REVIEW

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Transferring biodiversity models for conservation: Opportunities and challenges

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Abstract

1. After decades of extensive surveying, knowledge of the global distribution of species still remains inadequate for many purposes. In the short to medium term, such knowledge is unlikely to improve greatly given the often prohibitive costs of surveying and the typically limited resources available.

2. By forecasting biodiversity patterns in time and space, predictive models can help fill critical knowledge gaps and prioritise research to support better conservation and management.

3. The ability of a model to predict biodiversity metrics in novel environments is termed "transferability," and models with high transferability will be the most useful in this context.

4. Despite their potentially broad utility, little guidance exists on what confers high transferability to biodiversity models.

5. We synthesise recent advances in biodiversity model transfers to facilitate increased understanding of what underpins successful model transferability, demonstrating that a consistent approach has so far been lacking but is essential for achieving high levels of repeatability, transparency and accountability of model transfers.

6. We provide a set of guidelines to support efficient learning and the improvement of model transferability.

KEYWORDS

applied ecology, biodiversity, conservation, extrapolation, forecasting, modelling, statistics

1 | MODEL TRANSFERABILITY AS A TOOL FOR CONSERVATION AND MANAGEMENT

Effective conservation and management of biodiversity requires a robust understanding of the distribution and status of wildlife species. However, our existing knowledge of biological systems is frequently inadequate and field surveys too costly to generate the data necessary for addressing many immediate management needs (Margules & Pressey, 2000). As a result, spatial planning is often constrained to proceed in the absence of relevant ecological information (Possingham, Grantham, & Rondinini, 2007). In these cases, indirect methods for estimating biodiversity patterns, such
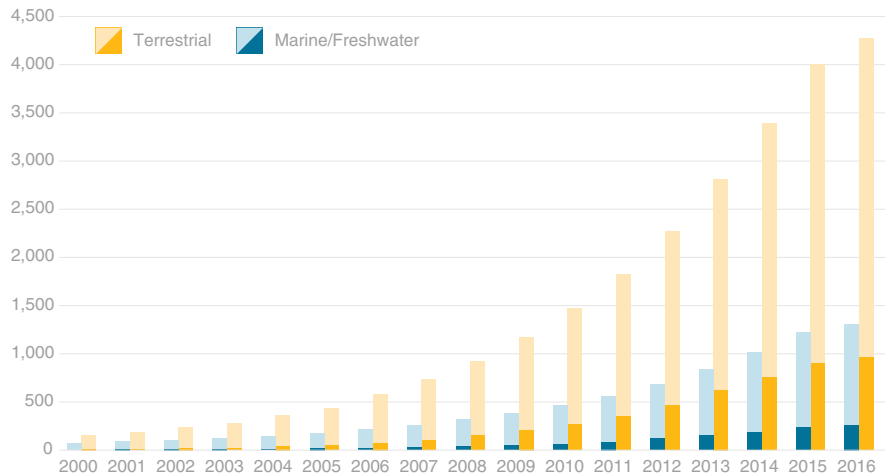
FIGURE 1 Temporal trends in published papers related to biodiversity models (lighter colours) and model transferability (darker colours). Bars indicate the cumulative number of peer-reviewed journal articles listed on the ISI Web of Science (webofknowledge. com). Search details are included in Supplementary Information

as predictive models, could be of great utility for decision-making. Indeed, correlative models relating ecological metrics to environmental and spatial predictors (henceforth biodiversity models) are now commonplace (see e.g. Franklin, 2010 for a summary of methods used and a framework for spatial prediction of species occurrence) and play a critical role in supporting management and conservation efforts world-wide (Margules & Pressey, 2000; Robinson et al., 2011). Such models are increasingly sought where data are scarce or non-existent, for example when predicting the distributions of threatened or invasive species into unsampled locations or under future climates (Austin & Meyers, 1996; Duque-Lazo, van Gils, Groen, & Navarro-Cerrillo, 2016; Elith, Kearney, & Phillips, 2010). While the literature on biodiversity models is now extensive, little guidance exists on how to maximise the utility of transferring these models.

The ability of a model developed for a specific site and/or time and/or taxon to predict biodiversity in a different time or place or for a different taxon defines its transferability. Transferability, therefore, encompasses the statistical concept of extrapolation which is embedded in the broader topic of model validation, but it is not synonymous of (mathematical) extrapolation. Transferability has the potential to leverage legacy investments in sampling and increase the efficiency of management and conservation actions. However, while the development of biodiversity models and model validation has proceeded rapidly in the last decade (Figure 1) (Elith & Leathwick, 2009; Elith et al., 2006), their transferability remains poorly understood (Robinson et al., 2011), particularly in marine systems (e.g. Lauria, Power, Lordan, Weetman, & Johnson, 2015; Sequeira et al., 2016). Moreover, transferability assessments have not yet been standardised, leading to disparate interpretations that preclude comparisons of relative performance among model transfers. To address these knowledge gaps, we synthesise the emerging field of model transferability with the aim of fostering consistent and transparent model transfers in ecological studies. We begin by defining multiple scenarios under which model transfers can take place, reviewing lessons learnt and describing modelling approaches applied to date. We then clarify critical, yet commonly ignored assumptions,

discussing perceived constraints and limitations of model transferability, and highlighting the diversity of assessment metrics currently available. Building on these observations, we describe how the standardisation of transferability assessments among studies could catalyse the widespread application of model transfers in marine and terrestrial environments. We make practical recommendations on ways to achieve such consistency and advocate for future research that would improve the transferability of biodiversity models.

