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Scale mismatches between predictor and response variables in species distribution modelling: A review of practices for appropriate grain selection

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1 **Title:** Scale mismatches between predictor and response variables in species distribution modelling:
2 a review of practices for appropriate grain selection

3

4 **Abstract**

5 There is a lack of guidance on the choice of the spatial grain of predictor and response variables in species
6 distribution models (SDM). This review summarises the current state of the art with regard to the following
7 points: (i) the effects of changing the resolution of predictor and response variables on model performance;
8 (ii) the effect of conducting multi-grain vs single-grain analysis on model performance; and (iii) the role of
9 land cover type and spatial autocorrelation in selecting the appropriate grain size. In the reviewed literature,
10 we found that coarsening the resolution of the response variable typically leads to declining model
11 performance. Therefore, we recommend aiming for finer resolutions unless there is a reason to do otherwise
12 (e.g., expert knowledge of the ecological scale). We also found that so far, the improvements in model
13 performance reported for multi-grain models have been relatively low and that useful predictions can be
14 generated even from single-scale models. In addition, the use of high-resolution predictors improves model
15 performance; however, there is only limited evidence on whether this applies to models with coarser-
16 resolution response variables (e.g. 100 km² and coarser). Low-resolution predictors are usually sufficient for
17 species associated with fairly common environmental conditions but not for species associated with less
18 common ones (e.g., common vs rare land cover category). This is because coarsening the resolution reduces
19 variability within heterogeneous predictors and leads to underrepresentation of rare environments, which can
20 lead to a decrease in model performance. Thus, assessing the spatial autocorrelation of the predictors at
21 multiple grains can provide insights into the impacts of coarsening their resolution on model performance.
22 Overall, we observed a lack of studies examining the simultaneous manipulation of the resolution of predictor
23 and response variables. We stress the need to explicitly report the resolution of all predictor and response
24 variables.

25

26

27 **Keywords:** Environmental niche modelling, Grain, Land cover, Predictor, Resolution, Scale, SDM, Variable

29 **1. Introduction**

30 Species distribution models (SDMs) are widely used to assess species–environment relationships and to make
31 predictions of species distributions in both space and time (Elith and Leathwick, 2009; Ferrier et al., 2017;
32 Wiersma et al., 2011). To this end, SDMs relate a biodiversity-related response variable (e.g., the geographic
33 distribution of one or more species) to explanatory variables (i.e., predictors, covariates, or features). The
34 strength of these relationships infere species’ niches, and can be used to predict a species’ occurrence in
35 unsurveyed locations. Although SDMs are a fundamental tool for answering many ecological, evolutionary,
36 and conservation-related questions, some methodological issues remain unresolved (Araújo et al., 2019;
37 Moudrý et al., 2017; Rocchini et al., 2011; Santini et al., 2021).

38 One such issue is the choice of *spatial resolution*, or *grain*, of the input data (Dungan et al., 2002). It has been
39 hypothesized that organisms respond to their environment more strongly at some grains than at others; these
40 grains have been referred to as ‘ecological scales’ (Lecours et al., 2015), ‘characteristic scales’ (Holland et al.,
41 2004), ‘intrinsic scales’ (Wu and Li, 2006) and ‘response grains’ (Mertes and Jetz, 2018). This concept
42 implies that for every species, there are one or more grains that best capture the scales at which organisms
43 most strongly respond to specific environmental variables. For example, it is assumed that climate constrains
44 species distributions at broader spatial scales (e.g., at the extent of a whole continent, with phenomena that
45 can be measured at a coarse resolution like $> 100 \text{ km}^2$). At successively finer resolutions and over smaller
46 geographic extents, topography or biotic interactions may be the dominant variables in controlling species
47 distribution, whereas at even finer resolutions, microclimate, vegetation structure, or the presence of
48 individual land cover categories such as water bodies might drive local species distribution (Austin and Van
49 Niel, 2011; Field et al., 2009; Pearson and Dawson, 2003; Wiens, 1989). However, previous studies have
50 suggested that some of the abovementioned variables may shape species distribution across multiple grains
51 (e.g., Alexander et al., 2015; Bütikofer et al., 2020; Wisz et al., 2013). Consequently, the choice of grain
52 adopted in models can strongly influence our ability to detect and measure species’ response to the
53 environment (de Knegt et al., 2010; Huston, 2002; Levin, 1992; Soberón, 2007; Cord et al. 2014).

