REVIEW

A practical overview of transferability in species distribution modeling

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Abstract: Species distribution models (SDMs) are basic tools in ecology, biogeography, and biodiversity. The usefulness of SDMs has expanded beyond the realm of ecological sciences, and their application in other research areas is currently frequent, e.g., spatial epidemiology. In any research area, the principal interest in these models resides in their capacity to predict species response in new scenarios, i.e., the models' transferability. Although the transferability of SDMs has been the subject of interest for many years, only in the 2000s did this topic gain particular attention. This article reviews the concept of the transferability of SDMs to new spatial scenarios, temporal periods, and (or) spatial resolutions, along with the potential constraints of the model's transferability, and more specifically: (*i*) the type of predictors and multicollinearity, (*ii*) the model complexity, and (*iii*) the species' intrinsic traits. Finally, we describe a practicable analytical protocol to be assessed before transferring a model to a new scenario. This protocol is based on three fundamental pillars: the environmental equilibrium of the species with the environment, the environmental similarity between the new scenario, and the areas used to model parametrisation and the correlation structure among predictors.

Key words: species distribution model, spatially explicit model, spatial transferability, temporal transferability, downscaling, multicollinearity.

Résumé : Les modèles de répartition des espèces (MRE) sont des outils de base en écologie, en géographie et en biodiversité. L'utilité des MRE s'est étendue au-delà de la sphère des sciences écologiques, et leur application dans d'autres domaines de recherche est actuellement fréquente, p. ex. l'épidémiologie spatiale. Dans n'importe quel domaine de recherche, l'intérêt principal de ces modèles provient de leur capacité à prédire la réponse des espèces dans de nouveaux scénarios, c.-à-d. la transférabilité des modèles. Bien que la transférabilité des MRE ait été le sujet d'intérêt depuis de nombreuses années, ce n'est que dans les années 2000 que ce sujet attira une attention particulière. Cet article passe en revue le concept de transférabilité des MRE à de nouveaux scénarios spatiaux, à de nouvelles périodes temporelles et/ou à de nouvelles résolutions spatiales, avec des contraintes possibles de transférabilité du modèle, et plus spécifiquement : (*i*) le type de prédicteurs et de multicolinéarité, (*ii*) la complexité du modèle et (*iii*) les caractères intrinsèques des espèces. Finalement, nous décrivons un protocole analytique praticable à être évalué avant de transférer un modèle à un nouveau scénario. Ce protocole est fondé sur trois piliers fondamentaux : l'équilibre environnemental des espèces avec l'environnement, la similitude environnementale entre le nouveau scénario et les domaines utilisés pour modéliser le paramétrage, et la structure des corrélations entre les prédicteurs. [Traduit par la Rédaction]

Mots-clés : modèle de répartition des espèces, modèle spatialement explicite, transférabilité spatiale, transférabilité temporelle, réduction d'échelle, multicolinéarité.

Introduction

The study of species distributions developed significantly during the last decades of the twentieth century. The first theoretical models and predictive approaches appeared in the late 1970s and during the 1980s (Kessel 1979; Busby 1986; Nix 1986; Austin 1987; see also Booth et al. 2014). The increasing use and development of geographic information systems and the growing ability and capacity to handle large databases provided fundamental tools with which to carry out large-scale studies on species ranges (e.g., Guisan and Zimmermann 2000; see also Elith and Leathwick 2009). Nowadays, species distribution models (SDMs) have become basic tools in ecology, biogeography, biodiversity, and conservation (e.g., Franklin 2010).

An SDM is basically a correlative or mechanistic model that relates the localities in which one species is present — or its abundance — with the ecological and geographical characteristics of the territory (Guisan and Zimmermann 2000). These kinds of spatially explicit models make it possible to determine the main environmental gradients to which species are able to respond and to predict the potential of a territory for the species according to the local environmental characteristics. Scientific literature has denominated these models in accordance with the interpretation that is made of their outcomes, and the terms "niche models", "predictive models of habitat", or "suitability models" have, for example, been used. Researchers are currently attempting to reach a consensus as to what name to apply to these approaches, and the term "species distribution models" is now becoming generalised as a more theoretically neutral term (Mateo et al. 2011).