2 | FROM REFERENCE TO TARGET SYSTEMS

A model must be developed for a reference system at a specific location, time or taxon where data are available at a number of sampling locations before being transferred. This reference model is calibrated within a range of values for each predictor, and then projected, or transferred, to a target system at some other location, time or taxon. Model transferability can take many forms depending on the predictors available for the target system, their range of values, as well as those of the response variable (Figure 2). The most straightforward situations occur where both response and predictor variables are within the same ranges in both the reference and target systems (e.g. Mannocci, Monestiez, Jerôme, & Ridoux, 2015) (Figure 2a, External 1; and Figure 2b, blue ellipse). In this scenario, the environmental space is the same in both systems, and the realised niche in the target system is fully contained in the model created for the reference system. Under these conditions, good transferability can be expected, assuming reasonable overlap in the combinations of response and predictor variables. When the range of predictors in the target system is within that used for model calibration in the reference system, but the response variable is not (e.g. when observed abundances are different in the target and reference systems) (e.g. Owens et al., 2013; Thogmartin, Knutson, & Sauer, 2006), two situations can arise: (i) poor transferability should be expected where the relationship between response and predictor variables differs (Figure 2b,
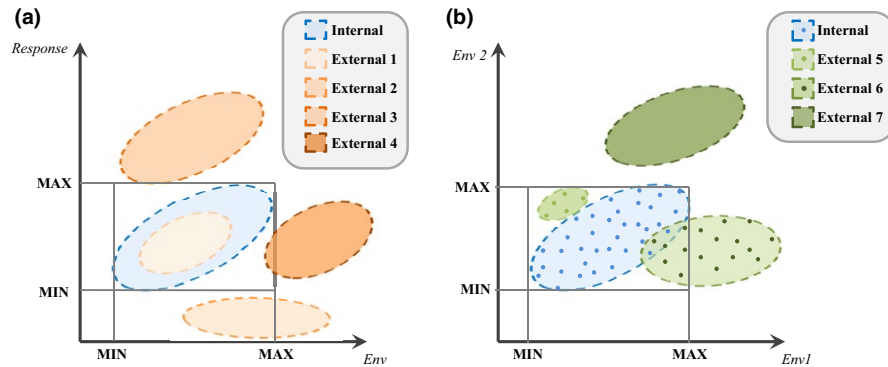
FIGURE 2 Conceptual summary of possible conditions under which model transferability can be tested. "Internal" refers to conditions found in the reference system, and "External" to those in a target system (adapted from Mesgaran et al., 2014). The slope of each ellipse reflects the nature of the relationship between the variables represented on the x and y axes. Dots represent available samples (data points). In (a), we consider scenarios in which the range of both response and predictor variables may differ between the reference and target systems. In External 1, the range of predictor and response variables overlaps. In External 2, predictor values in the target system fall partially, within the internal range but the response variable in the target system is completely outside reference conditions, and the relationship between response and predictors takes a different form. In External 3, predictor values overlap in both systems but the range of responses does not. In External 4, the range of predictors might differ in both systems but the range of responses is the same, as is the relationship (slope) between response and predictor variables. In (b), we consider a pair of environmental predictors and illustrate scenarios where: the external range of predictors lies within the range of internal predictors (External 5), there is some overlap in predictor range (External 6), and no overlap in predictors (External 7)

External 2), and (ii) when this relationship is similar (Figure 2b, External 3), transferred predictions will always be biased. If this bias is relatively consistent (e.g. always lower or higher), then a simple correction to the resulting predictions could allow for good transferability. For example, the probability of occurrence of a species in the target system might always be 20% lower than in the reference system, in which case a simple correction to account for this bias could result in a shift from poor to good model transferability. Where sample sizes are sufficiently large, the predictive performance of the transferred model can be robustly tested, yielding potential insights into how model transferability is affected by novel conditions. When predictor values are within the range of those used in the reference model (Figure 2a, External 5), models transferred from an information-rich area may successfully predict species distributions and help inform new sampling designs in spite of data scarcity in the target system. However, when the range of predictor values in the target system extends beyond that encountered during model building for the reference system, model transfers will involve some mathematical extrapolation (Figure 2b, External 4, and Figure 2a, Externals 6 and 7). If the range of predictors in the target system is entirely outside that used in the reference model (Figure 2d, External 7), transferability tests would only serve to capture potential distributions of species within novel environmental conditions. Despite many possible different scenarios, confidence in the resulting predictions derived from transferred models is paramount and will depend strongly on the identification of opportunities for robust model validation. Therefore, the form of the transferability test being performed should always be explicitly described when models are transferred, including a summary of the relationships between

predictor and response variables for data from reference and target systems.

The amount of data available in each system will also be a key determinant of the model transfer protocols chosen in any given situation, and three different scenarios can be considered. First, where sufficient information exists for both response and predictor variables in the reference and target systems (data-rich), it is possible to directly test model transferability through empirical validation (Barbosa, Real, & Vargas, 2009; Sequeira et al., 2016). Such scenarios are useful to better understand the factors affecting model transfers (Figure 3; data-rich scenario) and inform model transfer endeavours elsewhere. Second, when data for both response and predictor variables at the target system are insufficient (data-deficient), testing model transferability is only possible if alternative data sources for predictor variables are sought and/or if assumptions are made about the similarity of the covariate space and relationships between the response and predictor variables (Figure 3, data-deficient scenario) (Schadt et al., 2002). Third, when information is lacking for either response or predictor variables in the target system (Figure 3, data-sparse scenario), several courses of action are possible (e.g. Sequeira, Mellin, Fordham, Meekan, & Bradshaw, 2014). Where data for the target system are available for predictor variables, but not response variables, the same set of predictor variables (p) need to be considered in both the reference and target systems, and it is preferable that the range of each predictor in both systems is similar, as detailed above. If the range of predictors in the target system exceeds that in the reference system, caution is advised (see extrapolation section). Examples and recommendations for each of these three scenarios are included in Figure 3.
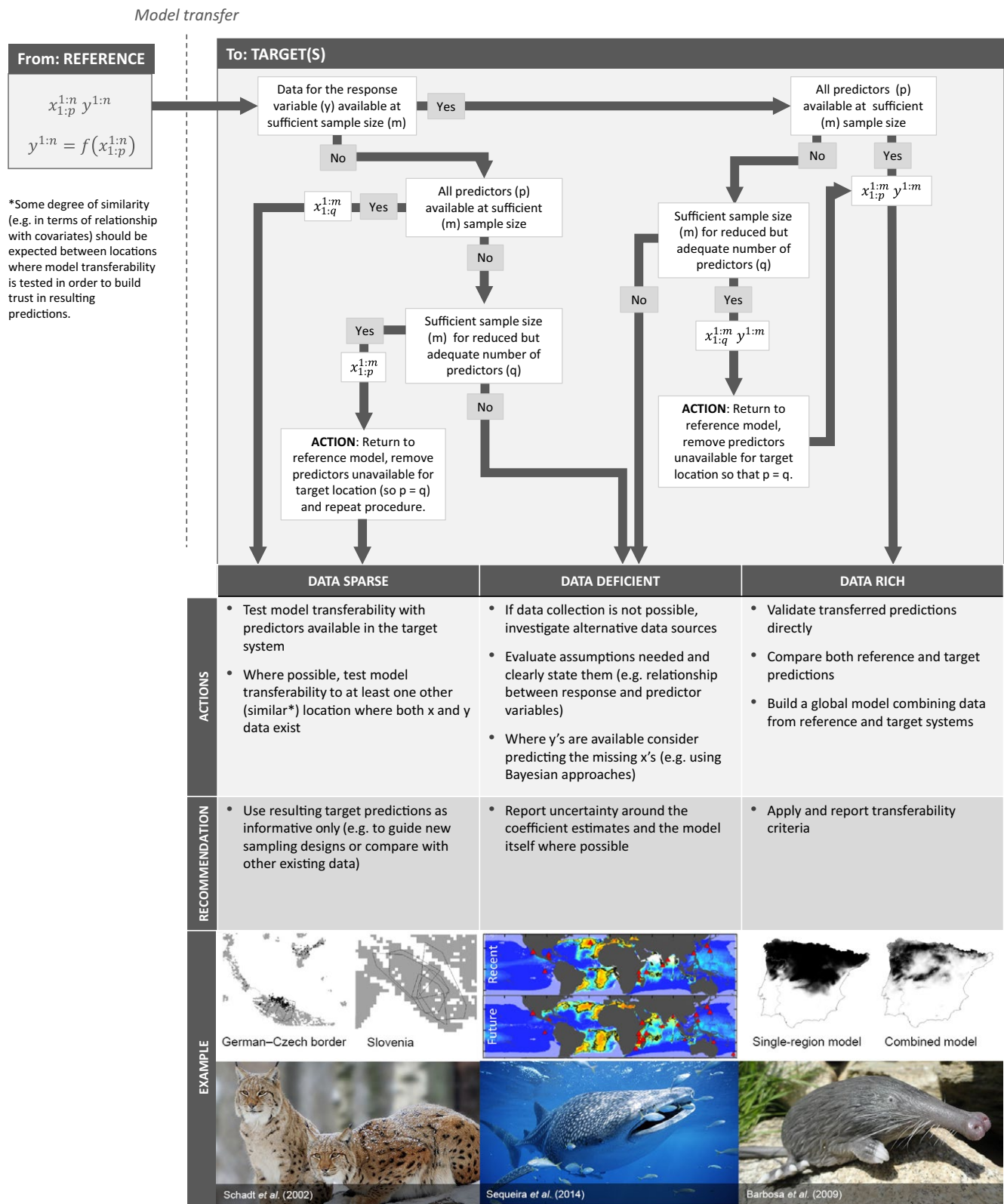
Model transfer