54 Ideally, both species occurrence data and predictor variables are available at relatively fine resolutions,
55 allowing the researchers to coarsen the resolutions iteratively to find the best match between the predictor and
56 response variables. While the response data should preferably be available at resolutions at which the species
57 are expected to respond to the environment, predictor variables should be detailed enough to allow
58 distinguishing important features of the environment that are hypothesized to affect species distribution (e.g.,
59 a certain habitat type or specific microclimatic conditions). However, this is not always the case due to
60 limitations in data availability. Usually, the original spatial resolution of different datasets that need to be
61 integrated for modelling purposes varies significantly, and thus finding an optimal match remains a significant
62 challenge.

63 It is a common practice to modify the resolution of the input data so that it matches the resolution at which the
64 study is intended, for example, by averaging environmental variables within field plots. Both continuous (e.g.,
65 bioclimatic variables, terrain characteristics such as slope) and categorical (e.g., land cover) predictors are
66 often aggregated or resampled to match the resolution of the response variable ([Grohmann, 2015](#); [Moudrý et al., 2019](#)). While not commonly implemented, an alternative approach consists of retaining the discrepancy
67 between the grain sizes of the response and predictor variables through hierarchical modelling. This allows
68 modelling species distribution using fine-grain species data and coarse-grain environmental data ([McInerney
69 and Purves, 2011](#)), coarse-grain species data using fine-grain environmental data ([Keil et al., 2013, 2014](#)), or
70 modelling the grain-dependency of the species-environment relationships. The latter can be done using an
71 extra parameter in the model to quantify the relationship across a continuum of spatial scales ([Keil & Chase,
72 2019](#)).

74 Any end user should know how changing the spatial resolution of predictor and response variables can affect
75 SDM performance and which data characteristics play a role in how profound the effect of changing the
76 resolution will be. Therefore, here we review methodological issues related to the choice of the spatial
77 resolution of predictor and response variables in SDM. In particular, we focus on the following issues: (i) the
78 effects of changing the resolution of predictor and response variables on model performance, (ii) the effect of
79 conducting multi-grain vs single-grain analysis on model performance, and (iii) the role of land cover type
80 and spatial autocorrelation in the selection of appropriate grain sizes. Accordingly, we aim at providing
81 recommendations for the critical assessment of the input data.

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2. Effects of changing the resolution of predictor and response variables on model performance

Numerous studies examined the grain dependence of species-environment relationships (see the review by [Moudrý and Šímová, 2012](#)). Some authors coarsened the resolution of the response variable (section 2.1), others coarsened the resolution of predictor variables so that the resulting predictor was coarser than the response variable (section 2.2). Finally, in some studies the resolution of predictor variables was coarsened so that the resulting predictor was finer than the response variable (section 2.3). These three scenarios are shown in Figure 1. The distinction between these three approaches is often not made in the respective studies, and the effect of changing any resolution can be mistakenly understood as a single problem. We found no studies manipulating the resolution of predictors from finer to coarser resolution compared to the response variable, nor did we find studies manipulating the resolution of both the predictors and the response simultaneously (but see [Tobalske, 2002](#)).

2.1 How the resolution of the response variable affects model performance

The availability of species data at a much coarser resolution than commonly used environmental variables (e.g., species occurrence locations only available aggregated at a municipal or county level; [Cheng et al., 2021](#); [Jetz et al., 2012](#)) can significantly limit our ability to model species-environment relationships. Studies using species data at such coarse resolutions are not uncommon, especially for less studied taxa. As examples of such data, we can name gridded atlases ([Jalas and Suominen, 1988](#); [Št'astný et al., 2021](#)), the resolutions of which can range from hundreds of meters to tens of kilometres. However, monitoring programs collecting atlas data are organizationally and financially demanding. The choice of grid resolution then becomes a trade-off between the level of detail and the feasibility of fieldwork. It is increasingly common to supplement

109 atlases with maps generated with SDMs (e.g., [Flousek et al., 2015](#); [Šťastný et al., 2021](#)). As field data may
110 nowadays be gathered with the knowledge that they will also be used for modelling, it is important to know
111 how the resolution of the response affects model performance.

