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Biological invasions reveal how niche change affects the transferability of species distribution models

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Abstract

Species distribution models (SDMs) have been widely applied to predict geographic ranges of species across space and time under the assumption of niche conservatism (i.e., species niches change very slowly). However, an increasing number of studies have reported evidence of rapid niche changes across space and time, which has sparked a widespread debate on whether SDMs can be transferred to new areas or time periods. Understanding how niche changes affect SDM transferability is thus crucial for the future application and improvement of SDMs. Biological invasions provide an opportunity to address this question due to the geographically independent distributions and diverse patterns of niche changes between species' native and introduced ranges. Here, we synthesized findings on 217 species from 50 studies to elucidate the effects of niche change on the spatial transferability of SDMs. When niche change was considered as a categorical classification (conserved vs. shifted niches) in tests of the niche conservatism hypothesis, SDM transferability was markedly lower for species with a shifted niche in their introduced range. When niche change was measured as numerical dynamics between native and introduced niches, SDM transferability was high for species occupying similar environmental conditions in both ranges and low for species with more environmental space remaining unoccupied in the introduced range. Surprisingly, the number of presence points used for developing SDMs turned out to have an even stronger effect on transferability. Our results thus reveal detrimental effects of both niche change and lack of presence points on SDM transferability. It is necessary to consider both niche change and data quality for improving the transferability of SDMs, so that they can better support conservation management and policy decisions.

KEYWORDS
Bayesian inference, biogeographical experiments, biological invasions, ecological niche models, invasive alien species, niche dynamics, niche shift, quantitative synthesis

INTRODUCTION

The ecological niche is a key concept in the field of ecology, biogeography, and conservation biology (Guisan et al., 2014; Wiens et al., 2009). Central to niche theory is the niche conservatism hypothesis, which posits that species largely conserve their niches across space and time: Niches only slowly change, so species can only sustain populations under similar conditions compared to the environment in which they evolved (Soberón & Nakamura, 2009; Wiens et al., 2010). The niche conservatism hypothesis has been considered an important foundation for understanding biogeographical patterns, elucidating species adaptation to changing environments, and reconstructing the evolutionary histories of clades (Pearman et al., 2008; Wiens et al., 2009).

Niche conservatism is also a fundamental assumption of species distribution models (SDMs), which are a crucial tool for predicting the potential distribution of species and supporting the design of conservation strategies (Feng et al., 2019; Guisan & Thuiller, 2005; Jeschke & Strayer, 2008). SDMs are developed on the basis of the realized ecological niche (i.e., the environmental conditions in which a species persists in nature) by fitting the relationship between species distributions and environmental predictors (D'Amen & Azzurro, 2020; Guisan & Thuiller, 2005; Petitpierre et al., 2017). In recent decades, a number of SDMs have been developed using data obtained from one region and transferred to other regions or time periods under the assumption of niche conservatism (Jeschke & Strayer, 2008; Werkowska et al., 2017). Transferred SDMs are widely used for forecasting species responses to climate change, determining the probability of disease outbreaks, and hindcasting species distributions under historical environments (Morán-Ordóñez et al., 2017; Nogués-Bravo, 2009; Yates et al., 2018). Since species conserve their niche, it has been suggested that SDMs are only transferred to environmental conditions similar to the ones in which the model is developed (Qiao et al., 2019; Sequeira et al., 2018; Werkowska et al., 2017).

However, recent studies have frequently reported that species tend to change their niche when transported to a new geographic region, challenging the transfer of SDMs in new space and time (Atwater & Barney, 2021; Broennimann et al., 2007; Guisan et al., 2014; Pearman et al., 2008). A changed species–environment relationship has been considered the main limitation for the spatiotemporal transferability of SDMs (Guisan & Thuiller, 2005; Parravicini et al., 2015; Yates et al., 2018). To facilitate the application of SDMs across space and time, it is important to understand the degree to which niche change affects SDM transferability in general (Atwater & Barney, 2021; Pearman

et al., 2008; Petitpierre et al., 2012, 2017) and why some SDMs are more transferable under certain conditions (Petitpierre et al., 2017; Sequeira et al., 2018).

Biological invasions represent an opportunity to address these questions because of two unparalleled advantages (Jeschke & Strayer, 2008; Tingley et al., 2014). First, invasive species have demonstrated a wide range of patterns in niche change in their introduced range as a consequence of adaptive evolution, residence time, changes in biotic interactions, and dispersal limitations (Atwater et al., 2018; Broennimann et al., 2007; Guisan et al., 2014; Pearman et al., 2008). Patterns of niche changes range from cases where the niche in the introduced range (i.e., introduced niche) is only a subset of the niche in the native range (i.e., native niche) to cases where the introduced niche completely encompasses the native niche (Liu et al., 2020a). Second, a crucial premise of assessing SDM transferability is that the distribution data used for developing and evaluating SDMs are spatiotemporally independent (Feng et al., 2019; Jeschke & Strayer, 2008). In the Anthropocene, thousands of invasive species have been introduced around the world, yielding many geographically independent data sets between species' native and introduced ranges (Parravicini et al., 2015; Petitpierre et al., 2017).