From: REFERENCE

$$x_{1:p}^{1:n}\ y^{1:n}$$

$$y^{1:n} = f\left(x_{1:p}^{1:n}\right)$$

Some degree of similarity (e.g. in terms of relationship with covariates) should be expected between locations where model transferability is tested in order to build trust in resulting predictions.

To: TARGET(S)

Data for the response variable (y) available at sufficient sample size (m) — Yes → All predictors (p) available at sufficient (m) sample size

No

$x_{1:q}^{1:m}$ — Yes

All predictors (p) available at sufficient (m) sample size

No

Yes

$x_{1:p}^{1:m}$

Sufficient sample size (m) for reduced but adequate number of predictors (q)

No

No — Yes

$x_{1:p}^{1:m}\ y^{1:m}$

Sufficient sample size (m) for reduced but adequate number of predictors (q)

No

Yes

$x_{1:q}^{1:m}\ y^{1:m}$

ACTION: Return to reference model, remove predictors unavailable for target location (so p = q) and repeat procedure.

ACTION: Return to reference model, remove predictors unavailable for target location so that p = q.

	DATA SPARSE	DATA DEFICIENT	DATA RICH
ACTIONS	• Test model transferability with predictors available in the target system • Where possible, test model transferability to at least one other (similar*) location where both x and y data exist	• If data collection is not possible, investigate alternative data sources • Evaluate assumptions needed and clearly state them (e.g. relationship between response and predictor variables) • Where y's are available consider predicting the missing x's (e.g. using Bayesian approaches)	• Validate transferred predictions directly • Compare both reference and target predictions • Build a global model combining data from reference and target systems
RECOMMENDATION	• Use resulting target predictions as informative only (e.g. to guide new sampling designs or compare with other existing data)	• Report uncertainty around the coefficient estimates and the model itself where possible	• Apply and report transferability criteria
EXAMPLE	German–Czech border Slovenia Schadt *et al.* (2002)	Recent Future Sequeira *et al.* (2014)	Single-region model Combined model Barbosa *et al.* (2009)

3 | CHOICE OF MODELLING ALGORITHMS CAN AFFECT MODEL TRANSFERABILITY

The transferability of predictive models can be dataset, question and algorithm-specific (Duque-Lazo et al., 2016; Elith et al., 2006).

It is often thought that model simplicity and parsimony should be preferred over complexity. Simpler models are easier to interpret and also return smoother response curves that are relatively immune to overfitting and may therefore be more widely applicable (Lauria et al., 2015; Vaughan & Ormerod, 2005). However, defining

FIGURE 3 Summary of possible scenarios and recommended actions when testing model transferability. Transferability refers to the predictive performance of a model developed for a reference location, time or taxon, and used to make predictions for a different target location, time or taxon. The transfer possibilities and the actions that can be undertaken depend on the availability of data for the response and predictor variables. For example, in a "data-sparse" situation, home ranges for Eurasian Lynx were predicted in Germany based on data from the Swiss Jura Mountains (action 1) and then results were validated using telemetry data from the Czech Republic and Slovenia (2nd action point) (image adapted from Schadt et al. (2002) and photo credit to National Geographic). The future geographical distribution of whales sharks ("data-deficient" situation) was predicted based on existing knowledge of their occurrence and using modelled sea surface temperature for 2070 (1st action point) while assuming that relationships between response and predictors will be maintained (2nd action point) (image adapted from Sequeira et al. (2014), and photo credit to Brian J. Skerry; National Geographic). The distributions of the Iberian desman were predicted comparing results from a reference and target model with validation data (1st and 2nd action points, "data-rich" situation) before producing a general model combining data from both reference and target locations (3rd action point) (image adapted from Barbosa et al. (2009) and photo credit to Réseau Education Pyrénées Vivantes)

complexity of biodiversity models is not straightforward as it depends on the interplay between the complexity of the underlying processes and the amount of data available to build the model. For these reasons, past comparisons of model performance as a function of complexity may have been unfair (García-Callejas & Araújo, 2015). New complexity indices are being studied (Bell & Schlaepfer, 2016; García-Callejas & Araújo, 2015; Moreno-Amat et al., 2015), but further testing of their influence on the interpretation of model transferability is needed before clear advice can be given.

