental data, and grid cells containing multiple occurrences were counted as a single presence. We filtered out records with listed geospatial issues within GBIF and coordinate uncertainty greater than 5 km (the resolution of our environmental data). We applied standardized cleaning using the 'CoordinateCleaner' package (Zizka et al., 2019), which removed any records with equal or zero/zero coordinates, found in urban areas, near biodiversity institutions, outside of their listed country, or at the centroids of countries and its subdivisions. We excluded sightings dated before 1970 to match the temporal resolution of our environmental datasets (therefore, occurrences ranged between 1970 and 2020).

Species occurrences were classified as either native or exotic at the country level using the Centre for Agriculture and Bioscience International (CABI) Invasive Species Compendium (CABI, 2020) and the International Union for Conservation of Nature (IUCN) Global Invasive Species Database (GISD, 2015). We defined 'regions' and 'ranges' as physical areas and the contiguous geographic extent of the species, respectively. Regions were generated at the sub-national level (state/province/equivalent), using the Global Administrative Areas Database (2018). Exotic ranges were defined as the set of contiguous regions (that is, regions that share a land border with each other) containing at least one occurrence point. Therefore, an SDM fitted on the native range for a species may be extrapolated to one or more exotic ranges, each comprising one or more connected regions. Records were excluded in regions where the species was considered both native and exotic, or not classified. Ranges (both native and exotic) with fewer than 20 occurrences were excluded to avoid overfitting. The species included in the study, along with relevant taxonomic information are presented in Supporting Information Table S2.

2.3 | Background environment selection

SDMs were fitted using presence-background data within the native range of the species, and evaluated by extrapolating to one or more invaded ranges, also comprising presences and background sites. We sampled up to a maximum of 10,000 background sites for each fitting set and separately for each validation set (Barbet-Massin et al., 2012; Capinha et al., 2011). While the number of background points included in the model affects the absolute probabilities of prediction, the likelihood of presences could still be interpreted in a relative manner, termed discrimination (Pearce & Boyce, 2005). We used the 'target-group background' approach to select our background sites (TGB; Phillips et al., 2009) by randomly sampling GBIF records within the same range and belonging to the same taxonomic class as the species of interest (see Supporting Information Table S3

for the GBIF DOIs). This accounted for observation biases associated with presence-only data by mimicking the sampling approach of the occurrence records. We set a minimum requirement of 4,000 background sites, to remain large enough to estimate the background distributions of environmental conditions (excluding 38 species from the analyses). We applied the same data cleaning procedure to our target-group background sites as the occurrence records.

2.4 | Modelling species distributions

We applied two modelling approaches as the framework of the SDMs in this study: generalized additive models (GAMs; Hastie & Tibshirani, 1990; using the 'mgcv' package in R; Wood, 2017) and MaxEnt (Phillips et al., 2006; using the 'maxnet' package in R; Phillips, 2017). GAMs and MaxEnt both attempt to account for complexity by allowing nonlinear fitting, albeit through differing algorithms, with GAMs using 'smooth functions' and MaxEnt using 'transformed features', described below. For GAMs, nonlinear relationships (the 'smooth' terms in the model) are defined by segments specified by the number of knots, each of which may have their own polynomial functional form.

$$z_{ij} = b_0 + s(x_{1,i}) + s(x_{2,i}) + \dots + s(x_{m,i}) \quad (1)$$

$$y_{ij} = \frac{1}{1 + e^{-z_{ij}}} \quad (2)$$

Where y_{ij} is the binary presence or background at site i and species j , and $x_{1,i} \dots x_{m,i}$ are the m continuous climatic predictors with smoothing terms s . We used a maximum of five knots to allow each smoothing function to remain flexible, but computationally efficient. To prevent overfitting, we allowed terms to be excluded by setting the 'select' argument to true within the 'gam' function. Additionally, we removed variables showing concavity, the nonlinear extension of multicollinearity for GAMs (Buja et al., 1989; Morlini, 2006). We applied the 'concurvity' function from the package 'mgcv' (Wood, 2017) to remove the predictor with the highest 'worst' case concavity value. We refit the GAM, iterating this procedure until all concavity values were less than .8.

MaxEnt is a machine learning method designed specifically for presence-background modelling (Phillips et al., 2006; Phillips & Dudík, 2008). MaxEnt estimates the distribution across geographic space with the greatest spread (i.e., maximum entropy) in relation to the environmental variables, and can fit increasingly complex models through the use of the 'transformed features' of variables (of different classes, including linear, quadratic, product and hinge features), constrained using regularization. Like GAMs, MaxEnt may be subject to similar issues of overfitting given its flexible modelling procedures. To reduce possible overfitting, we limited the model complexity to only include linear, quadratic and product features (Merow et al., 2014). We used the default arguments in 'maxnet' (Phillips, 2017) for the rest of the settings, with the regularization applied.

To estimate model performance, we used the area under the receiver operating characteristic curve (AUC; Hanley & McNeil, 1982). An AUC value of 1 indicates perfect discrimination, while a value of .5 indicates discrimination no better than chance. We compared AUC in the fitted range against AUC in the exotic ranges, to determine transferability. We considered AUC values greater than or equal to .7 to have useful model performance (Morán-Ordóñez et al., 2017; Swets, 1988). While several authors have criticized the use of AUC due to the equal weighting of omission and commission errors (Jiménez-Valverde, 2012; Lobo et al., 2007), AUC remains one of the most commonly used metrics of discrimination for SDMs and is suited for the relative behaviour of presence-background models (Phillips et al., 2006). We considered the continuous Boyce index (CBI; Hirzel et al., 2006), but using simulation analyses we found that CBI was sensitive to the proportion of unsampled presences, while AUC was robust (Supporting Information Text S2, Figure S1). Therefore, we only report the AUC in the main text (but provide the CBI results in Supporting Information Text S2).