112 In studies specifically examining the effect of grain size of the response variable on SDM performance,
113 response grain ranges from a few metres to hundreds of kilometres, depending on the predictors tested (Figure
114 1a; Table 1; see review by [Miguet et al., 2015](#)). These studies typically ask: at what scale(s) is the species
115 distribution most driven or constrained by specific environmental conditions? At finer resolutions, studies
116 typically concentrate on the role of landscape structure (composition and configuration) in driving species
117 distribution ([Heikkinen et al., 2007](#); [Holland et al., 2004](#); [Tobalske, 2002](#)). With coarser response grains,
118 studies often include (bio)climatic variables ([Chauvier et al., 2022](#); [Kaliontzopoulou et al., 2008](#); [Seo et al.,](#)
119 [2009](#)). Typically, such studies report declining model performance with the coarsening of the resolution of the
120 response variable ([Chauvier et al., 2022](#); [Gábor et al., 2022a](#); [Heikkinen et al., 2007](#); [Kaliontzopoulou et al.,](#)
121 [2008](#); [Seo et al., 2009](#); [Zarzo-Arias et al., 2022](#)), suggesting that modelling species at coarser resolutions is not
122 optimal. However, these studies typically focus on the general performance of the models and do not report
123 the effect of changing the response grain on the variables' importance, which may provide valuable insights
124 into which variables shape species distributions at individual grain sizes (but see [Chauvier et al., 2022](#);
125 [Hanberry, 2013](#)).

126 **2.2 How the resolution of the predictor variable (coarser than the** 127 **response variable) affects model performance?**

128 Instead of coarsening the resolution of the response variable, some studies have coarsened the resolution of
129 predictor variables, so that the resulting predictor is coarser than the response variable (Figure 1b; Table 2).
130 They came to different conclusions. [Ferrier and Watson \(1997\)](#) concluded that coarse environmental data lead
131 to poorer model performance. [Graf et al. \(2005\)](#) found that the predictive power was highest at resolutions of
132 about 1 and 2 km². In contrast, [Guisan et al. \(2007\)](#) and [Pradervand et al. \(2014\)](#) concluded that coarsening the
133 predictor variables' resolution did not substantially change model performance, meaning that refining the
134 resolution may not be sufficient to improve the models.

135

136 **2.3 How the resolution of the predictor variable (finer than the**
137 **response variable) affects model performance?**

138 Studies that manipulate the resolution of predictor variables, so that the resulting predictor was finer than the
139 response variable (Figure 1c; Table 3), are mostly concerned with the importance of fine-scale habitat features
140 for analyzing species-environment relationships (e.g., [Gottschalk et al., 2011](#); [Šímová et al., 2019](#)). They
141 combine response variables at a coarse resolution with predictor variables at a fine resolution. These studies
142 typically ask: do we need fine-resolution predictors to explain species distribution at a relatively coarse
143 resolution?

144 High-resolution predictor variables suitable for modelling at multiple levels of detail may not be readily
145 available for the particular study area, their acquisition may be prohibitively expensive (especially for studies
146 conducted over large extents), and their use may require excessive data processing and significantly increase
147 computational time ([Kissling et al. 2022](#); [Moudrý et al. 2022](#)). Hence, researchers face trade-offs between data
148 detail and availability, data processing, and analytical optimization. Several studies have examined the
149 importance of fine-grain habitat features for the analysis of species-environment relationships using a
150 relatively coarse-grained response variable (Figure 1c; Table 3). In this type of study, authors typically use
151 predictor variables of various origins, collected, for example, by remote sensing ([Leitão & Santos 2019](#)),
152 fieldwork, or crowd-sourcing ([Šímová et al., 2019](#); [Thomas et al., 2002](#); [Venier et al., 2004](#)). Others have
153 coarsened the grain of the original predictors to examine the grain dependency of species-environment
154 relationships (e.g. [Gottschalk et al., 2011](#)).

155 [Thomas et al. \(2002\)](#) found that field-collected fine-grain predictors and predictor variables derived from a 30
156 m digital elevation model lead to the same model performance at a 1 km resolution. [Seoane et al. \(2004\)](#)
157 found that models derived from land cover at a 250 m resolution are comparable to those based on the same
158 variables derived from satellite images at a 30 m resolution, in agreement with [Venier et al. \(2004\)](#).
159 Consequently, it is commonly assumed that coarse-resolution habitat predictors at continental (e.g., CORINE
160 Land cover; [Büttner et al., 2004](#)) or global (e.g., Global Consensus Land cover; [Tuanmu and Jetz, 2014](#))
161 geographic extents are sufficient for use in combination with coarse-resolution responses.