The applications of SDMs in ecology are varied and numerous: from basic studies whose aim is to determine the ecogeographical determinants of species ranges, to multispecies interdisciplinary studies focused on relevant ecological questions, both for basic and applied ecology (e.g., Guisan et al. 2006; Acevedo et al. 2010; Franklin 2013). However, the principal driving force behind SDMs

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was their use to predict species response in unsampled spatio-temporal scenarios. Models can be used to forecast the distribution of a species in different scenarios, such as past climatic scenarios, to reconstruct the evolutionary history of the species (e.g., Nogués-Bravo 2009), future scenarios of climate and land-use changes to assess species sensitivity to environmental changes (e.g., Pearson and Dawson 2003; Acevedo et al. 2011), for an invasive species in a new territory to assess potential invasion patterns (e.g., Peterson and Vieglais 2001; Peterson 2003), or similarly, for a species in unsampled territories (e.g., Randin et al. 2006; Barbosa et al. 2009). This concept of the cross applicability of the models in both space and time has been defined as generality (Fielding and Haworth 1995) or transferability (e.g., Thomas and Bovee 1993; Glozier et al. 1997; hereafter transferability) and it is now widely used to expand the potential of SDMs. But the transference of a SDM is not a straightforward task (see below) and requires modellers to handle both a conceptual background and analytical procedures to avoid the inclusion of bias in the results. However, most of the SDMs transferences in studies not directly focused in testing transferability are uncritically performed (but see e.g., Acevedo et al. 2014a; Ray et al. 2016). In this context, we provide a practical overview of SDMs transferability aimed to (*i*) define the concept of the transferability of SDMs to new spatial scenarios, temporal periods, and (or) spatial resolutions, and identify the potential constraints of the model's transferability, and (*ii*) describe a practicable analytical protocol to be assessed before transferring a model to a new scenario.

The transferability of SDMs

Modellers employ SDMs when seeking the environmental conditions of the species and when interested in registering general responses to environmental gradients and not only to local conditions. The fit among predictions and observed data — when available — is an empirical validation of the ecological significance of the model; a general and validated model can therefore be transferred to other scenarios to predict the pattern of the species in a scenario in which very little sampling has taken place. The validation of the model is a key step for getting success in its transference. In the last few years, further advances were produced on validation in SDM, and nowadays there are both conceptual frameworks and analytical protocols to consistently perform validation (e.g., Roberts and Hamann 2012; Muscarella et al. 2014; Radosavljevic and Anderson 2014). Finally, the transference of an SDM to outside the context used for model calibration helps drive return on investment for the development of the model, which often requires intensive fieldwork and (or) laboratory analyses. At times of low investment in science in general and in the management of natural resources in particular, the use of published models to predict species patterns in areas for which little information is of the species available is an extremely interesting line of research (Acevedo et al. 2014b).

Models can be transferred to different spatial scenarios, temporal periods, and (or) spatial resolution. *Spatial transferability* is a means to assess the degree to which a parameterised model can be generalised to other territories (Randin et al. 2006; Barbosa et al. 2009). It is possible to differentiate two types of spatial transferability as regards whether predictions are made within (interpolation) or outside (extrapolation) the geographical domain of the model (Elith and Leathwick 2009). Spatial transferability has been used widely to improve sampling design (e.g., Rebelo and Jones 2010), to determine the environmental potential for invasive/introduced species (e.g., Jiménez-Valverde et al. 2011; Torres et al. 2016), or to assess the niche similarities between related taxa (e.g., Acevedo et al. 2014a), among others. For instance, SDM extrapolation was recently used to evaluate niche relationships between two allopatric species, *Lepus castroviejoi* and *Lepus corsicanus*, which inhabit the northern Iberian Peninsula and mainland Italy and

Sicily, respectively (Acevedo et al. 2014a), to reinforce the molecular evidence on their status as sister species (Alves et al. 2008). In the study in question, individual models were transferred to the territory of the sister species to evidence their ecological similarities.