Recent studies have taken advantage of this opportunity to evaluate SDMs that are developed in the native range and transferred to the introduced range, as well as to assess niche changes between ranges (Liu et al., 2020a, 2020b). The effects of niche changes on SDM transferability have been investigated for multiple taxa, including invasive birds (e.g., Strubbe et al., 2013), insects (e.g., Hill et al., 2017), marine fishes (e.g., Parravicini et al., 2015), and plants (e.g., Petitpierre et al., 2012), but these studies yielded different findings. For example, Petitpierre et al. (2012) reported that SDMs were more transferable for plant invaders with a small magnitude of niche change, while Rodrigues et al. (2016) did not detect a clear influence of niche change for invasive turtles.

A possible reason for these conflicting findings is the inconsistency in how niche changes have been assessed. Most studies simply assessed whether a species' niche was conserved or shifted (i.e., qualitatively concluding yes or no in tests of the niche conservatism hypothesis), using different techniques or criteria. For example, taking the univariate approach (i.e., niche is compared along an individual environmental variable), some studies concluded a niche shift had taken place if there was no overlap in the range of an environmental predictor between species' native and introduced ranges (e.g., Rödder et al., 2009), whereas others based the conclusion on significance tests of predictor values between ranges (e.g., Gallardo et al., 2013). For those applying the ordination approach (i.e., comparing species niche in a two-

dimensional environmental space) (Guisan et al., 2014), many studies adopted the magnitude of niche matching between ranges as a criterion (e.g., Capinha et al., 2011), and a few studies focused on whether there was a significant difference in breadth between native and introduced niches (e.g., Steiner et al., 2008). To date, at least 22 techniques and 13 criteria have been applied to yield such categorical classification by testing the niche conservatism hypothesis for invasive species (Liu et al., 2020a). However, contrasting classifications are frequently reported for a given species if niche change is assessed by more than one technique or criterion (Liu et al., 2020a). For example, Zhu et al. (2012) used the univariate and ordination approaches to test the niche conservatism hypothesis for the invasive common reed *Phragmites australis* and concluded that the niche had been conserved and shifted, respectively.

Besides the categorical classification, another commonly used method of assessing niche change is to measure the numerical dynamics (i.e., based on a gradual scale) between native and introduced niches (Guisan et al., 2014). The Centroid shift, Overlap, Unfilling, and Expansion (COUE) scheme is efficient and robust, and is considered the gold standard for estimating numerical niche dynamics (di Cola et al., 2017; Petitpierre et al., 2012). This scheme first delineates a species' global niche in a two-dimensional space constructed based on associated environmental predictors using a principal component analysis (PCA) and then decomposes the global niche into three components according to the environmental space that is occupied: (1) in both the native and introduced range (stability [S]); (2) in the introduced range only (expansion [E]); and (3) in the native range only (unfilling [U]) (Figure 1) (for more details, see Broennimann et al. [2012] and Guisan et al. [2014]). A few studies estimating the niche dynamics of invasive species using the COUE scheme also evaluated the spatial transferability of SDMs between native and introduced ranges (e.g., Sales et al., 2017; Strubbe et al., 2015; Tingley et al., 2014), paving the way for assessing the association between niche dynamics and SDM transferability.

Here we consider biological invasions as large-scale natural experiments that allow us to investigate the effects of niche changes on SDM transferability. We specifically focused on the spatial transferability of SDMs that were developed based on species distributions and environmental predictors in the native range (native-range SDM) and evaluated based on the distribution data of invasive species in their introduced range, which was much more frequently evaluated than that of SDMs transferred from the introduced range to the native range (Liu et al., 2020b). Since no technique or metric is currently considered as the most appropriate (Qiao et al., 2015; Sofaer et al., 2019; Yates et al., 2018), some studies used more than one
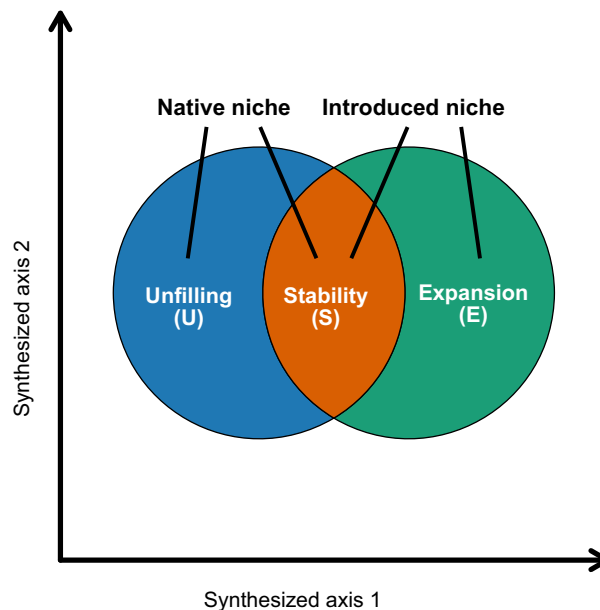

FIGURE 1 Schematic plot showing niche dynamics of invasive species between native and introduced ranges quantified by Centroid shift, Overlap, Unfilling, and Expansion (COUE) scheme (Petitpierre et al., 2012). The global niche is decomposed into three components: stability (*S*), unfilling (*U*), and expansion (*E*), according to environmental space occupied in both native and introduced ranges, in the native range only, and in the introduced range only, respectively

technique to develop SDMs or applied more than one metric to evaluate the developed SDM (e.g., Strubbe et al., 2013; see *Materials and Methods* for more details).