Similarly, best practice regarding algorithm choice for testing model transferability is, so far, not settled. For example, previous studies have reported better transferability in generalised additive or linear models (GAMs or GLMs), maximum entropy models (MaxEnt) and boosted regression trees (BRTs) compared to random forests (RFs) (Dobrowski et al., 2011; Heikkinen, Marmion, & Luoto, 2012). GAMs have also been seen as robust when predictions are needed beyond the range of sampled values (i.e. when extrapolating) (Fronzek, Carter, & Luoto, 2011), despite being unconstrained outside the bounds of the observations used during model calibration (unlike RFs, MaxEnt and BRTs). Similarly, despite some evidence that genetic algorithms can better accommodate regional spatial effects, no clear preference for a specific method has yet emerged in comparisons of machine learning approaches (Fielding, 1999; Hsieh, 2009). Without consensus on the best algorithms or methods to develop more transferable models (Araujo & Guisan, 2006; Randin et al., 2006), three different approaches to multi-model comparisons have been suggested: (1) adopt a single modelling procedure regarded as the most suitable to the research problem being addressed; (2) implement a suite of algorithms and proceed with the best performing one; or (3) combine several approaches to generate "ensemble" forecasts. While it is hard to provide general guidance, ensemble approaches have been suggested to offer superior predictive power (Grenouillet, Buisson, Casajus, & Lek, 2011; Marmion, Parviainen, Luoto, Heikkinen, & Thuiller, 2009).

All of the approaches described above relate to correlative models. Although beyond the scope of this review, process-based mechanistic models are also worth considering in the context of transferability because they can explicitly incorporate the dynamics of biological processes thought to limit species' ranges (Buckley et al., 2010), such as dispersal, connectivity and trophic interactions. Mechanistic models, however, tend to be more challenging to construct and test, owing to greater demands on computational resources and data needed for calibration and validation. Consequently, the transfer of mechanistic models in predictive ecology remains rare despite their considerable promise in strengthening and guiding conservation practice under climate change and biological invasions (Cuddington et al., 2013; Kearney, Wintle, & Porter, 2010).

4 | COMMON ASSUMPTIONS UNDERLYING MODEL TRANSFERS

Irrespective of the approach used, model transferability hinges on a number of assumptions that are commonly overlooked (Mesgaran, Cousens, & Webber, 2014; Werkowska, Márquez, Real, & Acevedo, 2017) and may explain some difficulties in obtaining good model transferability. For example, species are often assumed to be at equilibrium with their environment and present in all suitable sites (Araujo & Pearson, 2005). However, such equilibrium is taxon-dependent and inversely related to a taxon's ability to track dynamic conditions, and should therefore be explicitly considered beforehand (Araujo & Pearson, 2005). The set of conditions under which species can persist (niche, *sensu* Hutchinson, 1957) is also commonly assumed to be stationary in both space and time (Wiens & Graham, 2005). A discussion on the reasoning behind this assumption should be clearly specified for any transfer, as this assumption may not hold if existing biotic or abiotic interactions break down, shift, or new ones form (Broennimann et al., 2007; Martinez-Freiria, Tarroso, Rebelo, & Brito, 2016). Moreover, increasing evidence for rapid niche shifts (Broennimann et al., 2007) may render static models invalid for predicting into space or time (Forester, DeChaine, & Bunn, 2013). Integrating information from mechanistic models can improve trust in the resulting predictions in this context (Elith et al., 2010). Species occurrences are also commonly assumed to be solely driven by environmental forces, but realised distributions can reflect current/past disturbances and human uses, and so historical events should be considered when interpreting transferability results (Beans, Kilkenny, & Galloway, 2012; Davis, Malas, & Minor, 2014). Another common assumption is space-for-time substitutability (Blois, Williams, Fitzpatrick, Jackson, & Ferrier, 2013), under which unobservable past or future temporal trends are inferred from contemporary spatial models of different aged locations. However, conflicting predictions generated by different models (Kharouba, Algar, & Kerr, 2009) challenge the general validity of this assumption,

and the current best advice is, whenever possible, to use models that have been successful at hindcasting (Kharouba et al. 2009).

Overall, the transferability of biodiversity models can be affected by a wide range of factors associated with the choice of study design, model algorithm or target taxa, as well as with the type, quantity and quality of input data, and the characteristics of the environment (Table 1 and references within). To understand what confers transferability on biodiversity models, more will need to be learned about the consequences of violating assumptions. This highlights the need to encourage best practice when testing model transferability by explicitly checking the validity of assumptions wherever possible (Werkowska et al., 2017) or explicitly reporting why they cannot be checked and if they are likely to affect the results of the transferred model. Results of these checks need to be reported as they will be crucial for better understanding and improving model transferability.

5 | COMMON METHODS FOR ASSESSING MODEL TRANSFERABILITY

Model accuracy generally decreases when a model is transferred (Kharouba et al. 2009, Dobrowski et al., 2011; Torres et al., 2015). Assessments of model results beyond where and when data were available (external evaluations) are commonly more variable than within the same location or time (internal evaluations) (Dobrowski et al., 2011). Furthermore, better fit during internal evaluation has not always resulted in greater model transferability (Heikkinen et al., 2012; Sequeira et al., 2016) and the reported ability of transferred models to predict well has varied widely (Fielding & Haworth, 1995; Martin et al., 2012; Randin et al., 2006; Sequeira et al., 2016).

Part of this variability in transferability across studies may stem from the range of different metrics used during evaluation of the results of model transfers (Wang & Jackson, 2014), with at least 17 different metrics reported to date (Table 2). Metrics derived from confusion matrices, such as sensitivity, area under the curve (AUC)/receiver operating characteristic (ROC), Cohen's kappa statistic or the c-index (Vaughan & Ormerod, 2005), which are based on the number of true and false positives and negatives, have been favoured for models of presence/absence or presence-only data (Randin et al., 2006). ROC has, however, been considered weak (Peterson, Papes, & Eaton, 2007), but see Phillips (2008). Spearman rank and coefficients of determination (R^2) from linear regressions are commonly used for models using count data (Lauria et al., 2015) to assess the relationship between observed and predicted values. Compound performance metrics have also been proposed and applied, including the AUC-based transferability index TRI (Randin et al., 2006) (Table 2), which compares internal and external evaluations made in both directions. Reciprocal model transferability is, however, not always possible or warranted (e.g. Sequeira et al., 2016), and being AUC-based, TRI only applies to models of presence/absence data. Furthermore,

indices focusing on the evaluation of model fit only provide partial assessments of transferability; they do not evaluate maps of transferred predictions (as detailed by Randin et al., 2006). To assess the resulting maps, other metrics have been proposed, including Kulczynski's coefficient (Legendre & Legendre, 2012), Schoener's D (Warren, Glor, & Turelli, 2010) and the I similarity statistic (or Modified Hellinger Distance) (Warren, Glor, & Turelli, 2008). In the face of such heterogeneity in assessments of model transferability, standardisation of results across studies, modelling techniques, datasets and environmental settings are needed to improve the utility of model transfers for conservation. Such standardised assessments will facilitate direct comparisons across studies and promote their transparent interpretation, thereby strengthening our ability to meaningfully address key knowledge gaps in model transferability.