162 However, it is essential to know if a given spatial resolution of a predictor variable captures the details that are
163 important for explaining the distribution of the species of interest. [Gottschalk et al. \(2011\)](#) concluded that a
164 higher spatial resolution of predictors could be essential for accurate predictions. In addition, they attributed
165 the improvement in models using detailed land cover maps to the high level of detail in the species response
166 variable (2 km diameter around survey points). This contrasts with results by [Šímová et al. \(2019\)](#) that
167 demonstrated improvement in model performance when using high-resolution land cover data despite the
168 coarse resolution of species data (12 x 11.2 km). They showed that the area and perimeter of water bodies
169 derived from high-resolution land cover datasets (raster data at 30 m resolution) explain distributions of
170 waterbirds better than predictors derived from coarser 1 km data. In line with these findings, it has been
171 recently recommended to first coarsen the resolution of the predictors to match the resolution of the assumed
172 ecological scale before calculating prediction metrics (e.g., standard deviation, Shannon-Wiener diversity
173 index, or Rao's Q) at the resolution of a response variable ([Graham et al., 2019](#)). In this context, the recent
174 finding by [Gábor et al. \(2022b\)](#), who showed that in the case of species inhabiting rare habitats, using simple
175 binary predictors (i.e. presence/absence of the habitat) might be sufficient, is of particular interest.
176 In conclusion, coarse-resolution land cover or terrain predictors may lack details to capture potentially
177 suitable habitats such as wetlands or cliffs. Thus, using high-resolution data could benefit models utilizing
178 coarser-resolution species data (e.g. from gridded atlases). The question of whether the need for fine-scale
179 predictors is somehow related to the resolution of the response variable or whether it can be generalized
180 should be further explored for different taxa and sets of predictors.

181

182 **3. Single-grain versus multi-grain analysis**

183 Up to this point, we have neglected discussing the possibility of considering species-environment
184 relationships at multiple grains in a single model. Typically, experimental studies use a single grain for the
185 response variable. Therefore, they implicitly assume the existence of a common ecological scale for all
186 predictor variables. However, it has been shown that the ecological scale is variable-specific since species
187 often respond to different environmental variables at different spatial scales, and sometimes even respond
188 differently to a single environmental variable at multiple grains ([Leitão et al. 2010](#); [Lecours et al., 2020](#);

189 [Miguet et al., 2016](#); [Roilo et al. 2022](#)). However, despite theoretical concepts and extensive empirical
190 evidence that species respond to their environment at different spatial grains (e.g. [Bergman et al., 2012](#); [Graf](#)
191 [et al., 2005](#); [Holland et al., 2004](#); [Stuber and Fontaine, 2019](#); [Zweifel-Schielly et al., 2009](#)), the appropriate
192 approach to select the grain of response variable remains unclear ([Jackson and Fahrig, 2015](#); [Martin and](#)
193 [Fahrig, 2012](#); [Stuber and Gruber, 2020](#)). For example, [Mertes et al. \(2020\)](#) recognized two primary spatial
194 grains at which species typically respond to their environment: they denoted the term “occupancy grain” for
195 the grain equivalent to a species’ typical home range and the term “response grain” for the grain at which an
196 individual uses an environmental resource. They also developed an optimization procedure for their
197 identification. However, studies usually use grains of response variables coarser than the assumed occupancy
198 and response grain, and it is unclear how to incorporate occupancy and response grains in such studies (but
199 see [Graham et al., 2019](#)).

200

201 In theory, species distributions are driven by environmental variables at a range of scales ([Levin, 1992](#)), and
202 there is no single “correct” spatial grain at which to characterize species-environment associations ([Mitchell et](#)
203 [al., 2001](#); [Wiens, 1989](#)). Therefore, models using multiple grains should, in theory, outperform models that
204 assume a common ecological scale for all variables. However, scale-sensitive applications that aim to align
205 the grain of the response variable (or predictor variables; see [Graham et al., 2019](#)) with the ecological scale
206 are rare ([McGarigal et al., 2016](#)). In addition, studies have come up with different conclusions. Some have
207 suggested that the performance of models using multiple response variable grains is better than that of single-
208 grain models ([Mertes et al., 2020](#)), while others have not drawn similar conclusions ([Martin and Fahrig,](#)
209 [2012](#)). Of note is that the improvements reported for multi-grain models were often relatively low, in the order
210 of hundredths of the area under the receiver operating characteristic curve (AUC) values ([Boscolo and](#)
211 [Metzger, 2009](#); [Graf et al., 2005](#); [Kuhn et al., 2011](#); [Mateo Sánchez et al., 2014](#)). In other words, valuable
212 predictions can still be generated from models using a single arbitrarily selected scale. Hence, it remains
213 unclear whether the increased complexity caused by the use of multiple grains is beneficial, particularly in the
214 case of SDMs used for the projection of species distributions under future climate conditions, which are
215 generally uncertain (e.g. [Sinclair et al., 2010](#)).

