



**A practical overview of transferability in species distribution modelling**

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1 **A practical overview of transferability in species distribution**  
2 **modelling**

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**11 Abstract**

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

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

29

## 30 **Introduction**

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

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

52 The applications of SDMs in ecology are varied and numerous: from basic studies  
53 whose aim is to determine the ecogeographical determinants of species ranges, to  
54 multispecies interdisciplinary studies focused on relevant ecological questions, both for  
55 basic and applied ecology (e.g. Guisan et al. 2006; Acevedo et al. 2010; Franklin 2013).  
56 However, the principal driving force behind SDMs was their use to predict species  
57 response in unsampled spatio-temporal scenarios. Models can be used to forecast the  
58 distribution of a species in different scenarios, such as past climatic scenarios in order  
59 to reconstruct the evolutionary history of the species (e.g. Nogues-Bravo 2009), future  
60 scenarios of climate and land-use changes to assess species sensitivity to environmental  
61 changes (e.g. Pearson and Dawson 2003; Acevedo et al. 2011), for an invasive species

62 in a new territory to assess potential invasion patterns (e.g. Peterson and Vieglais 2001;  
63 Peterson 2003), or similarly, for a species in unsampled territories (e.g. Randin et al.  
64 2006; Barbosa et al. 2009). This concept of the cross applicability of the models in both  
65 space and time has been defined as generality (Fielding and Haworth 1995) or  
66 transferability (e.g. Thomas and Bovee 1993; Glozier et al. 1997; hereafter  
67 transferability) and it is now widely used to expand the potential of SDMs. But the  
68 transference of a SDM is not a straightforward task (see below) and requires to handle  
69 both a conceptual background and analytical procedures in order to avoid the inclusion  
70 of bias in the results. However, most of the SDMs transferences in studies not directly  
71 focused in testing transferability are uncritically performed (but see e.g. Acevedo et al.  
72 2014a; Ray et al. 2016). In this context, we provide a practical overview of SDMs  
73 transferability aimed to i) define the concept of the transferability of SDMs to new  
74 spatial scenarios, temporal periods and/or spatial resolutions, and identify the potential  
75 constraints of the model's transferability, and ii) describe a practicable analytical  
76 protocol to be assessed before transferring a model to a new scenario.

77

### 78 **The transferability of SDMs**

79 Modellers employ SDMs when seeking the environmental conditions of the species and  
80 when interested in registering general responses to environmental gradients and not only  
81 to local conditions. The fit among predictions and observed data – when available – is  
82 an empirical validation of the ecological significance of the model; a general and  
83 validated model can therefore be transferred to other scenarios so as to predict the  
84 pattern of the species in a scenario in which very little sampling has taken place. The  
85 validation of the model is a key step for getting success in its transference. In the last  
86 years further advances were produced on validation step in SDM and nowadays there  
87 are both conceptual framework and analytical protocols to consistently perform it (e.g.  
88 Roberts and Hamann 2012; Muscarella et al. 2014; Radosavljevic and Anderson 2014).  
89 Finally, the transference of an SDM to outside the context used for model calibration  
90 helps drive return on investment for the development of the model, which often requires  
91 intensive fieldwork and/or laboratory analyses. At times of low investment in science in  
92 general and in the management of natural resources in particular, the use of published

93 models to predict species patterns in areas for which little information is of the species  
94 available is an extremely interesting line of research (Acevedo et al. 2014b).