The transferability of the model to other periods of time is known as *temporal transferability*. It permits the evaluation of the effects that environmental changes have had and will have on species ranges (e.g., Dobrowski et al. 2011; Tuanmu et al. 2011) — i.e., to determine the species' sensitivity to environmental changes — to anticipate the effects of global change on species distributions (e.g., Brook et al. 2008), and to design conservation plans in the context of environmental change (Araújo et al. 2011; Thuiller et al. 2011). The transference of SDMs to future climate change scenarios was the area that stimulated further progress in both conceptual and analytical strategies of SDMs. It is not, however, possible to adequately assess predictions for future scenarios owing to the obvious lack of data (but see Araújo et al. 2005a). Therefore, predictions should be considered with relative caution since several sources of uncertainty emerge at each step (e.g., Real et al. 2010) and propagate throughout the modelling procedure (e.g., Rocchini et al. 2011). A huge number of studies are based on the temporal transferability of SDM. For instance, Maiorano et al. (2011) assessed the future of terrestrial mammals in the Mediterranean basin in climate change scenarios. These authors concluded that a substantial number of species, and mainly endemic species, will have been severely affected by the ongoing climate change by 2100.

The integration of macroecology and phylogeny is currently a cutting-edge research area in biogeography. In this respect, SDMs are hindcasted to past environmental scenarios as a means to provide ecological scenarios in which to test evolutionary hypotheses (e.g., Wielstra and Arntzen 2012). However, SDMs can perform poorly when projected to distant time periods and climatic dissimilar scenarios (Maguire et al. 2016). Thus, predictions for past scenarios should be validated by using fossil records and (or) phylogenies (e.g., Collevatti et al. 2013; Diniz-Filho et al. 2013; Maguire et al. 2015). For instance, the application of SDMs in evolutionary studies allows researchers to propose and validate hypotheses regarding the existence and location of glacial refugia (e.g., Carnaval and Moritz 2008; Acevedo et al. 2012), to explore ecological relationships within and between phylogenetically related taxa (Peterson et al. 1999; Wiens and Graham 2005), or to reconstruct the conditions that allowed, among other things, historical hybridisation and genetic introgression to occur (Acevedo et al. 2015).

The resolution at which distribution data are available does not always coincide with the interests of conservation and management. The *changes in the spatial resolution* of a model's predictions — i.e., the projection of models built at one resolution to a larger (upscaling) or a finer (downscaling) spatial resolution — are potentially highly beneficial for ecology and conservation (Araújo et al. 2005b). The large-scale data available are usually too coarse to enable spatial resolutions to be applied in local conservation planning, while the collection of data at a finer resolution requires high sampling efforts, which are only feasible for a few species and over small areas. For instance, Barbosa et al. (2010) successfully downscaled SDMs for a restricted endemic insectivore, the Iberian desman (*Galemys pyrenaicus*), and a more widespread carnivore, the Eurasian otter (*Lutra lutra*), in the Iberian Peninsula. This and other studies suggest the potential usefulness of downscaled projections of environmental quality as a proxy for expensive and time-consuming field studies when field studies are not feasible.