Using data compiled from 50 published studies that assessed niche change and SDM transferability for 217 invasive species, we addressed two research questions. First, does niche change negatively affect SDM transferability? To address this question, we first investigated whether SDM transferability was higher for species with a conserved versus shifted niche, using data from studies that applied the previously described categorical classification to test the niche conservatism hypothesis. We then investigated the association of SDM transferability with the magnitude of niche expansion (*E*), stability (*S*), and unfilling (*U*), using data from studies that assessed numerical dynamics between native and introduced niches based on the COUE scheme. Given that SDMs are deeply rooted in niche theory, our second research question of whether niche change (categorical or numerical) has a stronger influence on SDM transferability than other factors. To address this question, we applied a Bayesian multivariate response model, a form of path analysis, to assess the influence of niche change, data used, and invasion history on SDM transferability.

MATERIALS AND METHODS

Study compilation

We conducted a systematic search for publications reporting both niche change and SDM transferability for invasive species following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Moher et al., 2009). First, we searched Clarivate Analytics' Web of Science database using the following terms: ([Introduce* OR inva* OR alien OR non-native OR nonnative OR exotic OR naturaliz* OR nonindigenous OR non-indigenous] AND niche). Literature searches were first conducted in December 2018 and updated in July 2020. We did not include terms related to transferability ("transfer*") because some candidate publications described SDM transferability using synonyms (e.g., cross-applicability, generality) (Yates et al., 2018) and were not found if "transfer*" was included in the search query (e.g., Broennimann et al., 2007; Parravicini et al., 2015). The titles and abstracts of publications returned by the search were screened for relevance. Second, we screened the reference section of each relevant article to find additional publications. After scanning the titles and abstracts of 8227 publications, we identified 306 potentially relevant articles. Finally, we downloaded these articles and screened the full texts to only include studies that evaluated SDM transferability between species' native and introduced ranges, as well as assessed niche change as the categorical classification by testing the niche conservatism hypothesis or as numerical dynamics using the COUE scheme. The final data set included empirical findings on 217 species from 50 studies and is provided in Liu et al. (2021).

Data compilation and transformation

From all identified studies we collected the estimates of the spatial transferability of native-range SDM in each introduced range for each species, following the authors' definition of species' native and introduced range. Given SDM transferability may vary with different modeling techniques or evaluation metrics, we collected the data for each SDM technique and each metric. For example, Strubbe et al. (2013) developed SDMs for 28 invasive birds using four techniques (generalized boosted models, generalized linear models, random forests, maximum entropy) and evaluated each developed SDM using both the area under the curve (AUC) (Fielding & Bell, 1997) and Boyce index (Boyce) (Boyce et al., 2002), resulting in more than 200 estimates of SDM transferability (Liu et al., 2021). In our data set, most studies (82%) applied only one SDM

technique, with the maximum entropy method (MaxEnt) (Phillips et al., 2006) being the most popular across studies (37.2%) and ensemble modeling across species (32.7%) (Araújo & New, 2007; Liu et al., 2021). Similarly, most studies (70%) adopted only one evaluation metric, with AUC as the most popular across studies (32.3%) and Boyce across species (59.8%) (Liu et al., 2021).

Given the great heterogeneity in evaluation metrics across studies and the lack of an agreed-upon metric for evaluating SDMs, the values of all evaluation metrics were transformed to the same scale from 0 to 10 following Liu et al. (2020b) as

$$t = (o - w)/(b - w) \times 10,$$

where o and t are the original and transformed values of each evaluation metric, respectively; and w and b are values denoting the worst (i.e., no absence and presence point is correctly predicted) and best performance (i.e., all absence and presence points are correctly predicted), respectively (Appendix S1: Table S1). After transformation, 0 and 10 represent the worst and best performance, respectively. For each SDM, we averaged the transformed values of different metrics to avoid pseudoreplication of model evaluation, which is supported by the insignificant difference in values between two metrics evaluating the same SDM (Wilcoxon matched pair test, $p = 0.51$, df = 142).

For 49 studies testing the niche conservatism hypothesis, we collected all categorical classifications made by 16 techniques and 12 criteria (Appendix S1: Tables S2 and S3). We excluded the categorical classifications made by four techniques based on SDM transferability, because the assessment of niche change and SDM transferability is dependent (Appendix S1: Table S2; also see Guisan et al. [2014]). Most studies (87.8%) only applied one niche approach, with the ordination approach being used in 91.8% of studies. The frequency of studies using the univariate approach and the hypervolume approach (i.e., species niche is compared in a multidimensional space constructed by more than two predictors) was only 16.3% and 4.1%, respectively. To avoid pseudoreplication, all classifications made by different techniques and criteria to each pair of species' native and introduced ranges were grouped into three categories: (1) conserved, if all techniques and criteria concluded that the niche did not shift but was conserved between the native and introduced range; (2) shifted, if all techniques and criteria concluded that the niche shifted between ranges; and (3) ambiguous, if different techniques and criteria led to contrasting classifications. Among 195 species being tested for the hypothesis, 18 species were included in more than one study, and within one study, 49 species were tested between the native range and multiple introduced ranges (Liu et al., 2021).