2.5 | Predictors of SDM transferability

We examined several factors based on characteristics of the SDMs and species that may relate to model transferability in general, as well as characteristics related specifically to biological invasions (Table 1). We included AUC in the native range (based on 10-fold cross-validation) as a predictor of model transferability to invaded ranges. We considered the number of occurrences used to fit the model, as models with few sample points may lead to the species-environment relationships being poorly captured (Wisz et al., 2008). We included the number of occurrences in the exotic range, as stochasticity may also lead to poor predictive performance, particularly at low numbers (Yates et al., 2018). To examine generalities within large geographic areas, we included the invaded continent as a categorical predictor. Multi-continental invasions were treated as a unique level within the factor (for example, an invaded range occupying both Asia and Europe was treated as its own level). We considered differences in transferability between taxonomic classes, which were obtained using the 'taxize' package in R (Chamberlain & Szöcs, 2013).

We examined the effects of ecological generalism on transferability (Brotons et al., 2004; Zhang et al., 2015) using two environment-based predictors: environmental breadth and environmental coverage (Supporting Information Text S3). We quantified the environmental breadth and coverage of each native species distribution by projecting the occurrence cells, as well as the background environment cells into a two-dimensional environment space using principal component analysis (PCA; Pearson, 1901). The environmental breadth of a species was defined as the area of the environment space encompassing the occurrences in the native range, representing their specialization. Environmental coverage was calculated by dividing the environmental breadth of the projected

occurrences by the environmental breadth of all cells in the range (i.e., the occurrence and background cells combined; Supporting Information Figure S2). We incorporated environmental coverage to estimate how much of the available environment the species occupied, where high environmental coverage may result in an SDM that cannot distinguish between occurrences and background sites.

We expected species to be farther from equilibrium, with lower exposure (i.e., lower propagule pressure and more recent invasions) resulting in distributions being driven by other factors besides environmental constraints (Leung et al., 2012; Runquist et al., 2019). We used GDP as a proxy of propagule pressure, which is strongly correlated with human-mediated transport of invasive species (Sardain et al., 2019). The GDP of the range was calculated using the sum of all cells within its regions using a gridded GDP dataset (at 5-arcmin resolution) provided by Kumm et al. (2018). We also examined time since invasion, using the year of first record within an invaded range as a surrogate, using all invasions since 1700 from the first records database by Seebens et al. (2017), and supplemented with the earliest recorded GBIF presence for that species and range (GBIF, 2020).

As transferability may be influenced by non-analogous conditions when extrapolating (Yates et al., 2018), we examined the dissimilarity between the native and exotic ranges using geographic and environmental distances as well as islands versus mainlands. We calculated geographic distances as Haversine distance (in kilometres) between the centroids of the native and exotic ranges with background environment points included. Additionally, we compared ranges using a multivariate environmental similarity (MES) surface (Elith et al., 2010). MES values measure the similarity of a given point to a set of reference points for each environmental predictor, providing a continuous measure with positive values indicating environmental similarity and negative values indicating dissimilarity (Elith et al., 2010). We calculated environmental similarity as the proportion of negative MES values in the exotic range with the native range as reference sites and the environmental predictors used to fit the SDMs, using the 'MESS' function from the 'modEVA' package (Barbosa et al., 2013). For our analysis of islands, each range was classified as island or mainland based on whether all its regions were contained within the global shoreline vector and islands database by Sayre et al. (2018).

We included all predictors in a 'transferability model', examining the potential factors that influence the predictive success of SDMs in the exotic range measured as AUC for the invaded range as the response variable. The transferability model was generated as a linear mixed-effects model (LMM; Breslow & Clayton, 1993) for GAMs and MaxEnt separately, using the 'lmer' function from the 'lme4' package (Bates et al., 2015). We included species as a random effects factor, as species could invade multiple disjoint ranges. Nominal variables use one level of the factor as reference, which we set as Mammalia and North America for taxonomic class and continent, respectively. Continuous variables were scaled to a mean of zero and standard deviation of one to allow comparability between fitted model parameters. Native and exotic AUC values were logit-transformed, while the number of occurrences, environmental breadth and GDP

were log-transformed (Table 1). We identified (and removed) multicollinear variables using a variance inflation factor (VIF), which quantifies the level of multicollinearity by regressing each predictor against the rest (Kock & Lynn, 2012). We used a conservative threshold of $VIF \geq 5$, using the 'vif' function within the 'car' package in R (Fox & Weisberg, 2019). Consequently, two predictors were excluded: environmental breadth and GDP in the exotic range. We excluded species locations that did not have available data for the factors, resulting in 647 species and 1,867 species–location combinations. The vast majority of species in the analyses were plants (Supporting Information Table S2), comprising 591 of the 647 species and 4 of the 8 classes (Liliopsida, Magnoliopsida, Pinopsida, and Polypodiopsida). Other classes were examined, consisting of 12 mammals (Mammalia), 21 birds (Aves), 19 insects (Insecta) and 4 reptiles (Reptilia). We reported the R^2 following Nakagawa et al. (2017) for the LMMs to provide the conditional (the variance explained by both the fixed and random factors) and marginal (the variance explained solely by the fixed factors) R^2 values.