The opposite process, upscaling, is not as frequent as downscaling in studies on species distribution (but see Harvey 2000). Data on species distribution at fine spatial resolution are able to contain more reliable and precise information on species ecology

Fig. 1. Overview of the model building process when the dataset is split into two parts, one with which to fit and another with which to evaluate the model. The transferability of the model to a new scenario is also schematised. In each step, the main factors that can compromise the model's transferability are highlighted in red, along with the three (1–3) fundamental requirements that should be checked before the transference of the model to the new scenario (see text for details). [Colour online.]
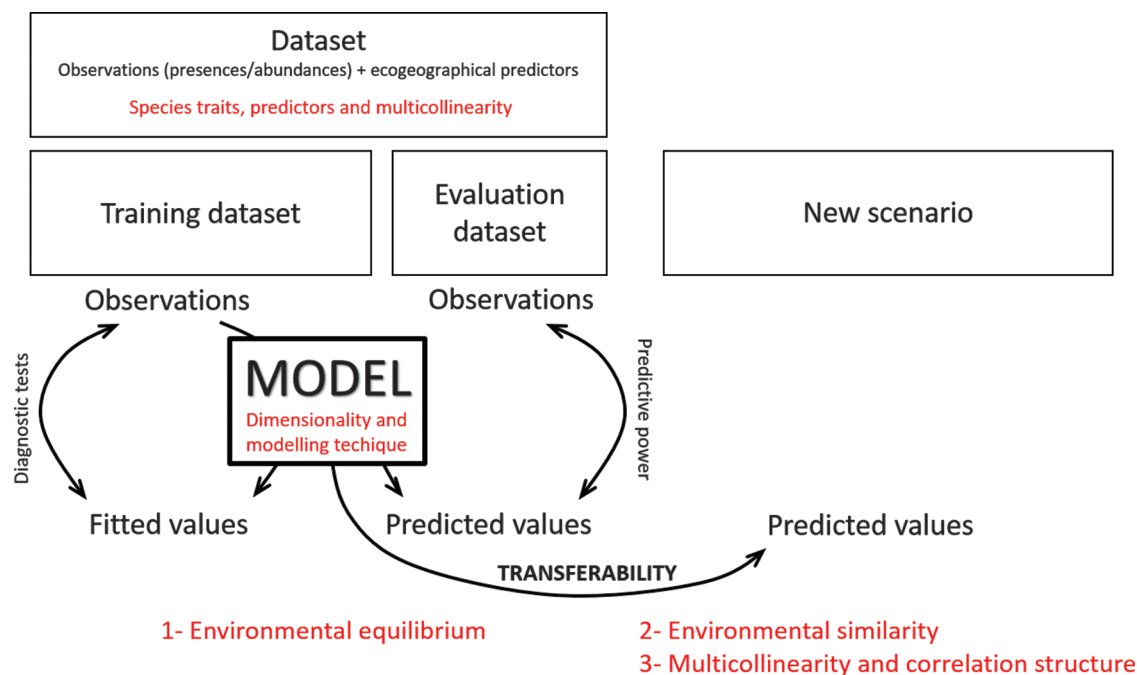
than data obtained for coarser resolutions, but the former are patchy within the species range. However, factors that are associated with the occurrence of individuals on a local scale may not be associated with factors explaining a large-scale species distribution range (Jiménez-Valverde et al. 2008), and SDMs derived from fine resolution data are, therefore, sometimes not able to provide a good explanation of data represented at coarser resolutions. This indicates that SDMs at both fine and coarse resolution do not explain the same species distribution pattern, as was discovered by Marcer et al. (2012) when studying vascular plants in Spain; the models at a fine resolution probably explain the habitat selection within the area favourable for species distribution, but they fail to discriminate between the areas that are favourable and unfavourable for the species. Despite the relevance of this topic to both fit the spatial resolution of SDM adequate to data and goals, and determine the limits for changing spatial resolution, the studies are scarce and therefore further research would be valuable in this area.

Potential constraints regarding a model's transferability

Researchers have for many years found the transferability of statistical models to be a subject of interest, but it was not until the 2000s that this topic gained particular attention (Randin et al. 2006; Vanreusel et al. 2007; Barbosa et al. 2009). Many studies have indicated factors that may affect and hinder a model's transferability, such as the type of predictor variables and their multicollinearity, the model complexity (dimensionality and algorithm), and the species' intrinsic traits (see Fig. 1).