Transferability assessments can also be model-focused, instead of data-focused, in which case the onus is on finding the most general model (Wenger & Olden, 2012). So, when testing model transferability, a thorough assessment of model generality should also be performed (Wenger & Olden, 2012). As a general principle, only models demonstrating good fit and evaluation for the reference system should be transferred, even if they do not always result in good transferability. For example, better transferability is expected of models developed for large, heterogeneous ecosystems where sampling effort has been sufficient to capture the full range of environmental conditions available (*sensu* Sequeira et al., 2016). Therefore, when transferring models it is important to clearly justify the choice of a particular model for any particular situation.

6 | A STANDARDISED ROADMAP FOR MODEL TRANSFERABILITY STUDIES

When quantifying transferability, three aspects of model performance are commonly compared (adapted from Randin et al., 2006). These include the fit to the set of observations on which the model was built in the reference system, evaluation against observed data in the reference system not used for model training, and the model's predictive power for the target system determined by comparing these predictions with observations or to the results of models developed for the new location, time or taxon.

Comparisons of model fit between reference and target systems are relevant for transferability assessments (see Figure 3 for options when model fit in the target system is poor) but are not universally applicable. This is because comparable results are only expected in special cases, such as when covariance structures are similar in both systems. By contrast, focusing on model evaluation and comparisons of prediction results should allow meaningful insights regarding the relevance of distinct modelling approaches relative to available datasets and study sites. Even though the choice of metric for comparing predictions might vary between studies (Table 2), most metrics can be derived from a small set of basic statistics. These include confusion matrices (TP, FP, TN and FN; refer to Table 2) and comparisons

TABLE 1 Summary of features previously reported to affect model transferability, by improving (green; +), or impairing it (red; −). For features that have yielded conflicting results in empirical studies, here we consider their influence unclear (grey; +/−). References are provided in the Supplementary Information Appendix S1

Feature	Effect	Explanation	References (see Appendix S1)
Field sampling			
Larger than known geographic extent	+	Guarantees that the tails of a species' response curve are adequately captured	[1, 2]
Central position within the species range	+	Because species thrive in a more varied array of habitats at the centre of their distribution and are more restricted to specialised habitats towards the margins	[3, 4]
Large sample size	+	Captures variability in habitat conditions and to allows more precise estimates of model parameters	[5–7]
Systematic vs. random design	+/−	Systematic sampling may lead to wider environmental coverage and reduce autocorrelation. However, random sampling has desirable statistical properties and avoids spatial bias	[8, 9]
Uneven or incomplete coverage	−	Because biased sampling may add noise to the data, constrain the range of habitat variability being captured, and introduce taxonomic and environmental biases	[10–12]
Imperfect detectability	−	May lead to biased samples and misleading inferences of species-environment relationships	[13, 14]
Model building, calibration and validation			
Model training in more than one region	+	Multi-region models place less emphasis on locally dominant environmental features making them more structurally similar and transferable	[15–17]
Correct choice of calibration areas	+	May reduce the rate of false positives	[18]
Validation with independent data	+	Allows for objective assessment of predictions to novel conditions and of the relative importance and nature of uncertainty sources	[16, 19–21]
Accounting for true absences	+	True absences contain valuable information on the conditions that are unfavourable for a given species, and support the modelling of the realised, rather than potential, distributions	[22]
Choice of model algorithm	+/−	No superior method has yet been identified (refer to text for details)	[23]
Model complexity	+/−	Complex models may overfit data while simpler models often yield better transferability (but more needs to be learned)	[24–30]
Direction of model transferability test	+/−	Can depend on asymmetries in environments or be taxon-specific	[3, 31, 32]
Calibration and projection at different scales (local vs. regional)	+/−	Regional model stability tends to be site- and taxon-specific while adjacent areas are more likely to be similar	[33–37]
Accounting for autocorrelation	+/−	Reducing autocorrelation may be necessary, but the added autocorrelation term may fail to account for some biological structure affecting transferability	[38–41]
Multi-model inference and model averaging	+/−	Consensus forecasts are generally seen as more robust, although recent studies suggest that their extrapolative performance may be taxon- and context-specific	[42–44]
Model misspecification	−	Erroneous choices of error distributions may limit the effectiveness of model transferability	[26]
Overfitting	−	Can lead to weak correlations among variables and incorrect inferences	[3, 45]
Data and predictor variables			
Use of direct, functional and ecologically relevant predictors	+	Allow estimation of ecologically sound predictor–response relationships	[3, 16, 17, 32, 46]
Large training dataset	+	Minimise the variance in parameter estimates	[47, 48]
Including biotic interactions	+	Better describe species distributions and range margins at broad spatial extents, thereby maximising model transferability	[49–56]

(Continues)

TABLE 1 (Continued)

Feature	Effect	Explanation	References (see Appendix S1)
Higher quality and resolution of predictors	+	Better capture relevant ecological processes and detect local variations more effectively	[1, 17, 57, 58]
Adequate geographical projection	+	Minimise biases associated with grid-cell sizes (i.e. increased apparent sample size at high latitudes as a degree of longitude decreases in length from the equator to the poles)	[59]
Use of independent remote sensing data	+	Captures complex spatial features in the data, and allows measuring environmental variability to directly indicate limiting environmental conditions beyond climatic suitability	[60, 61]
Inclusion of climatic extremes	+	Because they affect demographic processes including growth, regeneration and mortality in some organisms	[62]
Contingent absences	+	Improve descriptive and predictive potential of models	[1]
Use of surrogate predictors	–	May fail to express the true habitat requirements of the species, particularly if relationships vary spatially and temporally	[3, 16, 17, 32, 46]
Multicollinearity	–	Can lead to the misidentification of the most relevant predictors and biases in estimated coefficients and their standard errors	[63–65]
Type of scenario in climate projections	–	May lead to over-confidence in single maps of future distributions	[66, 67]
Niche shifts	–	Can compromise model predictions	[68]
Species			
Abundance data	+	Can improve detection of the relative suitability of habitats, particularly for species with low prevalence	[69]
Assemblage composition	+	Enables the detection of general trends that are more immune to the idiosyncrasies of individual taxa	[36, 70, 71]
Free movement in space	+	May provide better representation of suitable habitats	[31]
Ecological traits	+/–	Are a species-specific characteristic but can result in greater model transferability	[3, 19, 72–77]
Endemism	+/–	Should result in better species-habitat relationships but some studies have found better transferability of models based on non-endemic species	[19, 31]
Prevalence and rarity	+/–	Common species yield more false positive predictions, whilst more false negatives are expected for rarer taxa, suggesting that intermediate levels of prevalence may be optimal for transferability	[3, 19, 20, 78–80]
Eurytopic species	–	May persist in a wide array of conditions that are not easily defined by data, independent variables or model design	[47, 81, 82]
Dispersal ability	–	Is a source of autocorrelation likely to influence the accuracy of projections across time and space in changing environments	[19, 38, 83]
Behavioural plasticity	–	Model projections may be misleading if the capacity of a species to adapt to new conditions is ignored	[84]
Ecotypes	–	Being selectively adapted to localised environmental conditions, model transferability may not be applicable	[3]
Environment			
Non-analogue conditions	–	May result in the truncation of species response curves under unobserved conditions rendering extrapolating risky	[2, 37, 85–92]
Non-stationarity	–	Will impede model transferability due to inconsistent relationships across space or time	[31, 93]
History of human use	–	May lead to inconsistent model transferability due to different disturbance regimes, management practices, or histories of human use between regions/times	[27, 94–96]