For 27 studies estimating niche dynamics using the COUE scheme, we collected the numerical values of the three dynamic metrics (E, S, and U). We only kept 23 studies that estimated niche dynamics in analogous environments (i.e., environmental conditions present in both native and introduced ranges) (Guisan et al., 2014). Excluding nonanalogous environments is a key premise of assessing niche dynamics for invasive species to avoid pseudoniche change caused by environmental non-availability in one range (Guisan et al., 2014; Petitpierre et al., 2012). Because the values of S and E are weighted by environmental density in the introduced range, whereas the value of U is weighted by environmental density in the native range (for more details, see Broennimann et al. [2012] and Di Cola et al. [2017]), we followed Liu et al. (2020a) to transform the value of U to the magnitude relative to the environmental density in the introduced range:

$$U_T = S/(1 - U_O) \times U_O,$$

where U_O and U_T are the original and transformed values of U, respectively; S is the value of stability, which is directly calculated as $1 - E$ based on the environmental density in the introduced range (di Cola et al., 2017). We further excluded one species with $S = 0$, for which the value of U could not be transformed. For each set of metric values, the values of E, S, and U were divided by their sum to get the relative contributions to the global niche. Among 166 species with estimated niche dynamics, ten were included in more than one study, and in one study, 42 species were estimated between the native range and more than one introduced range (Liu et al., 2021).

We collected the information related to the type and quality of the data used in each study, including (1) spatial resolution, (2) number of predictors, (3) number of presence points in the native range (hereafter, native presences), and (4) number of presence points in the introduced range (hereafter, introduced presences). We also collected information on the earliest year in which a species was introduced to each range from each study and further supplemented our data set using the Global Alien Species First Records Database (Seebens et al., 2018). We requested such data from the authors if they were not available in the study or online, as well as the results of niche dynamics and SDM transferability.

Bayesian analyses

We performed all analyses within a Bayesian inference framework using the brms package (Bürkner, 2017).

Bayesian analyses have the advantage of estimating parameter probabilities by controlling for the influence of noisy data and insufficient samples (Ellison, 2004). To address whether SDMs are more transferable for species with a conserved niche, we compared SDM transferability among species with three classifications (i.e., conserved, shifted, and ambiguous) using a Bayesian regression model. To address how niche dynamics (based on the COUE scheme) affect SDM transferability, we assessed the strength of the association between each dynamic metric (E, S, and U) and SDM transferability, using a Bayesian multilevel model. Because these two analyses used data from different studies, we also performed the foregoing analyses using the data from a subset of studies that both tested the niche conservatism hypothesis and estimated niche dynamics using the COUE scheme. Besides exploring the general pattern across studies, we also assessed the influence of niche changes on SDM transferability for individual studies with sufficient data using the Bayesian models described previously.

Last, we compared the direct effects of niche change and five other factors (i.e., resolution of species distribution and environmental predictors, number of predictors, number of native presences, number of introduced presences, and year of introduction) on SDM transferability using the data of studies that yielded categorical classifications and estimated numerical dynamics, respectively. Since niche changes are closely associated with the data used and the invasion history of the focal invader (Li et al., 2014; Liu et al., 2020a; Petitpierre et al., 2012), we further considered the indirect effects of these factors mediated by niche change. For example, the magnitude of niche unfilling is negatively related to the number of introduced presences (Liu et al., 2020a), which increases in the process of species invading new areas (Atwater et al., 2018; Guisan et al., 2014). A higher number of introduced presence points in turn improves SDM transferability because more introduced presences can buffer against an SDM evaluation bias caused by outliers (Guisan & Thuiller, 2005; Liu et al., 2020b). Here, we used a Bayesian multivariate response model, a form of path analysis (Bürkner, 2018), to assess the effect of each factor on SDM transferability. Path analysis is particularly useful for assessing the independent influence of the data used on niche changes and SDM transferability because the same data set is used for assessing niche changes and developing SDMs.

For path analysis based on data from studies applying a categorical classification of niche change, we excluded species with the ambiguous conclusion and coded "conserved" and "shifted" niches as 0 and 1, respectively, so that the analyses could be performed in one model to specifically assess the influence of niche shift. Given the

equivalent roles of three dynamic metrics (expansion, unfilling, and stability), we performed the path analysis for each dynamic metric separately. Note that the number of predictors is the same for the development of SDMs and the assessment of niche change, despite the fact that COUE scheme consequently synthesizes all environmental predictors to two PCA components (Broennimann et al., 2012; Guisan et al., 2014). The numbers of native and introduced presences were log-transformed, and the values of all variables were standardized with the mean of 0 and SD of 1 for comparing their effects.

For all Bayesian models, the study was set as a random factor. We further set the technique used for developing SDMs as a random factor nested within the study, because the SDM technique can affect transferability (Sequeira et al., 2018; Yates et al., 2018). In our data set, different values of transferability can be obtained from SDMs developed using different techniques, even with the same set of data (Appendix S1: Figure S1). The mean and credible interval of parameters were estimated based on 12,000 posterior values calculated from 4 chains of 5000 iterations with the first 2000 steps as burn-in. Weakly informative priors were used for all variables, with 0 as the mean and 2 as SD. We confirmed a good chain convergence according to Rhat (the potential scale-reduction factor), which had values below 1.01 for all models (Bürkner, 2017). All analyses were conducted in R (version 3.5.0.) (R Development Core Team, 2019).