Type of predictors and multicollinearity

The choice of predictor variables for modelling affects a model's predictive performance (e.g., Synes and Osborne 2011) and therefore the SDM's transferability. Most of the abiotic predictors used for modelling explain animal distribution indirectly, through their correlation with ecological functional resources (Austin 2002; Guisan and Thuiller 2005; Austin et al. 2006). Extrapolations

will be particularly error-prone if only indirect predictors are used, because the correlations between them and the functional resources vary in both space and time (Austin 2002). When these correlations depend on area-specific conditions, models could be overfitted to the local conditions, which may compromise the model's transferability (Luoto et al. 2002) — in SDMs overfitting occurs when a model closely fits the calibration data and thus fails when predicting on independent data. The use of more ecologically relevant predictors is now increasingly possible as remotely sensed data are more readily available (e.g., Pettorelli et al. 2016). Remote sensing therefore provides data that can play a role in improving the performance of SDMs and therefore their transferability (e.g., He et al. 2015), especially spatial transferability and changes in spatial resolution, since remote sensing data are not available for different past, e.g., in an evolutionary context, or future temporal scenarios. Despite these advances, many studies appear to use only data that are readily available, while failing to explain the relevance of the predictors selected and probably missing important ecological drivers.

When an SDM is extrapolated, the proper quantification of the effect of each predictor on current geographic ranges is a must for an accurate estimation of the potential for the species (Braunisch et al. 2013). But the effect of a factor can only be adequately estimated in the context of the other influential factors (e.g., Márquez et al. 2011). This signifies that the real effect of a factor on species distributions could be masked (under- or over-rated) by confounding correlated factors, becoming evident only when the effects of the other factors are subtracted from the weights of the predictors and subsequently from the predictions of the models (e.g., Lavergne et al. 2005; Real et al. 2013; Record et al. 2013). One of the main challenges in this respect is to filter out (control for) the variation caused by spatial structures (Griffith and Peres-Neto 2006; Dormann et al. 2007; Hawkins et al. 2007), since the spatial structure in species distribution and environmental processes can increases type I errors and can potentially affect model estimations (e.g., Legendre et al. 2002). Briefly, the solution is again to produce combined models in which both environmental and spa-

tial gradients should be considered (for details, see Peres-Neto and Legendre 2010). For instance, Real et al. (2013) estimated the pure climatic effect (i.e., not affected by covariation with non-climatic factors) and the apparent climatic effect (i.e., including shared effects between climate and non-climatic factors) on species distribution, and suggested that both the pure and apparent fractions could be interpreted as the lower and upper bounds of a range of possible scenarios for the future climatic potential for the species.

Model complexity

Model complexity can be characterized with the number of predictors (dimensionality), the algorithm, and the parameters within the same algorithm (e.g., Merow et al. 2014; Duque-Lazo et al. 2016). A simpler model typically has relatively fewer parameters and fewer relationships among predictors compared to a more complex model. Simple models, with insufficient flexibility to describe occurrence-environment relationships, can misunderstand the factors driving species distributions. Complex models, with excessive flexibility and number of parameters, can inadvertently ascribe pattern to noise. Therefore, in the framework of the transferability, complex models should be avoided.

The dimensionality — i.e., number of predictors — of the models determines the transferability of SDMs (e.g., Peterson 2011) and must be declared and weighed carefully from the beginning of the analysis (see also Warren et al. 2014). Transferability decreases as the number of predictors in the model increases; models developed using too many dimensions may run the risk of overfitting to local conditions that restrict the predictive power of the model.