of grid-cell values, such as predicted probabilities from a presence-only model, predicted abundances or differences between observed and predicted values. If these basic statistics are reported alongside the results for the metric(s) chosen in each study, they can then be used to derive most other metrics commonly used. They can also be used to calculate additional descriptive statistics (e.g. mean, standard

deviation, covariance, collinearity or correlation) for datasets resulting from any model type. Such reporting will facilitate comparisons across studies (Koricheva, Gurevitch, & Mengersen, 2013), and improve our ability to provide clearer guidance in the future. Moreover, to further expedite comparisons, we suggest as a minimum that one metric, the coefficient of determination (R^2), should always be reported.

In relation to model predictive power, the assessment of predictions from transferred models should also estimate uncertainty and spatial dependencies among gridcells. This can be achieved using the structural similarity index (SSIM) (Jones, Rendell, Pirotta, & Long, 2016), which was designed to allow quantitative comparisons of pairs of spatial data (e.g. two distributions maps from different species groups). SSIM provides an overall measure of similarity between two sets of spatial observations (i.e. maps) ranging between −1 and 1, and could, therefore, be used in the context of model transferability to test the predictive power of transferred models through comparison of the predictions obtained with those from a model developed for the target system. SSIM also compares the mean, variance and covariance of both datasets, and provides information on where dissimilarities might be greatest. Such information will be relevant for understanding where and why a model may fail to transfer well (see example of application of SSIM to model transferability in Figure 4).

These ways of standardising transferability assessments are appropriate for data-rich scenarios. However, models are usually transferred because data are lacking for the target system, making direct validation challenging. Where sufficient predictor data are available, model transferability can still be tested and result in informative predictions (Figure 3; data-sparse scenarios). And trust in transferred predictions can be increased by selecting models that have already been successfully transferred to other analogous target system(s) (in a similar way as hindcasting is used to increase confidence in climate change predictions). Resulting predictions should then be used to inform new survey designs for the target system, and validation should proceed as these new data become available. Such procedures can provide transparent assessments prior to decision-making, and allow for adaptive learning in support of the best possible management outcomes at each step. The "holy grail" of model transferability is, clearly, to achieve reliable predictions for unsampled space/time/taxon, an exercise that involves some kind of extrapolation, whether mathematical, geographical or combinatorial (that is derived from novel combinations of covariates within the univariate range). Indeed, overcoming challenges associated with predicting into unknown space/time is becoming urgent in face of accelerating environmental change.

7 | THE UNCHARTED WATERS OF MATHEMATICAL EXTRAPOLATION: "HERE BE MONSTERS"?

Despite the dangers of extrapolation having long been known (Perrin, 1904), models are increasingly being projected into non-homologous environments (Elith et al., 2011). Predictions obtained under previously unobserved conditions are prone to both statistical and ecological error (Dormann, 2007; Perrin, 1904), yet the immediate need for solutions to wildlife management problems within new temporal or spatial domains often overrides caution in extrapolation, with forecasts frequently treated as reliable (Fitzpatrick & Hargrove, 2009; Jimenez-Valverde et al., 2011). Because attention to extrapolation risks is central to effective decision-making, the development of techniques that can diagnose or address the consequences of extrapolation when transferring models has been considered a research priority (Araujo & Guisan, 2006).

Various strategies have been suggested for dealing with extrapolation. These include avoidance, mitigation and explicit description. The "avoidance" strategy is based on the subjective rule of thumb that extrapolation errors increase with distance from the envelope of the observed data. It has been suggested that, if predictions are not made beyond one-tenth of the sampled parameter range, extrapolation might be considered negligible (Dormann, 2007). Extrapolation mitigation can be achieved by minimising the likelihood of encountering novel combinations of environmental conditions, for example by modelling the complete range of a species given its dispersal abilities and any major biogeographical transitions when projecting future distributions (Thuiller, Brotons, Araujo, & Lavorel, 2004). Methodologies have also been proposed to explicitly describe extrapolated predictions, for example by discriminating the areas where the data used most resemble the characteristics of the reference system, or by explicitly defining prediction intervals which highlight the probability that a new result will lie within certain values (e.g. Kampichler & Sierdsema, 2017). Examples include the multivariate environmental similarity surface (MESS) within MaxEnt (Elith et al., 2011), which relies on a rectilinear (univariate) detection of extrapolation. Other techniques are also capable of highlighting different types of environmental novelty arising from mathematical and combinatorial extrapolation (Capinha & Pateiro-López, 2014; Conn, Johnson, & Boveng, 2015) including: extrapolation detection (Mesgaran et al., 2014), environmental overlap masks (Owens et al., 2013), envelope uncertainty maps (Platts, McClean, Lovett, & Marchant, 2008), prediction uncertainty assessments using residual variation (Rödder & Engler, 2012) and mobility-oriented parity (Zurell, Elith, & Schröder, 2012). More generally, explicit description has been widely suggested as a way to deal with extrapolation, echoing Steel, Kennedy, Cunningham, and Stanovick's (2013) recommendation of "being honest", and some have highlighted the issues of extrapolation as being sometimes more philosophical than statistical (Conn et al. 2015).