95 Models can be transferred to different spatial scenarios, temporal periods and/or spatial  
96 resolution. *Spatial transferability* is a means to assess the degree to which a  
97 parameterised model can be generalised to other territories (Randin et al. 2006; Barbosa  
98 et al. 2009). It is possible to differentiate two types of spatial transferability as regards  
99 whether predictions are made within (interpolation) or outside (extrapolation) the  
100 geographical domain of the model (Elith and Leathwick 2009). Spatial transferability  
101 has been used widely to improve sampling design (e.g. Rebelo and Jones 2010), to  
102 determine the environmental potential for invasive/introduced species (e.g. Jimenez-  
103 Valverde et al. 2011; Torres et al. 2016), or to assess the niche similarities between  
104 related taxa (e.g. Acevedo et al. 2014a), among others. For instance, SDM extrapolation  
105 was recently used to evaluate niche relationships between two allopatric species, *Lepus*  
106 *castroviejoi* and *Lepus corsicanus*, which inhabit the northern Iberian Peninsula and  
107 mainland Italy and Sicily, respectively (Acevedo et al. 2014a), in order to reinforce the  
108 molecular evidence on their status as sister species (Alves et al. 2008). In the study in  
109 question, individual models were transferred to the territory of the sister species in order  
110 to evidence their ecological similarities.

111 The transferability of the model to other periods of time is known as *temporal*  
112 *transferability*. It permits the evaluation of the effects that environmental changes have  
113 had and will have on species ranges (e.g. Dobrowski et al. 2011; Tuanmu et al. 2011) –  
114 i.e. to determine the species' sensitivity to environmental changes – in order to  
115 anticipate the effects of global change on species distributions (e.g. Brook et al. 2008),  
116 and to design conservation plans in the context of environmental change (Araújo et al.  
117 2011; Thuiller et al. 2011). The transference of SDMs to future climate change  
118 scenarios was the area that stimulated further progress in both conceptual and analytical  
119 strategies of SDMs. It is not, however, possible to adequately assess predictions for  
120 future scenarios owing to the obvious lack of data (but see Araújo et al. 2005a).  
121 Therefore, predictions should be considered with relative caution since several sources  
122 of uncertainty emerge at each step (e.g. Real et al. 2010) and propagate throughout the  
123 modelling procedure (e.g. Rocchini et al. 2011). A huge amount of studies are based on  
124 the temporal transferability of SDM. For instance, Maiorano et al. (2011) assessed the

125 future of terrestrial mammals in the Mediterranean basin in climate change scenarios.  
126 These authors concluded that a substantial number of species, and mainly endemic  
127 species, will have been severely affected by the ongoing climate change by 2100.

128 The integration of macroecology and phylogeny is currently a cutting-edge research  
129 area in biogeography. In this respect, SDMs are hindcasted to past environmental  
130 scenarios as a means to provide ecological scenarios in which to test evolutionary  
131 hypotheses (e.g. Wielstra and Arntzen 2012). However, SDMs can perform poorly  
132 when projected to distant time periods and climatic dissimilar scenarios (Maguire et al.  
133 2016). Thus, predictions for past scenarios should be validated by using fossil records  
134 and/or phylogenies (e.g. Collevatti et al. 2013; Diniz-Filho et al. 2013; Maguire et al.  
135 2015). For instance, the application of SDMs in evolutionary studies allows researchers  
136 to propose and validate hypotheses regarding the existence and location of glacial  
137 refugia (e.g. Carnaval and Moritz 2008; Acevedo et al. 2012), to explore ecological  
138 relationships within and between phylogenetically related taxa (Peterson et al. 1999;  
139 Wiens and Graham 2005), or to reconstruct the conditions that allowed, among other  
140 things, historical hybridisation and genetic introgression to occur (Acevedo et al. 2015).

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

155 The opposite process, upscaling, is not as frequent as downscaling in studies on species  
156 distribution (but see Harvey 2000). Data on species distribution at fine spatial resolution

157 is able to contain more reliable and precise information on species ecology than data  
158 obtained for coarser resolutions, but the former are patchy within the species range.  
159 However, factors that are associated with the occurrence of individuals on a local scale  
160 may not be associated with factors explaining a large-scale species distribution range  
161 (Jimenez-Valverde et al. 2008), and SDMs derived from fine resolution data are,  
162 therefore, sometimes not able to provide a good explanation of data represented at  
163 coarser resolutions. This indicates that SDMs at both fine and coarse resolution do not  
164 explain the same species distribution pattern, as was discovered by Marcer et al. (2012)  
165 when studying vascular plants in Spain; the models at a fine resolution probably explain  
166 the habitat selection within the area favourable for species distribution, but they fail to  
167 discriminate between the areas that are favourable and unfavourable for the species.  
168 Despite the relevance of this topic in order to both fit the spatial resolution of SDM  
169 adequate to data and goals, and determine the limits for changing spatial resolution, the  
170 studies are scarce and, therefore, further research would be valuable in this area.