The complexity associated with the algorithm is, in this case, characterised as the shape of the inferred occurrence–environment relationships that are closely related to the number of parameters. Briefly, environmental envelopes (e.g., BIOCLIM or DOMAIN) and distance-based approaches in multivariate environmental spaces (e.g., ENFA, Malahanobis) are considered to be the simplest SDMs. Their response curves are simple functions with a reduced number of parameters (e.g., linear, hinge or step; Hirzel et al. 2002; Elith et al. 2005). Generalised linear models (GLMs), which are typically fitted with linear or polynomial features up to second-order terms (rarely third or fourth order) for SDMs, are considered to be simple even when they admit more complexity. However, this relative simplicity applies to the relationship between probability, which is the output of the model, and the logit function, whereas the relationship between probability and individual variables tends to be more complex owing to the collinearity between predictors (Acevedo and Real 2012). GARP and MAXENT are considered to be complex algorithms, since they allow high flexibility (Stockwell and Peters 1999; Phillips et al. 2006). Generalised additive models (GAMs) are also complex techniques, because they allow non-parametric smooth functions of variable flexibility (Hastie and Tibshirani 1990). Decision trees (Breiman et al. 1984) can also become quite complex, because they may use a large number of step functions (each requiring a parameter) and can implicitly include high order interaction terms with which to depict response curves of arbitrary complexity. In addition to the analytical protocols involving the use of a single modelling technique, "ensemble models" in which predictions from several techniques are considered, such as BIOMOD (Thuiller et al. 2009), are also frequently used. Different modelling techniques can achieve variable performance in the data-training set, even when they are calibrated with the same data (e.g., Segurado and Araújo 2004; de Pando and de Giles 2007; Mateo et al. 2011). The capability of the different techniques to be transferred is consequently also widely variable (e.g., Peterson et al. 2007). In addition, only models that produce commensurate outcomes, such as probability or favourability (see Acevedo and Real 2012), can be adequately combined in ensemble models, whereas models yielding suitability values that are idiosyncratic for each modelling technique lack the com-

mensurability required for combination (Romero et al. 2016). However, the ensemble models do not necessarily control or fix biases and (or) improve transferability (see e.g., Rodríguez-Rey et al. 2013).

Several studies were performed to assess the relationship between model complexity and predictive performance, both on the training and transference areas. For instance, Tsoar et al. (2007) compared the performance of six algorithms and concluded that flexible algorithms attain a higher predictive performance in the training data set than do non-flexible ones. This result resembles the insight provided by Elith et al. (2006), who also concluded that those that are able to fit complex responses are preferable to simple algorithms. However, complex algorithms are not preferred when the models should be transferred to new scenarios, because flexible algorithms tend to overfit to local conditions, thus losing generality (Jiménez-Valverde et al. 2008). A good transferability has been suggested for algorithms such as GLM and GAM (e.g., Austin et al. 2006; Meynard and Quinn 2007; Wenger and Olden 2012). Randin et al. (2006) reported that GLM was more robust than GAM, suggesting that overfitting can reduce the transferability of GAM models. With regard to GARP and MAXENT, two techniques based on data of presence, Peterson et al. (2007) compared these techniques and found the latter to be overfitted. However, if the sample size is small, it can extrapolate better than GARP (Papes and Gaubert 2007). Other techniques have proved to have worse predictive power and accuracy, such as GARP, Random Forest, and MARS (e.g., Prasad et al. 2006). Determining the most appropriate amount of complexity to be included in SDMs is therefore crucial for biological applications (Merow et al. 2014). Researchers must constrain model complexity on the basis of data attributes and study objectives, and an understanding of how they interact with the underlying biological processes.

Species intrinsic traits

Lack of transferability can be also caused by species specific traits not included in the model, for instance dispersal capacity, changes in the role of biotic interactions, and (or) changes in the realized niche (e.g., Urban et al. 2013; Williams et al. 2013). Despite this, the relationship between specific traits and model transferability has rarely been studied. Vanreusel et al. (2007) related model spatial transferability to the range of habitat use of two butterfly species. These authors observed that the model for the species with the smallest range of space use (*Callophrys rubi*) was more transferable than the model for a more mobile species (*Hipparchia semele*). Kharouba et al. (2009), also with butterflies, found that transferability declined for widely distributed species over time and showed inconclusive results for dispersal capability. After working with 133 vascular plant species, Dobrowski et al. (2011) found that models for non-endemic species with a greater dispersal capacity, intermediate levels of prevalence, and a low capacity to adapt to fire had a higher transferability over time than did endemic species with a limited dispersal capacity that rely on fire for reproduction (disturbance response). Heikkinen et al. (2012) found differences in models' spatial transferability between taxonomic groups; the best transferability was specifically found for birds, followed closely by butterflies, whereas plant species were found to have a weak transferability capability. There is thus a need for further research that will relate species' taxonomical and functional traits to model's transferability, taking into account potential discrepancies in their effects as regards the type of transferability: spatial *vs.* temporal.