Ultimately, the "monsters" that lurk in the waters of extrapolation will be less ferocious if the uncertainties underlying model projections are not ignored. Just as mean values should be reported with their associated confidence intervals, there is mounting support for reporting of extrapolated results in prediction maps (Fitzpatrick & Hargrove, 2009; Mesgaran et al., 2014). Because excluding areas as uninhabitable is currently impossible for most taxa, particularly data-poor ones (Fitzpatrick & Hargrove, 2009), validation of results will need to be prioritised and comparisons across models and modelling techniques (*sensu* Fielding, 1999; Hsieh,

TABLE 2 Metrics used for assessment of model transferability (i.e. external evaluation). All metrics are used for presence/absence, presence-only (PO), or abundance data and result in a score between 0 and 1 (or 0% and 100%), with the exception of the c-index, which varies between 0.5 and 1. P: probability distribution with x_1 and x_2 representing the response variable predicted by the two models being compared; cov: covariance; σ: standard deviation; A and B represent distinct spatial regions; TP, FP, FN and TN refer to each position in a confusion matrix including true positives, false positive, false negative and true negatives, respectively; N: sum of all positives and negatives. Examples of the use of each metric in a model transferability context are given in the last column. For AUC, "i" represents a range of cut-off values used to build the plot of sensitivity (SE) vs. 1 – specificity (SP)

| Metric	Calculation/definition	References (see Appendix S1)
Presence-only data		
Modified Hellinger Distance (I similarity statistic)	$I = 1 - \frac{1}{2}\sqrt{\sum_i \left(\sqrt{P_{X1}} - \sqrt{P_{X2}}\right)^2}$	[50, 66, 97, 98]
Schoener's D	$D = 1 - \frac{1}{2}\sum_i |P_{X1} - P_{X2}|$	[30, 98]
Presence/absence data		
Accuracy (overall)	$ACC = \dfrac{TP + TN}{N} \times 100$	[48]
Area under the curve (AUC) (or concordance c-index)	$AUC = \sum_{i=2} \dfrac{SE_i + SE_{i-1}}{2} \times |SP_{i-1} - SP_i|$	[1, 16, 19, 21, 27, 50]
Coefficient of determination (or Calibration curve; CU)	$R^2 = 1 - \dfrac{\text{Residual sum of squares}}{\text{Total sum of squares}}$	[37, 47, 99]
Cohen's Kappa	$K = \dfrac{(TP+TN) - \dfrac{(TP+FN)(TP+FP) + (FP+TN)(FN+TN)}{N}}{N - \dfrac{(TP+FN)(TP+FP) + (FP+TN)(FN+TN)}{N}}$	[3, 16, 74]
Correct classification rate	$CCR = \dfrac{TP + TN}{N}$	[1, 16, 47]
Extrapolative transferability index	$EX-TR = \dfrac{AUC_{Extrapolated}}{AUC_{Internal}}$	[74]
Minimal predicted area	$MPA = \dfrac{\text{Pixels above specified threshold}}{N}$	[65]
Percentage of FN or FP	–	[19]
Point biserial (Pearson correlation)	$\rho = \dfrac{cov(x,y)}{\sigma_x \sigma_y}$	[37]
Sensitivity	$SE = \dfrac{TP}{TP+FP}$	[1, 32, 40, 48]
Spearman Rank	$\rho = \dfrac{cov(x_{ranked}, y_{ranked})}{\sigma_{x_{ranked}} \sigma_{y_{ranked}}}$	[7, 26, 29, 37]
Specificity	$SP = \dfrac{TN}{FP + TN}$	[1]
Transferability index	$TRI = \dfrac{\frac{1}{2}\left(\left(1 - \frac{|AUC_{A\to A} - AUC_{A\to B}|}{0.5}\right) + \left(1 - \frac{|AUC_{B\to B} - AUC_{B\to A}|}{0.5}\right)\right)}{1 + \left||\frac{AUC_{A\to A} - AUC_{A\to B}}{0.5}| - |\frac{AUC_{B\to B} - AUC_{B\to A}}{0.5}|\right|}$	[3]
Transferability test (one-sided χ^2 test)	$TR = \dfrac{\sqrt{N}(TP\,TN - FP\,FN)}{\sqrt{(TP + FP)(FN + TN)(TP + FN)(FP + TN)}}$	[100, 101]
True skill statistic	$TSS = \dfrac{TP\,TN - FP\,FN}{(TP+FN)(FP+TN)}$	[102]
Abundance data		
Coefficient of determination (or Calibration curve; CU)	$R^2 = 1 - \dfrac{\text{Residual sum of squares}}{\text{Total sum of squares}}$	[37, 47, 99]
Spearman Rank	$\rho = \dfrac{cov(x_{ranked}, y_{ranked})}{\sigma_{x_{ranked}} \sigma_{y_{ranked}}}$	[7, 26, 29, 37]
Absolute difference (or root-mean square difference)	$Dif = |y_{target} - y_{reference}|$ $\left(RMS = \sqrt{\frac{1}{n}\left(x_1^2 + x_2^2 + \ldots + x_n^2\right)}\right)$	[36]
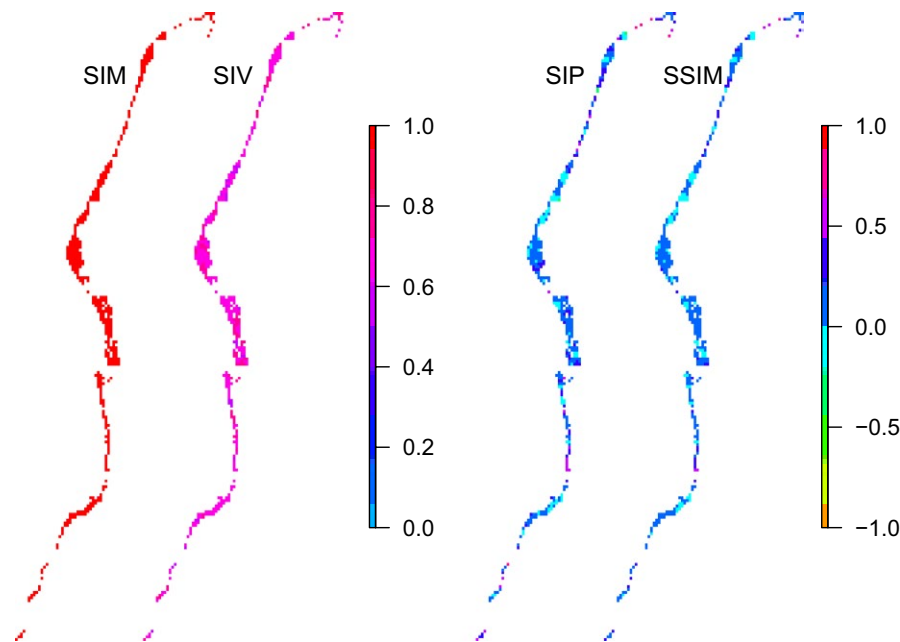
FIGURE 4 Application of the SSIM (structural similarity index) approach in a model transferability context, using the prediction results of a reference model developed for Ningaloo Reef (NR; on the west coast of Australia), and those from a model transferred from the Great Barrier Reef (on the east coast Australia) to NR; adapted from Sequeira et al. (2016). Here, we applied the SSIM index to both sets of prediction maps and results show that local means and variances are similar (SIM = 0.992; SIV = 0.691; left panel with red and pink indicating high similarity). When using SSIM to explore the pattern of spatial covariance, we obtained a positive correlation (>0) between both maps (SIP = 0.122; left map on the right panel). The resulting overall SSIM value is marginally positive as it reflects the combination of the three components (0.992 × 0. 691 × 0.122 = 0.080; right map on the right panel). These results highlight that the mean and variance obtained by the transferred and reference NR models are similar but the covariance patterns are only slightly correlated. These metrics allow better interpretation of model transferability results and provide insights for why a model may fail to transfer