We used the transferability model to identify where SDMs showed predictive success and where they did not. To communicate the contexts for strong/weak transferability more concretely, we discretized the 1,867 species–location extrapolations, and examined pairwise combinations of significant predictors. Higher-order combinations were not considered as the number of data points declined rapidly. We examined the AUCs in the exotic ranges for models categorized by the best and worst group for categorical variables, and the upper versus lower quantiles for continuous variables. We defined 'generalist' and 'specialist' species by the upper and lower quantiles of environmental breadth, respectively. High and low environmental coverage were 42.3 and 20.2%, respectively. High and low native range GDP were defined as 24.7 trillion and 3.94 trillion USD, while near and far geographic distances were 7,848 and 14,824 km, respectively. High and low numbers of occurrences within the native range were 3,302 and 170, respectively. We selected other high and low thresholds for variables when there was a rationale: for native AUC, we used thresholds of .8 and .7 as upper and lower values, respectively, as these have previously been identified as 'strong' and 'weak' (Hosmer et al., 2013; Morán-Ordóñez et al., 2017), and used 1970 as the threshold for the year of first record to separate recent versus older invasions, which was also the start date of most of our environmental data.

3 | RESULTS

3.1 | Species distribution modelling performance

Both SDM approaches, GAM and MaxEnt, were able to accurately discriminate between presences and background sites in the range used for fitting when tested using 10-fold cross-validation (Figure 2). GAMs had a mean AUC of .811 ($n = 647$; standard deviation $SD = 0.075$) when predicting the native range, while MaxEnt models performed slightly better within the fitting (native) range

with a mean AUC of .827 ($n = 647$; $SD = 0.070$). However, when extrapolated to one or more exotic ranges, a significant drop in model performance was observed with both model approaches performing similarly (Figure 2). The extrapolated GAMs had a mean AUC of .699 ($n = 1,867$; $SD = 0.127$), while MaxEnt models had a mean AUC of .692 ($SD = 0.123$). Roughly half of model extrapolations were poor, where 981 (52.5%) and 1,022 (54.7%) predicted exotic ranges had AUC values below .7 for GAMs and MaxEnt, respectively. Four hundred and sixteen (22.3%) and 445 (23.8%) predictions had AUC values between .7 and .8, and 470 (25.2%) and 400 (21.4%) predictions had AUC values greater than .8, for GAM and MaxEnt, respectively.

3.2 | Predictors of model performance

The transferability model for GAMs, fitted using LMM had a marginal R^2 value of .240, and a conditional R^2 value of .334. The transferability model for MaxEnt models explained less variation, with a marginal R^2 value of .183 and conditional R^2 value of .239. Of the 14 fixed effects used to characterize model transferability, 10 predictors were significant within the transferability models fitted for either GAMs or MaxEnt (Table 2; Figure 3; Supporting Information Tables S4 and S5).

We found that higher discriminatory ability (AUC) in the native range was positively related to AUC in the exotic range, as expected (Table 2; Figure 3). Additionally, the number of occurrences within the native ranges was negatively related to model performance for GAMs, contrary to our hypotheses. Transferability varied geographically, with significant differences between continents (Table 2; Figure 4; Supporting Information Table S6). SDMs showed the lowest average transferability in Asia, with mean AUCs of .651 ($SD = 0.108$; $n = 163$) and .659 ($SD = 106$) for GAM and MaxEnt, respectively, and highest in North America, with mean AUCs of .734 ($SD = 0.132$; $n = 514$) and .713 ($SD = 0.129$). South America, Africa, Europe, and Oceania showed mean AUCs of .653 ($SD = 0.109$; $n = 152$), .661 ($SD = 0.109$; $n = 204$), .675 ($SD = 0.118$; $n = 252$) and .718 ($SD = 0.129$; $n = 582$) for GAMs, and .659 ($SD = 0.103$), .664 ($SD = 0.106$), .665 ($SD = 0.112$) and .713 ($SD = 0.130$) for MaxEnt models, respectively. Multi-continental invasions comprised 127 ranges, with mean AUCs of .659 ($SD = 0.103$) and .665 ($SD = 0.110$) for GAMs and MaxEnt, respectively.

The transferability of the SDMs differed significantly between taxonomic classes for both GAMs and MaxEnt (Tables 2 and 3). Mammals, insects, and birds had the lowest discriminatory performance when predicting the invaded range. Mammals had mean AUCs of .645 ($n = 26$; $SD = 0.121$) and .655 ($SD = 0.108$) for GAMs and MaxEnt, respectively, while insects had mean AUCs of .692 ($n = 34$; $SD = 0.122$) and .663 ($SD = 0.122$). Birds also showed poor transferability, with mean AUC values of .663 ($n = 49$; $SD = 0.131$) and .673 ($SD = 0.116$) for GAMs and MaxEnt, respectively, while plants had overall means of .701 ($n = 1,752$; $SD = 0.127$) and .693 ($SD = 0.123$) across the four classes. Although reptiles performed well with mean AUC values of .768 ($SD = 0.143$) and .818 ($SD = 0.110$) for GAMs and