171

## 172 **Potential constraints as regards the model's transferability**

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

### 179 *Type of predictors and multicollinearity*

180 The choice of predictor variables for modelling affects the model's predictive  
181 performance (e.g. Synes & Osborne 2011) and, therefore, the SDM's transferability.  
182 Most of the abiotic predictors used for modelling explain animal distribution indirectly,  
183 through their correlation with ecological functional resources (Austin 2002; Guisan and  
184 Thuiller 2005; Austin et al. 2006). Extrapolations will be particularly error-prone if only  
185 indirect predictors are used, because the correlations between them and the functional  
186 resources vary in both space and time (Austin 2002). When these correlations depend



187 on area-specific conditions, models could be overfitted to the local conditions, which  
188 may compromise the model's transferability (Luoto et al. 2002) – in SDMs overfitting  
189 occurs when a model closely fits the calibration data and, thus, fails when predicting on  
190 independent data. The use of more ecologically relevant predictors is now increasingly  
191 possible as remotely sensed data are more readily available (e.g. Pettorelli et al. 2016).  
192 Remote sensing therefore provides data that can play a role in improving the  
193 performance of SDMs and, therefore, their transferability (e.g. He et al. 2015),  
194 especially spatial transferability and changes in spatial resolution, since remote sensing  
195 data are not available for different past, e.g. in an evolutionary context, or future  
196 temporal scenarios. Despite these advances, many studies appear to use only data that  
197 are readily available, while failing to explain the relevance of the predictors selected,  
198 and probably missing important ecological drivers.

199 When an SDM is extrapolated, the proper quantification of the effect of each predictor  
200 on current geographic ranges is a must for an accurate estimation of the potential for the  
201 species (Braunisch et al. 2013). But the effect of a factor can only be adequately  
202 estimated in the context of the other influential factors (e.g. Márquez et al. 2011). This  
203 signifies that the real effect of a factor on species distributions could be masked (under  
204 or overrated) by confounding correlated factors, becoming evident only when the effects  
205 of the other factors are subtracted from the weights of the predictors and subsequently  
206 from the predictions of the models (e.g. Lavergne et al. 2005; Real et al. 2013; Record  
207 et al. 2013). One of the main challenges in this respect is to filter out (control for) the  
208 variation caused by spatial structures (Griffith and Peres-Neto 2006; Dormann et al.  
209 2007; Hawkins et al. 2007), since the spatial structure in species distribution and  
210 environmental processes can increase type I errors and can potentially affect model  
211 estimations (e.g. Legendre et al. 2002). Briefly, the solution is again to produce  
212 combined models in which both environmental and spatial gradients should be  
213 considered (for details, see Peres-Neto and Legendre 2010). For instance, Real et al.  
214 (2013) estimated the pure climatic effect (i.e. not affected by covariation with non-  
215 climatic factors) and the apparent climatic effect (i.e. including shared effects between  
216 climate and non-climatic factors) on species distribution, and suggested that both the  
217 pure and apparent fractions could be interpreted as the lower and upper bounds of a  
218 range of possible scenarios for the future climatic potential for the species.

219 *Model complexity*

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

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

235 The complexity associated to the algorithm is, in this case, characterised as the shape of  
236 the inferred occurrence–environment relationships that are closely related to the number  
237 of parameters. Briefly, environmental envelopes (e.g. BIOCLIM or DOMAIN) and  
238 distance-based approaches in multivariate environmental spaces (e.g. ENFA,  
239 Malahanobis) are considered to be the simplest SDMs. Their response curves are simple  
240 functions with a reduced number of parameters (e.g. linear, hinge or step; Hirzel et al.  
241 2002; Elith et al. 2005). Generalised linear models (GLM), which are typically fitted  
242 with linear or polynomial features up to second order terms (rarely third or fourth order)  
243 for SDMs, are considered to be simple even when they admit more complexity.  
244 However, this relative simplicity applies to the relationship between probability, which  
245 is the output of the model, and the logit function, whereas the relationship between  
246 probability and individual variables tends to be more complex owing to the collinearity  
247 between predictors (Acevedo and Real 2012). GARP and MAXENT are considered to  
248 be complex algorithms since they allow high flexibility (Stockwell and Peters 1999;  
249 Phillips et al. 2006). Generalised additive models (GAM) are also complex techniques  
250 because they allow non-parametric smooth functions of variable flexibility (Hastie and