RESULTS

SDM transferability for species with a conserved versus shifted niche

A strikingly similar number of cases was found for species reported with a conserved ($N = 115$) and shifted niche ($N = 114$) between the native and introduced ranges, though there was ambiguous evidence (both conserved and shifted niche, depending on the techniques or criteria applied) for 37 species (Appendix S1: Figure S2). Path analysis revealed a markedly negative effect of niche shift on SDM transferability (-0.54 ± 0.33; Figure 2, arrows from niche shift to transferability; hereafter, effect sizes are reported by the mean of Bayesian posterior values $\pm 80\%$ credible intervals). In addition, the data used and the invasion history of focal species imposed indirect effects on SDM transferability by affecting the categorical classification (Figure 2). For example, the number of native presences elevated SDM transferability both directly (0.51 ± 0.19) and indirectly (0.1 ± 0.03), resulting in a total effect of 0.56. The influence of niche shift was further confirmed by the lower SDM transferability for niche-
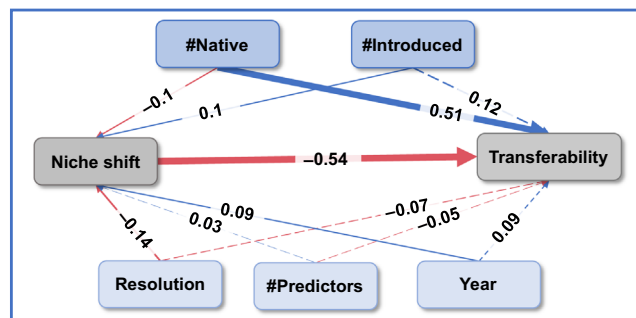

FIGURE 2 Path model showing direct effects of categorical classification of niche change (conserved vs. shifted niche), the data used, and the year of introduction on species distribution model (SDM) transferability, as well as the indirect effects of the data used and the year of introduction mediated by the categorical classification. The width of arrows is proportional to the mean of 12,000 Bayesian posterior values estimated from four chains, with the corresponding mean value on the arrow. Blue and red arrows represent positive and negative effects, respectively. Dashed and solid lines represent 80% credible intervals overlapping with zero or not, respectively

shifting (6.65 ± 0.5) than niche-conserving species (6.02 ± 0.31) without controlling for the effects of other factors (Appendix S1: Figure S2). Further, we found a high dispersion of transferability values for species both with conserved and shifted niches, contributing to a slight overlap of credible intervals between these two groups (Appendix S1: Figure S2). A similar pattern was found when using only data from studies that also estimated niche dynamics using the COUE scheme (Appendix S1: Figure S3). A lower SDM transferability for niche-shifting species and high dispersion of transferability values among species were also found in individual studies (Appendix S1: Figure S5).

Effects of numerical dynamics on SDM transferability

There were marked differences in the data used among studies that assessed numerical dynamics between native and introduced niches using the COUE scheme. Most SDMs were developed at a resolution of $0.5°$ (68.4% of SDMs) and with eight or nine predictors (45.8% and 40.4% of SDMs, respectively). Patterns of niche dynamics differed greatly among species (Figure 3), but most species showed limited (<10%) niche expansion (73.2% of species) or large (>50%) niche stability (65.4% of species).

SDM transferability was closely associated with niche dynamics (Figure 3). A weakly negative association was found between niche expansion and SDM transferability (-0.76 ± 0.78, with the credible interval slightly overlapping
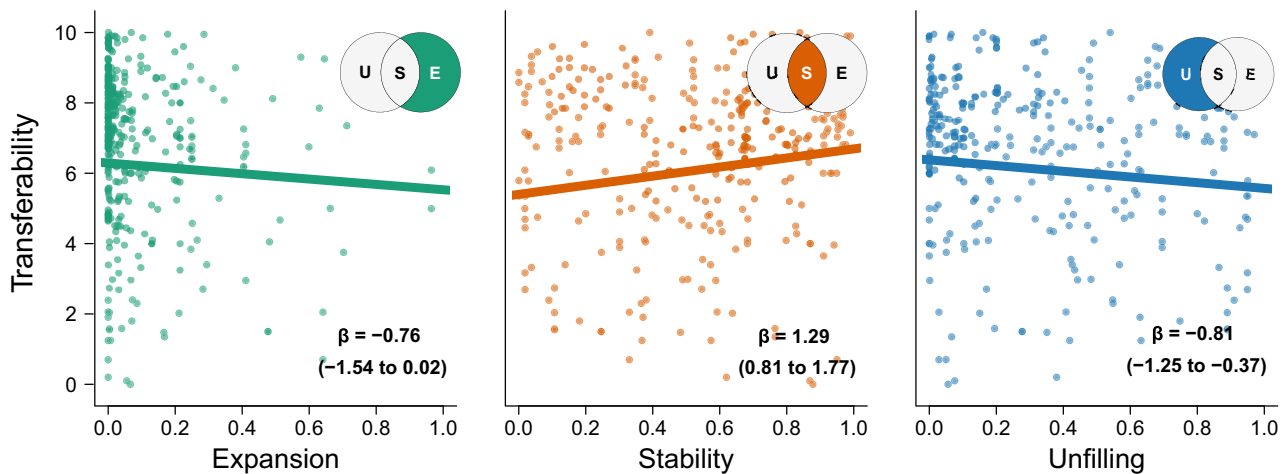
FIGURE 3 Associations between niche dynamics and species distribution model (SDM) transferability. Niche dynamics between native and introduced ranges were estimated using the Centroid shift, Overlap, Unfilling, and Expansion (COUE) scheme, with expansion representing the environmental space only occupied in the introduced range, stability representing the space in both native and introduced ranges, and unfilling representing the space only in the native range. Thick lines denote the mean of 12,000 Bayesian posterior values estimated from four chains, and the dots denote original data used for estimating the associations