216

217 **4. Land cover types and spatial autocorrelation**

218 In an early study on the effect of spatial resolution on the performance of species-habitat relationships, [Karl et al. \(2000\)](#) suggested that the effects of coarsening the resolution depend on the heterogeneity of the
219 environment. The difference in land cover types used in different analyses might, therefore, explain some
220 contrasting findings. For example, [Seoane et al. \(2004\)](#) and [Venier et al. \(2004\)](#) observed no improvement in
221 models when using finer-grain land cover data, while [Gottschalk et al. \(2011\)](#) and [Šímová et al. \(2019\)](#)
222 observed a significant improvement. Both [Seoane et al. \(2004\)](#) and [Venier et al. \(2004\)](#) used data on common
223 land cover types, such as the proportion of forests within mapping units. For homogeneous landscapes
224 displaying strong spatial autocorrelation (e.g., large blocks of forests), land cover information does not change
225 much when spatially aggregated to coarser resolutions. In contrast, [Šímová et al. \(2019\)](#) focused on water
226 bodies, a land cover category that can become virtually invisible at coarser resolutions; coarsening the
227 resolution often leads to a bias and underrepresentation of rare environments such as (especially linear) water
228 bodies in certain landscapes. Similarly, [Seoane et al. \(2004\)](#) observed considerable improvement in models for
229 riparian species when finer-resolutions predictors were used. This may be one of the reasons why [Tuanmu and](#)
230 [Jetz \(2014\)](#) found that the Global Consensus Land Cover that has a spatial resolution of 1 km²
231 (<https://www.earthenv.org/landcover>; see Table 2) performed worse for predicting aquatic species than
232 species inhabiting other environments. Similarly, [Cord et al. \(2014\)](#) showed for 30 tree species that SDM
233 performance was significantly positively correlated with the species-specific degree of association between
234 the focal species and different land cover types.

235
236
237 Environmental variables are typically spatially autocorrelated (i.e., values between two locations are more
238 similar the closer the locations are in space; [Legendre, 1993](#)). This spatial autocorrelation can be quantified
239 using an empirical variogram that can be used to calculate the characteristic distance within which spatial
240 autocorrelation operates (i.e., the ‘range’ of an empirical variogram). Recently, [Mertes and Jetz \(2018\)](#)
241 highlighted the importance of considering environmental autocorrelation for the ability of SDMs to estimate
242 species-environment associations. Similar results were obtained by [Kühn \(2006\)](#) for species richness. More
243 recently, [Smith and Santos \(2020\)](#) explored the effect of the resolution of predictor variables and their

244 autocorrelation on estimates of their importance. This body of literature shows that using coarser
245 environmental data in SDMs without consideration of the autocorrelation can mischaracterize species-
246 environment relationships (see [Miller, 2012](#), for review). This is particularly true for variables that vary
247 rapidly over space; i.e. heterogeneous landscapes characterized by spatial autocorrelation with relatively small
248 range values ([Mertes and Jetz, 2018](#)). Aggregating heterogeneous landscapes to a coarser resolution results in
249 the loss of a portion of that heterogeneity ([Graham et al., 2019](#); [Karl et al., 2000](#); [Mertes and Jetz, 2018](#)).
250 Lower autocorrelation means higher randomness; hence, very distinct values are aggregated together. In
251 contrast, if there is strong autocorrelation, aggregating over a larger area does not change the value much
252 because the values were similar even in the finer resolutions.