251 Tibshirani 1990). Decision trees (Breimann et al. 1984) can also become quite complex  
252 because they may use a large number of step functions (each requiring a parameter) and  
253 can implicitly include high order interaction terms with which to depict response curves  
254 of arbitrary complexity. In addition to the analytical protocols involving the use of a  
255 single modelling technique, "ensemble models" in which predictions from several  
256 techniques are considered, such as BIOMOD (Thuiller et al. 2009), are also frequently  
257 used. Different modelling techniques can achieve variable performance in the data-  
258 training set, even when they are calibrated with the same data (e.g. Segurado and Araújo  
259 2004; Benito de Pando and Peñas de Giles 2007; Mateo et al. 2011). The capability of  
260 the different techniques to be transferred is consequently also widely variable (e.g.  
261 Peterson et al. 2007). In addition, only models that produce commensurate outcomes,  
262 such as probability or favourability (see Acevedo & Real 2012), can be adequately  
263 combined in ensemble models, whereas models yielding suitability values that are  
264 idiosyncratic for each modelling technique lack the commensurability required for  
265 combination (Romero et al. 2016). However, the ensemble models does not necessarily  
266 control or fix biases and/or improve transferability (see e.g. Rodríguez-Rey et al. 2013).

267 Several studies were performed to assess the relationship between model complexity  
268 and predictive performance, both on the training and transference area. For instance,  
269 Tsoar et al. (2007) compared the performance of six algorithms and concluded that  
270 flexible algorithms attain a higher predictive performance in the training data set than  
271 do non-flexible ones. This result resembles the insight provided by Elith et al. (2006),  
272 who also concluded that those which are able to fit complex responses are preferable to  
273 simple algorithms. However, complex algorithms are not preferred when the models  
274 should be transferred to new scenarios, because flexible algorithms tend to overfit to  
275 local conditions, thus losing generality (Jimenez-Valverde et al. 2008). A good  
276 transferability has been suggested for algorithms such as GLM and GAM (e.g. Austin et  
277 al. 2006; Meynard and Quinn 2007; Wenger and Olden 2012). Randin et al. (2006)  
278 reported that GLM was more robust than GAM, suggesting that overfitting can reduce  
279 the transferability of GAM models. With regard to GARP and MAXENT, two  
280 techniques based on data of presence, Peterson et al. (2007) compared these techniques  
281 and found the latter to be overfitted. However, if the sample size is small, it can  
282 extrapolate better than GARP (Papes and Gaubert 2007). Other techniques have proved  
283 to have worse predictive power and accuracy, such as GARP, Random Forest and

284 MARS (e.g. Prasad et al. 2006). Determining the most appropriate amount of  
285 complexity to be included in SDMs is therefore crucial for biological applications  
286 (Merrow et al. 2014). Researchers must constrain model complexity on the basis of data  
287 attributes and study objectives, and an understanding of how they interact with the  
288 underlying biological processes.