with zero), suggesting a negative effect of environmental novelty on predicting invasion risks. SDM transferability was also negatively related to niche unfilling (-0.81 ± 0.44), indicating that transferred SDMs had a poorer predictability for species with more environmental space remaining unoccupied in the introduced range. By contrast, transferability was positively affected by niche stability (1.29 ± 0.48), suggesting that SDMs were more transferable for species with a larger overlap between native and introduced niches. There was no clear change in the direction and strength of the associations between niche dynamics and SDM transferability when using data only from those studies that also tested the niche conservatism hypothesis (Appendix S1: Figure S4). When focusing on individual studies, we found a markedly positive stability–transferability relationship and negative unfilling–transferability relationship only for studies with more than 20 species of plants or terrestrial endotherms (Appendix S1: Figure S6).

The direct effects of niche dynamics on SDM transferability were reflected in the path analysis, which showed that transferability positively correlated with stability (0.42 ± 0.15) and negatively with unfilling (-0.27 ± 0.14) (Figure 4b,c, with arrows from stability and unfilling to transferability). Estimates of niche dynamics were further influenced by the data used and invasion history, leading to consecutive effects on SDM transferability (Figure 4). For example, more introduced presences could increase the magnitude of stability (0.42 ± 0.09) (Figure 4b) and decrease the magnitude of unfilling (-0.36 ± 0.09) (Figure 4c).

Transferability was also directly affected by the number of native presences, the number of predictors, and invasion history, with the magnitude of their effects being consistent across the considered dynamic metrics (Figure 4a–c). Surprisingly, compared to niche dynamics (E, S, and U), the number of native presence points had a stronger effect on SDM transferability (0.55 ± 0.19, 0.53 ± 0.19, 0.56 ± 0.19, respectively) (Figure 4a–c), highlighting the importance of developing SDMs with a high number of presence points. The number of predictors also had positive effects on SDM transferability when accounting for expansion (0.38 ± 0.32; Figure 4a), stability (0.34 ± 0.33; Figure 4b), and unfilling (0.37 ± 0.34; Figure 4c). A slightly positive influence of the year of introduction on SDM transferability (0.18 ± 0.14) was found when accounting for stability.

DISCUSSION

Our synthesis clearly revealed negative effects of niche changes on the spatial transferability of SDMs for invasive species. When niche change was categorically assessed, SDM transferability was markedly lower for niche-shifting than niche-conserving species. When niche change was estimated as numerical dynamics based on the COUE scheme, SDM transferability was found to be closely associated with each dynamic metric (i.e., expansion, stability, and unfilling). Surprisingly, though, the number of native presence points had the strongest effect on SDM transferability overall.
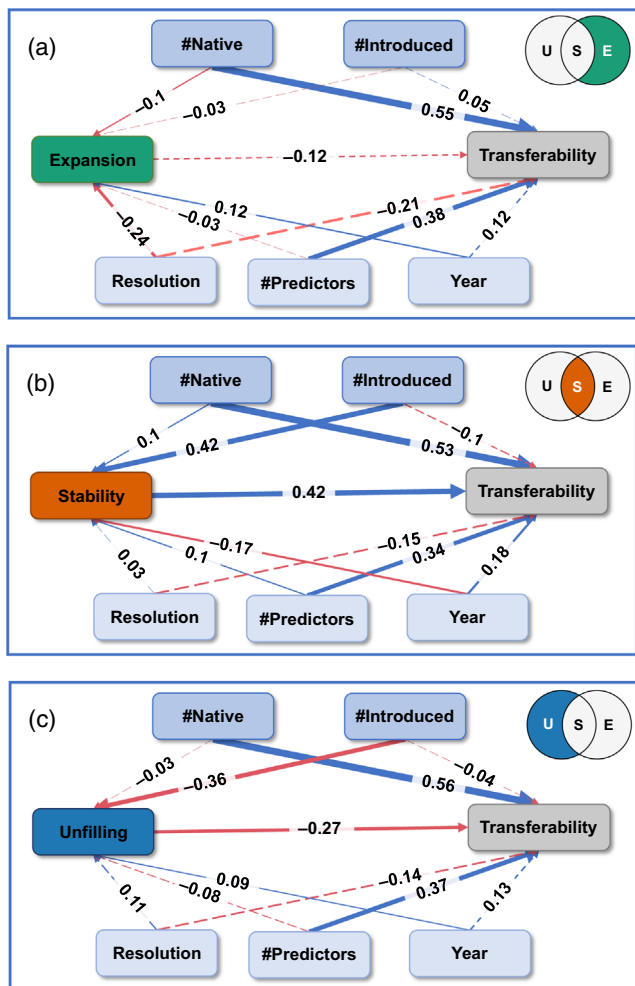
FIGURE 4 Path models showing direct effects of niche dynamics, the data used, and the year of introduction on species distribution model (SDM) transferability, as well as indirect effects of data used and year of introduction mediated by (a) expansion, (b) stability, and (c) unfilling. Arrow width is proportional to the mean of 12,000 Bayesian posterior values estimated from four chains, with the corresponding mean value on the arrow. Blue and red arrows represent positive and negative effects, respectively. Dashed and solid lines represent 80% credible intervals overlapping with zero or not