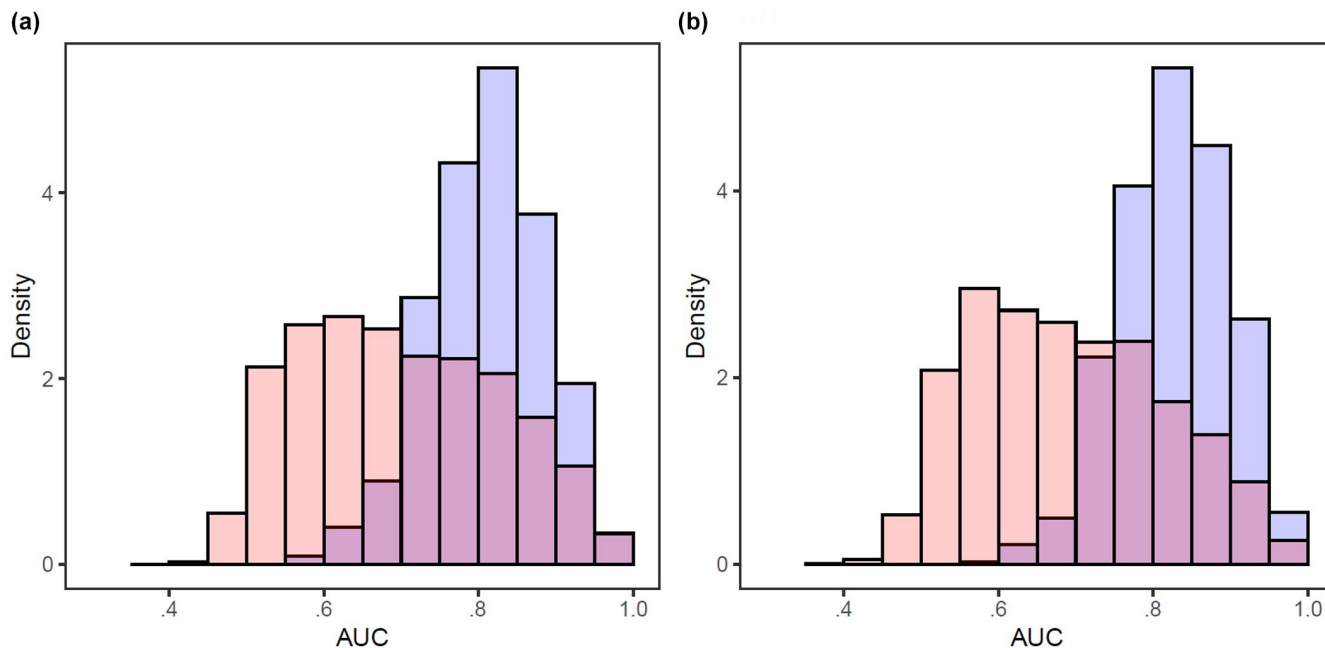


FIGURE 2 Density histogram of the performance of generalized additive models (GAMs; a) and MaxEnt (b) measured as area under the receiver operating characteristic curve (AUC) when predicting the native range, or fitting dataset (purple), using 10-fold cross-validation and when extrapolating to the exotic range, or validation dataset (pink)

TABLE 2 Estimated model parameters, with standard error, *t* value and *p* values of the fixed effects for the linear mixed model fitted using the full dataset for generalized additive models (GAMs) and MaxEnt with taxonomic class as a categorical predictor. An asterisk (*) next to the *p* values denotes significance

Variable	GAM				MaxEnt			
	Estimate	SE	<i>t</i> statistic	<i>p</i> value	Estimate	SE	<i>t</i> statistic	<i>p</i> value
AUC, native (NAUC)	0.070	0.020	3.495	<.001*	0.065	0.019	3.469	<.001*
Number of occurrences, native (NOCC)	-0.059	0.028	-2.078	.039 *	0.010	0.026	0.395	.693
Number of occurrences, exotic (EOCC)	0.007	0.021	0.337	.737	0.019	0.021	0.879	.380
Continent (CONT)	NA	NA	NA	<.001*	NA	NA	NA	<.001*
Taxonomic class (CLASS)	NA	NA	NA	.036*	NA	NA	NA	.002*
Environmental breadth, native (NEB)	0.155	0.032	4.890	<.001*	0.148	0.030	4.887	<.001*
Environmental coverage, native (NEC)	0.035	0.033	1.076	.284	-0.024	0.030	-0.779	.437
Environmental coverage, exotic (EEC)	-0.213	0.020	-10.683	<.001*	-0.189	0.020	-9.640	<.001*
GDP, native (NGDP)	-0.079	0.028	-2.861	.004*	-0.051	0.026	-1.976	.048*
Year of first records (YEAR)	0.027	0.017	1.584	.114	0.034	0.017	2.051	.041*
Geographic distance (DIST)	-0.067	0.019	-3.548	<.001*	-0.039	0.019	-2.105	.035*
Environmental similarity (ESIM)	0.008	0.019	0.415	.679	0.002	0.019	0.118	.907
Island, native (NISL)	-0.116	0.147	-0.787	.432	0.075	0.137	0.547	.585
Island, exotic (EISL)	-0.286	0.047	-6.114	<.001*	-0.238	0.046	-5.137	<.001*

Abbreviation: AUC, area under the receiver operating characteristic curve.

MaxEnt, respectively, only four species and six extrapolated species locations were examined.