Checking a model's transferability: analytical protocol

Before transferring an SDM beyond the data-training set, three fundamental requirements should be checked (see Fig. 1).

(*i*) Transferability requires the target species to have environmental equilibrium throughout its entire distribution area (Nogués-Bravo 2009). Species are said to be at equilibrium with the environment if they occur in all climatically suitable areas whilst being absent from all unsuitable ones (Araújo and Pearson 2005). However, even when the results obtained from a model suggest a climatic equilibrium, the model's transferability does not necessarily provide realistic results. This was the case of a study on *Crocuta crocuta* in which predictions for the last interglacial period were incoherent, because the current geographical range does not allow estimations of all of the environmental requirements of the species to be made (Varela et al. 2009). Paradoxically, the opposite — e.g., a model in disequilibrium that produce good predictions — can also occur when working, for instance, with an introduced invasive species (Muñoz and Real 2006; but see Jiménez-Valverde et al. 2011). A proxy metric of equilibrium between species distribution and the environment is the realised/potential range size ratio (Svenning and Skov 2004).

(*ii*) The environmental similarity of the new scenario with regard to the training area should be evaluated. As a general rule, SDMs may only be transferred to scenarios that are similar in environmental terms to that in which the model was calibrated. Similarity can be assessed using Mahalonobis distances and (or) multivariate environmental similarity surfaces (e.g., Elith et al. 2010). This kind of analyses also allow identifying the predictor that is driving to a given locality to be environmentally dissimilar (the most dissimilar predictor can thus be recognized). To remove the modelling procedure these dissimilar predictors is a way to improve the transferability of the model.

(*iii*) High levels of multicollinearity between the predictors included in a model can bias predictions when the model is transferred to a situation in which the correlation matrix between predictors is different. Collinearity can be quantified using the variance inflation factor (VIF), which should be calculated for each of the predictors in the model (see Zuur et al. 2010). There are more ways in which to detect collinearity, such as by examining the matrix of correlation coefficients between predictors to avoid including those that are highly correlated ($r > |0.8|$) in the model. However, multicollinearity is a real phenomenon in nature, and it cannot therefore be avoided in all cases, although it should be managed. When possible, the best ways in which to manage multicollinearity are by increasing the sample size by including external information and by removing highly correlated variables (e.g., Doran 1989). The maintenance of the correlation structure among predictors between training and transference areas should be assessed. As the coefficient for a predictor in a model depends on the coefficients for the other predictors (Fox 1997), changes in the correlation structure may include severe bias in models' predictions in the transference area. A Mantel test (Mantel 1967), or another similar means to determine the association between matrices (see Guillot and Rousset 2013), should therefore be carried out to avoid biased results.

In summary, various methodological requirements should be taken into account before transferring a model to another spatial/temporal scenario. This means that if the objective is to transfer a model, special attention should be paid to the species–environment equilibrium and to the selection of predictors. What is more, a calibrated model cannot be transferred just anywhere, but only to those scenarios that are environmentally similar to the scenario in which the model was calibrated. Despite the importance of transferring distribution models, studies designed to explore this feature and to assess the methodological and ecological factors that determine it are still scarce (e.g., Dobrowski et al. 2011). This is a line of interesting and timely research, given the high number of models that have been published in recent years (Lobo et al. 2010).

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