Lower transferability for species with shifted versus conserved niches

Our analyses based on studies that applied a categorical assessment of niche conservatism document the risks of applying native-range SDMs to anticipate the establishment and dispersal for niche-shifting species (Atwater & Barney, 2021; Petitpierre et al., 2017). Invasive species with a shifted niche require different environmental conditions for their growth and reproduction in new areas than the conditions in their native ranges. This has been considered as a key determinant of reduced transferability of SDMs

that are developed in the native range (Atwater & Barney, 2021; Petitpierre et al., 2012; Tingley et al., 2014). Nonetheless, we also found wide variation in SDM transferability for both niche-conserving and niche-shifting species, implying a potential limitation of the categorical assessment to guide the transfer of SDMs. Indeed, categorical assessments of niche conservatism have frequently reached conflicting conclusions (i.e., conserved or shifted niche) for a single species in a single study for different techniques or criteria (Guisan et al., 2014; Liu et al., 2020a). Some of these techniques have also been methodologically criticized (Peterson, 2011; Petitpierre et al., 2012; Strubbe et al., 2013). For example, the niche equivalency test draws conclusions based on the statistical significance of whether native and introduced niches are different, which is largely affected by sample sizes and background environments (Liu et al., 2020a; Peterson, 2011). Conclusions drawn from a univariate approach heavily depend on the focal environmental predictor, with contrasting conclusions likely being derived from different environmental axes (Lauzeral et al., 2011; Peterson, 2011). Because there is no commonly agreed-upon technique for testing the niche conservatism hypothesis, future studies should pay more attention to using techniques that can lead to biologically meaningful conclusions (Peterson, 2011).

Relationships between numerical niche dynamics and transferability

The negative effect of niche expansion on SDM transferability confirms the risk of extrapolating SDMs to novel environments, as a larger niche expansion indicates that SDMs are transferred to areas with a higher environmental novelty compared to species' native range (Liu et al., 2020b; Petitpierre et al., 2017). It has been widely accepted that the predictive performance of SDMs rapidly decreases under environmental conditions that differ from those for which SDMs were developed (Werkowska et al., 2017; Yates et al., 2018). The estimated niche expansion can thus serve as a useful proxy to infer the uncertainty underlying SDM predictions for invasive species (Hill et al., 2017; Qiao et al., 2019): When SDMs are applied to invaders showing high niche expansion, the confidence in native-range SDMs should be low (Li et al., 2014; Petitpierre et al., 2012; Strubbe et al., 2013). Note, though, that the limited niche expansion of most invasive species prevented us from obtaining a complete picture of the expansion–transferability relationship. We suggest future studies to focus more on species with large niche expansion to better understand its influence on SDM transferability.

The negative unfilling–transferability relationship is consistent with previous findings on invasive insects (Hill et al., 2017), plants (Petitpierre et al., 2012), and vertebrates (Strubbe et al., 2015), highlighting the caveat of predicting invasion risks for species that are in the process of colonizing new areas (Hill et al., 2017). Owing to the lag phase and dispersal limitation, the colonization processes of many invasive species are not yet complete (Strubbe et al., 2015; Tingley et al., 2016). A high unfilling value suggests that the focal species is in the early stage of invasion and has large potential to further colonize the new environment (Atwater et al., 2018; Guisan et al., 2014). The influence of colonization process on SDM transferability is also supported by the positive stability–transferability relationship, as the magnitude of niche stability increases with the residence time of invasive species in new ranges (Guisan et al., 2014, Liu et al., 2020a). Thus, for invaders in the process of colonizing new areas, a lower transferability should not be interpreted as a limited SDM performance to predict their future distributions (Atwater et al., 2018; Guisan et al., 2014; Liu et al., 2020a).

Limitations of assessing SDM transferability for invasive species

The colonizing process of invasive species also raises concerns on how best to evaluate the spatial transferability of native-range SDMs. One key aspect is the metrics used for evaluating transferability (Barbet-Massin et al., 2018; Sofaer et al., 2019). To date, most metrics are developed based on the confusion matrix in terms of presence/absence and under the assumption that species had sufficient time for colonization (Tingley et al., 2016; van Proosdij et al., 2016). However, such metrics can be misleading for species in the early invasion stage, which are still invading and have insufficient distribution data for SDM evaluation (Leroy et al., 2018; Sofaer et al., 2019). This limitation will probably be exaggerated by the threshold chosen to transform the probabilistic output of SDMs into species presence and absence in the introduced range (Guisan & Thuiller, 2005; Yackulic et al., 2013). A few studies adopt the threshold of binary conversion according to the prediction of SDMs that are developed using the data from the introduced range (e.g., Václavík & Meentemeyer, 2012). However, this approach very likely yields an overly optimistic estimation of SDM transferability: The data used for model development and evaluation are not independent, which leads to the selection of overparameterized SDMs with underestimated prediction errors (Jeschke & Strayer, 2008; Liu et al., 2020b). Moreover, in our data set, different strategies have been used to identify the threshold (Appendix S1: Table S1), with the highest number of studies (20%)

adopting the threshold that maximizes the evaluation metric value, while almost half of all studies (42%) do not provide such information. An elegant solution to consider ongoing colonization processes is to evaluate SDMs only for regions that have actually been accessible to focal invasive species since their introduction (Barve et al., 2011). Our study used the introduction year and the number of introduced presences to consider the colonization process, but these are rather rough proxies. It was unfortunately not possible to apply the approach used by Barve et al. (2011) for all species analyzed in this data set, as relevant information about introduction events, establishment status, and dispersal capacities was missing for most of them.