As expected, SDMs performed worse when species had a larger environmental coverage in the exotic range. Conversely, SDMs for generalist species with larger environmental breadths in their native range performed better when extrapolating to new ranges, contrary to our hypotheses (Table 2; Figure 3). Also contrary to our

hypotheses, models fitted on native ranges with larger GDPs tended to perform worse (Table 2; Figure 3), as did older invasions based on the year of first record, although only in MaxEnt models (GAMs were nearly significant with $p = .114$).

SDMs tended to perform worse when extrapolated across larger geographic distances, as predicted (Table 2; Figure 3). In contrast, the degree of environmental similarity did not significantly relate to

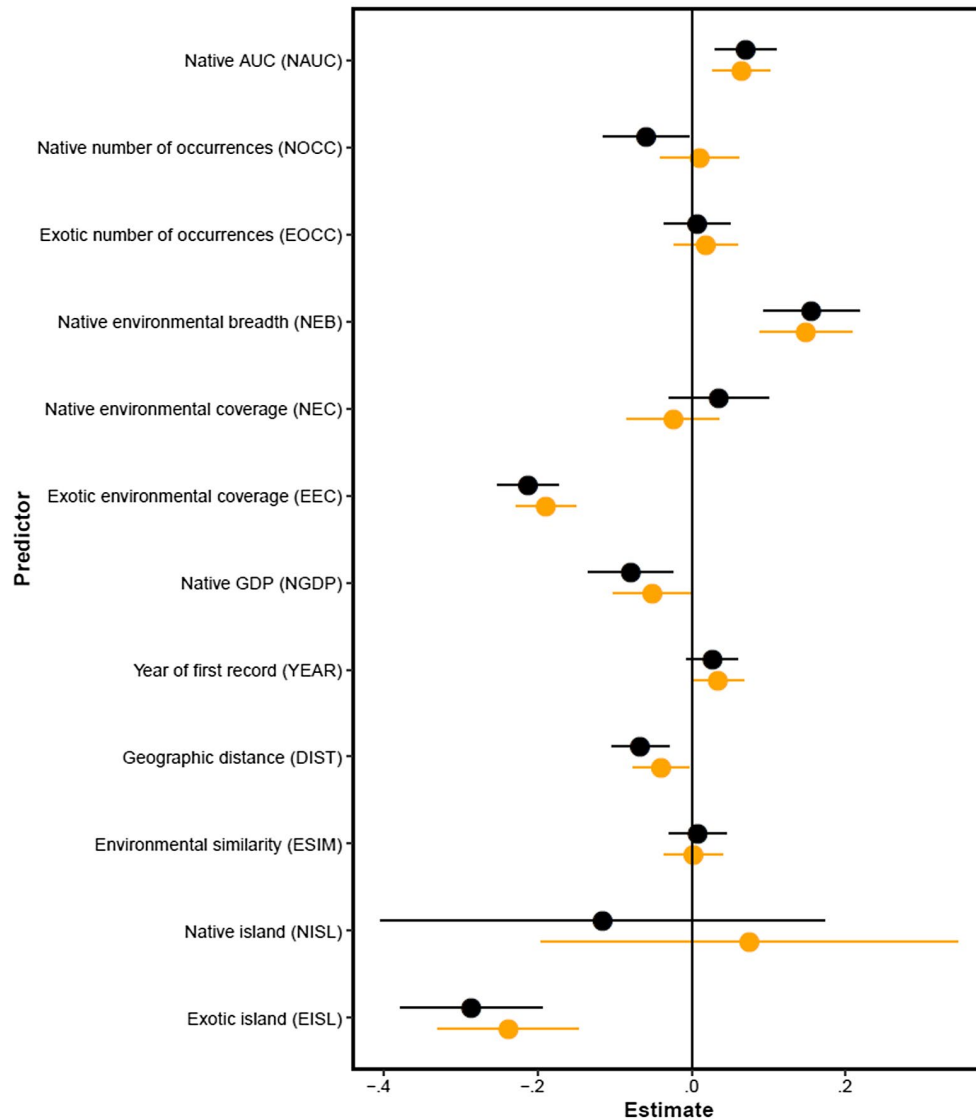


FIGURE 3 Dot-whisker plot of the parameter estimates for the binary and continuous predictors included in the linear mixed model for generalized additive models (GAMs; black) and MaxEnt (orange), with taxonomic class and continent as categorical predictors. Whiskers represent the 95 percent confidence intervals of the parameter estimates

the transferability of SDMs. However, there may have been insufficient differences to detect an effect, as only 11.8 and 13.4% of sites showed negative MES values on average for GAMs and MaxEnt, respectively. Finally, SDMs performed substantially worse when attempting to predict the distribution of species invading islands, as predicted. Species originating from islands, however, did not significantly affect model transferability, but only comprised 13 out of 647 species and so this result may reflect low power.

To further quantify and illustrate the contexts wherein SDMs may be transferable, we discretized the 1,867 species–location extrapolations, based on the significant predictors from the transferability model. We found that worse transferability occurred for exotic islands within Asia, and when high exotic environmental coverage (greater than 42%) occurred in Asia or on islands, with a mean AUC $\sim .6$ (Supporting Information Table S7). Conversely, we found that species invading North America recently (after the year 1970)

or with relatively few invaded sites (less than 20% environmental coverage) stood out as having stronger AUCs, with mean AUC $\sim .8$ (Supporting Information Table S8).