2009) will continue to be helpful in the context of model transferability. We suggest that, where extrapolation can't be avoided, the standardisation of the presentation of extrapolated results by explicitly using one of the three strategies suggested above, would support faster learning about model transferability. Importantly, wherever possible, extrapolation results should also be tested (e.g. validated with data collected after predictions have been made) to improve the performance of transferred models through adaptive learning (Dormann, 2007).

8 | TOWARDS BETTER PRACTICE IN MODEL TRANSFERABILITY

A number of rules of good practice for testing model transferability have been published and are summarised in Table 1. Key principles highlighted relate to the consideration of species characteristics, chosen predictors and modelling approaches (Werkowska et al., 2017). For example, it has been suggested that only models of species whose physiological constraints will remain similar throughout their ranges should be used for testing model transferability (Pearman et al., 2008). While such constraints might be difficult to establish, one possible way to promote best practice would be to compare forecasts from transferred models only for species for which hindcasting has demonstrated good predictive performance (Kharouba

et al. 2009). Predictions of species distributions in different areas should also be tested (Lauria et al., 2015) including those separated by thousands of kilometres (Sequeira et al., 2016; Sundblad, Härmä, Lappalainen, Urho, & Bergström, 2009). Suggestions that individual species traits and functional groups should be well known prior to testing transferability have also been put forward, as well as previous assessments of the effects of population demographics and conservation status. Furthermore, competition among species should also be considered, especially when such interactions are dynamic.

The careful choice of predictors has been advised due to potential effects of using proxy data and scale dependencies (see Table 1 for details). In particular, the discriminative ability and effect sizes of the predictor variables should be assessed before models are transferred. Also, predictors included in the models, their estimated coefficients and resulting predictions should all be fully reported. Exploration of other traits (e.g. fine scale traits such as molecular data) that might be more correlated with specific geographical features, has also been encouraged.

Best practice in modelling includes careful checks of model assumptions, and reporting of residuals to allow better interpretation of results. The use of multiple modelling approaches should also be considered to test appropriateness for different applications. This will be useful to reduce or quantify uncertainty, acknowledging though that models resulting in good internal evaluation (and

interpolation) will not always transfer well. The effects of model complexity should also be explored, as they are highly system- and data-dependent. Finally, best practice should also include standardisation of the presentation of results to facilitate cross-study comparisons and allow for general improvements in model transferability and in our understanding of what affects or hinders the transferability of biodiversity models. We therefore suggest that model transferability studies include a summary section where each of the steps in Box 1 are clearly considered.

9 | CONCLUSION

The future of model transferability and its utility for conservation and management will rely on the careful consideration of each of the above recommendations, together with the presentation of standardised results from transferability assessments. To promote advances in model transferability, we propose that ten key points should be addressed. While the focus of this manuscript is on correlative models, most of these guidelines will also be applicable to mechanistic models:

1. Define the situation according to the scheme presented in Figure 2.
2. Summarise the relationships between predictor and response variables in the reference and target systems.
3. Justify assumptions and check their validity where possible.
4. Decide on a strategy to deal with extrapolation: avoidance, mitigation or description.
5. Check the suggestions for best practise included in Table 1 and address the relevant points for the study.
6. Decide on the modelling approach; using the procedure most suitable for the study, implementing a suite of algorithms and selecting the best performing one, or using an ensemble approach.
7. Develop reference models following Figure 3, depending on the amount of data available for the study.
8. Check model fit and assess model performance focusing on:

   a. Evaluation by reporting the basic statistics (e.g. observed vs predicted comparisons or true and false positives and negatives, for continuous or categorical variables, respectively) that can be used to calculate common metrics, including, as a minimum, R^2, which can be considered equivalent to the normalised chi-squared (i.e. the ratio of the observed chi-squared to the maximum possible chi-squared for categorical data) (Rosenberg, 2010) and provides a score between 0 and 1 for the overall assessment.
   b. Predictive power using the SSIM where applicable (i.e. data-rich scenarios).
9. Clearly indicate where predictions are the result of extrapolation.
10. Report a minimum standardised set of results to facilitate comparisons between studies (see Box 1).

Transferring predictive biodiversity models has the potential to become a time- and cost-effective tool for management and conservation, provided it is done in a consistent way that guarantees transparency, comparability and confidence in model outputs. The information we synthesise here (Table 1 and Figure 3) can assist in dealing with different scenarios where model transfers may be helpful. The careful consideration of the issues we outline will improve the performance of model transfers in ecological studies and management practice, and more importantly, will help us learn what confers transferability on biodiversity models. As understanding increases, these recommendations may evolve but the need for standardisation will remain. Lastly, because model transferability is relevant in other fields, such as transport (Ibeas, Moura, Nuzzolo, & Comi, 2012; Rashidi, Auld, & Mohammadian, 2013), health and economics (Drummond et al., 2009), and urban pollution (Patton et al., 2015), cross-fertilisation among these communities of practice has the potential to further enhance our confidence in transferring models, their resulting predictions and their application to real-world situations.

AUTHORS' CONTRIBUTIONS

A.M.M.S., P.J.B. and M.J.C. conceived the paper; all author contributed to the development of the key ideas; A.M.M.S. and P.J.B. reviewed the literature with contributions from K.L.Y., K.M. and M.J.C.; A.M.M.S. led the writing of the manuscript; A.M.M.S., P.J.B.

BOX 1 Summary section needed for standardisation of the presentation of results from model transfer studies

1. Indication of type of transferability (as per Figure 2)
2. Summary of range of responses and predictors (e.g. boxplot)
3. Details on the assumptions made (equilibrium, stationarity, environment vs. human drivers, space-for-time substitutability)
4. Specification of the models and algorithms used
5. Details on the data scenario being tested: data-rich, data-sparse, data-deficient
6. Summary of model fit and performance (including R^2 as a minimum, and SSIM where applicable).

and K.L.Y. developed the figures; All authors contributed critically to the drafts and gave final approval for publication.

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