Strong effects of number of presences on transferability

The number of native presences was the factor with the highest contribution to SDM transferability overall. Although previous studies showed the positive effects of sample size on SDM performance (van Proosdij et al., 2016; Wisz et al., 2008), it was still surprising that the number of native presences had such a strong effect on SDM transferability.

We offer three nonexclusive explanations for the strong effect of the number of native presences. First, a large number of native presence points makes it possible to accurately capture the species–environment relationship across its native range (Guisan & Thuiller, 2005), which is a crucial premise of successfully transferring SDMs to new ranges (Liu et al., 2020b). Second, parameter estimates can be biased if insufficient samples are used for developing SDMs, because fewer presences fail to buffer the bias caused by noisy data, consequently causing a higher level of uncertainty in model parameterization (Guisan & Thuiller, 2005; Wisz et al., 2008). Third, more presences reduce the risk of overfitting when a relatively high number of predictors are used for developing SDMs (Petitpierre et al., 2017). Overfitted SDMs appear to perform well during the training process, but their predictive ability decreases when they are transferred to new environments (Qiao et al., 2019; Roberts et al., 2017). According to the close associations between niche dynamics and the number of native and introduced presences, the transferability can also be indirectly elevated by using more native and introduced presences. Given that previous studies only identified the positive effects of the number of presences on SDM performance (e.g., Liu et al., 2020b; Wisz et al., 2008), future studies should consider the direct and indirect effects of the number of native and introduced presences to better assess their relative influence on SDM performance.

In contrast to previous studies reporting a negative effect of overparameterization on SDM transferability (Liu et al., 2020b; Petitpierre et al., 2017), we found a positive effect of the number of predictors. This finding might be an artifact though, because 86.2% of the SDMs in our data set were developed with eight or nine predictors (see *Results*). Most (96.0%) of the SDMs with nine predictors were developed for terrestrial endotherms (Liu et al., 2021), the organismal group with the reportedly highest SDM transferability (Liu et al., 2020b), whereas most (95.9%) of the SDMs with eight predictors were developed for other organismal groups. More research is needed to understand how predictor selection affects SDM transferability (Fourcade et al., 2018; Petitpierre et al., 2017).

Limitations of this study

Despite offering new insights, this study could not disentangle how some other factors might influence the relationship between niche change and SDM transferability. The first one is biotic interactions (e.g., competition, predation, and parasitism), which directly shape species distributions at the local scale and are important determinants for both species' realized niches and SDM transferability (Jeschke & Strayer, 2008; Yates et al., 2018). For invasive species, variations in the composition and richness between native and introduced communities would inevitably result in different biotic interactions in new ranges (see Enders et al. [2020] for an overview). Such differences in biotic interactions are widely known for reducing SDM transferability, because native-range SDMs are developed by characterizing species' realized niches in consideration of biotic interactions in the native range (Guisan & Thuiller, 2005; Yates et al., 2018). To date, biotic interactions are not considered in most SDM studies (Guisan & Thuiller, 2005; Wiens et al., 2009). In our data set, information about biotic interactions was indeed lacking for all included studies, preventing us from assessing their influence.

The second important factor is the source population(s) since many invasive species have multiple geographical lineages in their native range, but only a subset has been introduced to new ranges (Jeschke & Strayer, 2008; Tingley et al., 2016). If those geographic lineages differ in their environmental tolerances, the introduced populations might occupy only a part of their entire niche. Thus, SDMs developed using data of all native lineages very likely fails to predict species distributions in the introduced range due to different species–environment relationships (Liu et al., 2020b; Tingley et al., 2016).

We are also unable to assess the role of several other factors, such as the background region for sampling pseudo-absence (Barve et al., 2011) or the threshold of binary conversion (Yackulic et al., 2013), for which the data are rarely reported (Feng et al., 2019). One reason for this lack of information is that there has not been a standard protocol to guide the operation and reporting of SDMs (Araújo et al., 2019; Nogués-Bravo, 2009). Recently, such protocols (e.g., ODMAP protocol; Zurell et al., 2020) have been proposed to enhance the transparency and reproducibility of SDM development and application (Araújo et al., 2019; Feng et al., 2019). We suggest future studies should consider state-of-the-art practices and report necessary information following standard protocols for better communicating the modeling methodology, which can in turn facilitate the understanding of SDM transferability (Liu et al., 2020b; Zurell et al., 2020).

CONCLUSIONS

Predicting species distributions in new geographic regions and time frames remains a core endeavor of invasion science, conservation biology, and related fields (Sequeira et al., 2018; Yates et al., 2018). Understanding the influence of niche change is crucial to improve the reliability of SDMs transferred to new areas and periods (Liu et al., 2020b; Yates et al., 2018). Our synthesis shows that SDM transferability is much lower for invasive species with shifted niche and is closely associated with the numerical dynamics between native and introduced niches. Moreover, we found the number of native presence points to be even more important for SDM transferability than niche change. In addition to considering niche change for improving the development of SDMs (D'Amen & Azzurro, 2020; Pearman et al., 2008), researchers modeling species distributions in exotic ranges should work in close collaboration with researchers who can obtain high-quality presence data of the species in their native range.

CONFLICT OF INTEREST

Theauthors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data supporting the results and R code supporting this work (Liu et al., 2022) are available in Figshare at https://doi.org/10.6084/m9.figshare.14959515.

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