4 | DISCUSSION

While many studies have used SDMs to forecast the distributions of exotic species (e.g., Vicente et al., 2013), evidence for reliable transferability to new locations has been equivocal (Yates et al., 2018). Recent studies have also found differences in predictiveness between methodological approaches, with MaxEnt performing better than regression-based models within the fitted range (Valavi et al., 2022). We also found that MaxEnt predicted better than GAMs in the range used for fitting; however, GAMs slightly outperformed MaxEnt when extrapolating to exotic ranges, demonstrating

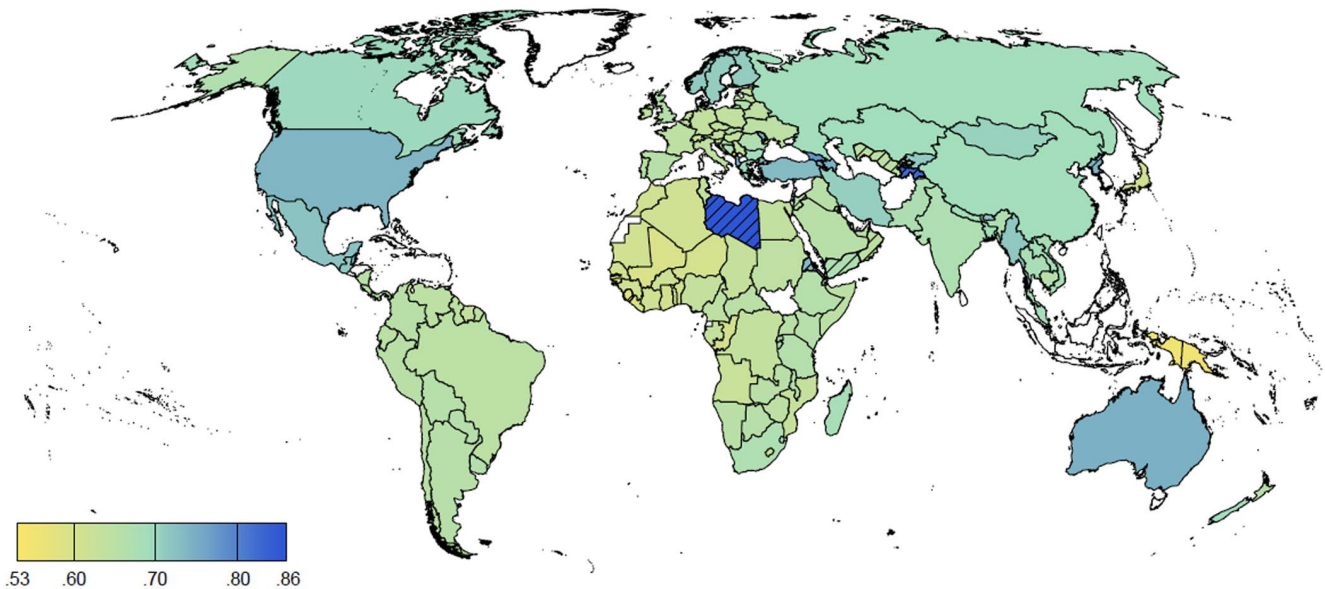


FIGURE 4 Map of the mean discriminatory performance (area under the receiver operating characteristic curve; AUC) of the models extrapolated to invaded regions, averaged between generalized additive models (GAMs) and MaxEnt. Striped regions represent areas that were invaded by fewer than three species

TABLE 3 Mean performance of the species distribution models divided between taxonomic groups, measured as area under the receiver operating characteristic curve (AUC), in both the native (fitting) range and the extrapolated (validation) range

Taxa	Native				Exotic					
	n	GAM		MaxEnt		n	GAM		MaxEnt	
		AUC	SD	AUC	SD		AUC	SD	AUC	SD
Mammalia	12	.780	0.106	.783	0.109	26	.645	0.121	.655	0.108
Insecta	19	.781	0.071	.790	0.058	34	.692	0.122	.663	0.122
Aves	21	.753	0.076	.772	0.079	49	.663	0.131	.673	0.116
Plants	591	.815	0.073	.831	0.068	1,752	.701	0.127	.693	0.123
Liliopsida	161	.819	0.070	.835	0.064	462	.692	0.127	.689	0.120
Magnoliopsida	416	.812	0.074	.828	0.070	1,266	.703	0.126	.693	0.124
Pinopsida	5	.908	0.073	.917	0.065	9	.702	0.142	.709	0.145
Polypodiopsida	9	.832	0.031	.860	0.031	15	.784	0.141	.803	0.126
Reptilia	4	.772	0.098	.787	0.091	6	.768	0.143	.818	0.110
TOTAL	647	.811	0.075	.827	0.070	1,867	.699	0.127	.692	0.123

Abbreviation: GAM, generalized additive model.

the importance of validation using spatially distinct data (Valavi et al., 2022). Moreover, we found half of the projections to exotic ranges to be unreliable despite strong performance in the native range (based on a .7 AUC threshold; Morán-Ordóñez et al., 2017; Swets, 1988). While AUC within the fitting data did positively relate to spatial transferability, high native range model performance was not sufficiently able to confer predictive success alone. This finding should inform our interpretations (and level of uncertainty) of invasion forecasts using environmental predictors. Notably, these were based on presence-only SDMs and mostly correlative climatic predictors, and thus alternative SDMs, such as those using

presence-absence or more mechanistic models, may provide superior transferability (but these possibilities need to be evaluated).