289

### 290 *Species intrinsic traits*

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

312

### 313 **Checking the model's transferability: analytical protocol**

314 Before transferring an SDM beyond the data-training set, three fundamental  
315 requirements should be checked (see Figure 1):

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

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

339 iii) High levels of multicollinearity between the predictors included in a model can bias  
340 predictions when the model is transferred to a situation in which the correlation matrix  
341 between predictors is different. Collinearity can be quantified using the variance  
342 inflation factor (VIF), which should be calculated for each of the predictors in the model  
343 (see Zuur et al. 2010). There are more ways in which to detect collinearity, such as by  
344 examining the matrix of correlation coefficients between predictors in order to avoid  
345 including those that are highly correlated ( $r > |0.8|$ ) in the model. However,

346 multicollinearity is a real phenomenon in nature, and it cannot therefore be avoided in  
347 all cases, although it should be managed. When possible, the best ways in which to  
348 manage multicollinearity are by increasing the sample size by including external  
349 information and by removing highly correlated variables (e.g. Doran 1989). The  
350 maintenance of the correlation structure among predictors between training and  
351 transference areas should be assessed. As the coefficient for a predictor in a model  
352 depends on the coefficients for the other predictors (Fox 1997), changes in the  
353 correlation structure may include severe bias in models' predictions in the transference  
354 area. A Mantel test (Mantel 1967), or another similar means to determine the  
355 association between matrices (see Guillot and Rousset 2013), should therefore be  
356 carried out in order to avoid biased results.

357 In summary, various methodological requirements should be taken into account before  
358 transferring a model to another spatial/temporal scenario. This means that if the  
359 objective is to transfer a model, special attention should be paid to the species-  
360 environment equilibrium and to the selection of predictors. What is more, a calibrated  
361 model cannot be transferred just anywhere, but only to those scenarios that are  
362 environmentally similar to the scenario in which the model was calibrated. Despite the  
363 importance of transferring distribution models, studies designed to explore this feature  
364 and to assess the methodological and ecological factors which determine it are still  
365 scarce (e.g. Dobrowski et al. 2011). This is a line of interesting and timely research,  
366 given the high number of models that have been published in recent years (Lobo et al.  
367 2010).

368

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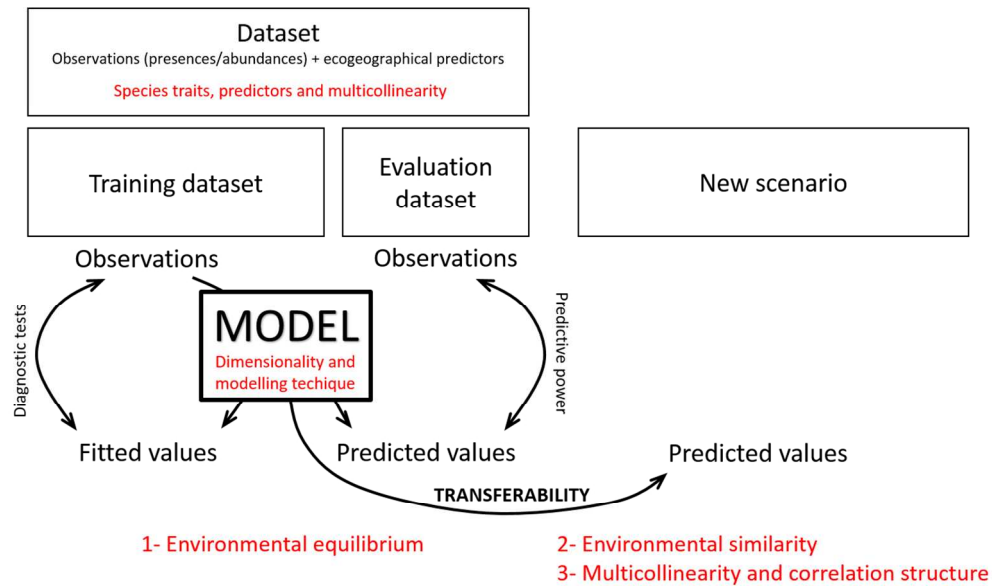
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738 Figure 1. Overview of the model building process when the dataset is split into two  
739 parts, one with which to fit and another with which to evaluate the model. The  
740 transferability of the model to a new scenario is also schematised. In each step, the main  
741 factors that can compromise the model's transferability are highlighted in red, along  
742 with the three (1-3) fundamental requirements that should be checked before the  
743 transference of the model to the new scenario (see text for details).

Draft



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).

Figure 1

368x219mm (96 x 96 DPI)