From a more optimistic perspective, half of the SDMs maintained some discriminatory ability ($AUC \geq .7$), and this method remains the best analysis possible given that alternatives (e.g., presence-absence data) are often unavailable. Further, although environmental similarity was not a significant predictor in the transferability model, this could be because successfully invaded ranges were environmentally similar to their corresponding native range, with few sites considered different on average (i.e., not enough variation to find a relationship). However, the environmental similarity between

ranges would also suggest that invasions are predictable at the regional level. Identifying which regions are at risk is also an important component of invasion biology (Ahmad et al., 2019). Regardless, much room exists for improving the transferability of SDMs (Yates et al., 2018).

A recent publication by Liu et al. (2020) also examined the spatial transferability of SDMs through meta-analysis, whereas we generated SDMs for this study. The authors' approach provided a valuable assessment of transferability, given how researchers have historically constructed SDMs (wherein model construction and quality control could vary considerably), while ours attempted to systematically control for quality and bias. In their study, Liu et al. found vastly higher accuracy in the range used for fitting, equivalent to an $AUC = .939$ based on their metric, but poorer transferability, equivalent to $AUC = .664$. In comparison, we found a less steep decline in performance and greater transferability, with a lower AUC in the native range ($AUC \sim .82$), but higher AUC in the exotic range ($AUC \sim .70$). Increasing quality control should reduce noise and overfitting and increase transferability (partially explaining the greater decline in transferability observed by Liu et al., 2020). However, the performance in the exotic range may differ more than these numbers suggest. Most SDMs historically do not control for bias (Yackulic et al., 2013) and thus, some of the signal in the exotic range in Liu et al. (2020) may reflect consistent detection bias between native and exotic ranges (e.g., due to distance to roads or human habitation; Yackulic et al., 2013), rather than the environmental drivers of interest. Therefore, transferability would likely have been even lower in Liu et al. (2020) if studies had controlled for biases.

4.1 | Predictors of transferability

Transferability differed between invaded continents, suggesting that SDMs may be more generally reliable in some areas than others. Liu et al. (2020) observed higher transferability in the Southern Hemisphere, contrary to our expectations, given greater data availability (Yesson et al., 2007) and research focus (Pyšek et al., 2008) in the Global North. Conversely, we found that Asia and Africa had worse transferability, possibly due to poorer sampling, while North America, with its high sampling intensity, showed the strongest performance. Surprisingly, we found that Europe showed low transferability, despite its high sampling intensity. Potentially, this may be because Europe has been heavily developed for centuries (Hulme, 2007), and the strong signal of transformed landscapes may weaken transferability based on climatic variables. As an additional factor, these large geographic areas differ considerably in biodiversity and species interactions (Willig et al., 2003). For instance, SDMs in practice rely on the realized niche, and higher species interactions in the tropics could reduce local predictions based on abiotic variables (Urban et al., 2016).

We found the strongest transferability for plants, and lower (but similar) levels of transferability for mammals, birds, and insects. Though we observed a higher average AUC for reptiles, these were

represented by only four species and therefore this should be interpreted with caution. One possible explanation is the mobility of species, which may influence the reliability of sightings records, as well as spread across areas within invaded areas (i.e., their dispersal ability; Elith & Leathwick, 2009; Urban et al., 2016). Contrary to this argument, Liu et al. (2020) observed higher transferability for terrestrial endotherms using meta-analysis. Yet, comparisons between our studies may be difficult to interpret, given differences in controlling for detection bias.

Increasing geographic distances between ranges resulted in poorer transferability, despite most invaded ranges being environmentally similar to the native range (based on the environmental traits measured). This suggests that other important factors varied over geographic distance, beyond those directly measured in our analysis (e.g., human demographics, Xu et al., 2019; community composition, Urban et al., 2016).

We found that SDMs often failed to predict the distribution of island invaders. Given that most species originated from mainlands, the overall poor transferability of SDMs to islands may be due to large ecological differences between ranges, for example through their differing community structure, and greater number of endemic species on mainlands (Vitousek, 1990). This poor discrimination on islands is particularly relevant for conservation, as island invasions are often of high concern due to their fragile recipient communities and risk to native biota (Lenzner et al., 2020; Simberloff, 1995).

Several of our findings differed from our a priori expectations, suggesting other processes were in play and requiring new hypotheses. While exotic environmental coverage negatively influenced model transferability, as models failed to differentiate between background sites and presences (Brotons et al., 2004; Zhang et al., 2015), environmental breadth in the native range was positively related to transferability. As a potential explanation, the positive relationship between native environmental breadth and SDM transferability may be due to a censoring effect, wherein we only analysed successful establishments. Smaller niche breadths may result in better discrimination in the native range in general, but most of these specialists may fail to establish in any exotic range (i.e., they would not exist within the study). Established species with narrow environmental breadths may then represent those restricted by other processes (e.g., biotic factors; Urban et al., 2016) that are released from these processes when invading a new region and may therefore occur outside of their realized niches and be poorly predicted. This post hoc hypothesis, however, requires further testing. For example, one possibility would be to examine successful and failed establishments in relation to their environmental breadth, using records of purposeful introductions to control for differential propagule pressures.

Also contrary to our initial hypotheses, we found a negative relationship between SDM transferability and GDP in the native range (which affects amount of trade with destination countries and thus propagule pressure, Sardain et al., 2019). We had expected that as species have greater opportunity to encounter more environments (more introduction events or more time to spread), exposure should become less of a limiting factor, thereby allowing environmental determinants to become

more important in shaping species distributions (Leung et al., 2012; Runquist et al., 2019). Second, we found that more recent invaders were more predictable. This was unexpected as earlier invasions should result in greater opportunities for exposure and be closer to equilibrium (an assumption of SDMs; Václavík & Meentemeyer, 2011). As a potential explanation, species may first establish in the most suitable habitats, resulting in good discrimination as these should offer the highest probabilities of survival. Species may begin to occupy less suitable sites with increased exposure, due to repeated introductions and processes such as competition, reducing overall transferability (Liu et al., 2020; McLoughlin et al., 2010). Finally, GAMs performed worse with higher number of native occurrences, contrary to our original expectation that more data may better inform model predictions. A previous study had found a positive relationship between transferability and the number of occurrences (Liu et al., 2020), more in line with our original hypothesis. While we cannot offer a mechanism underlying this relationship (beyond potentially a Type I error), we felt it was important to report findings even when they do not match our expectations to minimize confirmation biases in the literature.

Both SDM approaches tested in this study largely yielded concordant results, with similar levels of transferability and most predictors of transferability showing the same direction and significance. As such, there was no clear preference for one approach versus the other. While there were two differences (number of native occurrences and year of first record) out of 14 predictors examined, we would not expect the outcomes to be entirely identical between two alternative statistical models. As we were generally interested in the potential factors influencing model predictiveness, we considered the predictor if either GAM or MaxEnt provided evidence that a given factor affected transferability, albeit with less certainty than if the predictor was significant in both transferability models.

While overall transferability was modest, we observed strong predictions for SDMs occurred under certain contexts. Using the significant predictors of the transferability model, we identified concrete instances where SDMs may be successful. For example, we found higher transferability with more recent or less widespread invaders within North America, which is important from a management perspective as identifying the most likely sites of new invasions is often of interest (Kaiser & Burnett, 2010).

4.2 | Limitations and future directions

The SDMs in this study were generated using presence-only data, which is the most common approach due to the wide availability of occurrence records (Elith & Leathwick, 2009). Despite survey data representing a more rigorous sampling design, such data are less available for most species (Barbet-Massin et al., 2012). Thus, presence-only SDMs will likely remain an essential part of ecological modelling.

Although we found only low to moderate transferability, we acknowledge that this study primarily focused on correlative climate-based models, which may relate to species occurrences via other

(unknown) variables. The correlations between measured and other unknown variables need not remain consistent in exotic ranges, compromising transferability. Potentially, a loss in transferability may also be due to a temporal mismatch between species records, which ranged between 1970 and 2020, and environmental measures, which ranged from 1970 to 2000 for WorldClim and 2000 to 2020 for NDVI. Such differences may result in the models failing to characterize the species' actual relationship with its environment, resulting in poor predictive performance. More mechanistic processes of species distributions may confer better transferability (e.g., land use, ecosystem functional attributes and biotic factors; Arenas-Castro et al., 2018; Regos et al., 2019; Urban et al., 2016, respectively). However, unsurprisingly, the majority of ecological models have been based on such climatic predictors, given the challenges of applying experimental data to large geographic analyses (Werkowska et al., 2017) and the greater availability of high-resolution global climate data (e.g., Fick & Hijmans, 2017).

Finally, while we examined as many species as possible with the available data, the majority of species available were plants. However, non-plant groups still were comprised of 56 species and 115 exotic ranges within the dataset, and thus still represent an important component of the analysis, especially given the taxonomic differences in transferability detected.

4.3 | Conclusion

We conducted a large-scale systematic assessment by constructing 647 SDMs for individual species, to allow for the greatest comparability and rigor. Half of the SDMs exhibited poor discriminatory performance in the exotic range. However, SDM performance was heterogeneous, wherein SDMs may be reliable under certain contexts (e.g., invasions in North America after 1970), and only marginally better than random in others (e.g., exotic islands in Asia). Thus, inferences based on SDM projections to new ranges should be treated with caution, but SDMs still hold promise under some circumstances. Further analyses would be beneficial to identify additional conditions where SDMs may be reliable.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Species records are available through GBIF (<https://www.gbif.org/>), with DOIs for occurrences and background sites provided

in Supporting Information Text S1 and Table S3, respectively. Distributional data for invasive species are available through GISD (<http://www.iucngisd.org/gisd/>) and CABI Invasive Species Compendium (<https://www.cabi.org/isc>). GADM Environmental Systems Research Institute (ESRI) shapefiles for global subdivisions are available from <http://gadm.org/>. Global shoreline vector for islands is available from Sayre et al. (2018) (<https://rmgsc.cr.usgs.gov/outgoing/ecosystems/Global/>). Bioclimatic and elevation data are available through WorldClim v2 (<https://www.worldclim.org/>). MODIS NDVI data were accessed through NASA Land Processes Distributed Active Archive Center (<https://e4ftl01.cr.usgs.gov/MOLT/MOD13C2.006/>). First records data for invasive species were provided by Seebens et al.'s (2017) Alien Species First Records dataset (<https://doi.org/10.5281/zenodo.3690742>). Gridded GDP dataset is available through Kummu et al. (2018) (<https://doi.org/10.5061/dryad.dk1j0>). Code and data are available on Dryad (<https://doi.org/10.5061/dryad.gtht76hp6>).

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