253 Importantly, the inherent spatial autocorrelation of both species occurrences and predictor variables can result
254 in models that may inadvertently capture the spatial structure rather than true functional relationships ([Bahn
255 and McGill, 2007](#)). Indeed, it has been shown that spatial autocorrelation can lead to SDMs with high
256 discrimination ability even when there is no relationship between species occurrence and environmental
257 variables ([Chapman, 2010](#); [Fourcade et al., 2018](#)) and that many SDMs, despite a good fit, are not
258 significantly better than null models ([Osborne et al., 2022](#)). Therefore, it is a question of whether the loss of
259 explanatory power accompanying the coarsening of the resolution is due to the use of an inappropriate scale
260 (e.g. due to the lack of detail of potentially suitable environmental conditions) or due to changes in the spatial
261 structure; hence, this loss of power should be further explored for different resolutions and predictors. In any
262 case, selecting a relevant set of environmental predictors based on the known ecology of the species of interest
263 is essential to ensure fitting SDMs with an appropriate ecological interpretation ([Fourcade et al., 2018](#)). In
264 addition, it is necessary to carefully inspect whether SDMs estimated from the observed data perform better
265 than those generated from the null occurrence distributions, for example by using the recently-developed
266 “fauxcurrence” R package ([Osborne et al., 2022](#)).

267

268 **5. The ratio between the resolution of response and predictor variables**

269 A recently proposed standard protocol ([Zurell et al., 2020](#)) recommends reporting information on data,
270 modelling techniques, validation, and underlying questions ([Araújo et al., 2019](#); [Michener and Jones, 2012](#);

271 [Rocchini and Neteler, 2012](#)). However, many studies still lack it (see [Feng et al., 2019](#) for a review). When
272 evaluating the effect of changing the resolution of predictor variables, it is also important to consider the
273 resolution of the response variable (i.e., species occurrences). The opposite is also true: when evaluating the
274 role of the resolution of the response variable, one should be aware of the resolution of predictor variables.
275 Although this may seem like a trivial recommendation, it remains infrequent that studies evaluating the effects
276 of changing resolutions discuss their results with respect to the ratio between the resolutions of the response
277 variable and predictor variables (but see [Moudrý and Šímová, 2012](#)). The ratio between the resolution of the
278 response and the resolution(s) of the predictor variables differs among studies and might be the reason for
279 reported contradicting results (Figure 1). For example, in studies evaluating the importance of finer-resolution
280 predictors to explain species distributions, response grains can differ considerably (Table 4). It can be
281 expected that for small ratios, coarsening of the resolution of predictor variables will have a minimal effect on
282 model performance (e.g. [Seoane et al. 2004](#); [Venier et al. 2004](#)), while for high ratios (indicating a high
283 difference between the resolutions of the response and predictor variables), considerable effects can be
284 expected due to the aggregation of highly different values (e.g. [Gottschalk et al. 2011](#); [Šímová et al. 2019](#)).
285 Practices could be improved by reporting the resolution of predictor variables as well as that of the response
286 variable.

287

288 **6. Conclusions**

289 Spatial scale is one of the most critical issues in ecology and associated disciplines ([Levin, 1992](#)). Species
290 respond to their environment at different scales, and processes controlling species distribution operate at
291 various spatial scales. Unsurprisingly, the studies we reviewed found various optimal resolutions, depending
292 on the species and ecosystems analyzed. Besides, most studies analyzing multiple species usually report only
293 a general trend in models' behaviour with respect to changing resolution, and there are always some models
294 that do not conform to the general pattern (e.g., [Guisan et al., 2007](#); [Pradervand et al., 2014](#)). Our review
295 highlights that within the typically used resolutions (0.01 – 100 km²) finer-resolution models generally
296 perform better. Besides, the use of coarse-resolution response variables has implications for the predicted
297 distribution range ([Kunin, 1998](#)). When the resolution of the response variable is too coarse, there is a risk of

298 overestimating the occupied area (Connor et al., 2018; Hu and Jiang, 2010; Lauzeral et al., 2013; Seo et al.,
299 2009). Moreover, Gábor et al. (2022a) recently showed that coarsening the resolution does not compensate for
300 positional error in species occurrence data. Therefore, we recommend basing the choice of the resolution of
301 the response variable on practical aspects, such as aiming for finer resolutions unless there is a reason to do
302 otherwise (e.g., expert knowledge of the ecological scale of the species under study).

303
304 Coarsening the resolution of predictor variables has been shown to negatively affect model performance as it
305 obscures fine-scale heterogeneity in environmental variables. Therefore, we recommend (1) using finer-
306 resolution environmental variables when modelling species associated with rare environmental entities (e.g., a
307 rare habitat type), even when using species occurrence data at a coarse resolution (Šimová et al., 2019). When
308 species are associated with widespread environmental conditions, using low-resolution predictors is likely
309 sufficient. However, we recommend (2) assessing spatial autocorrelation or thematic resolution of predictors
310 at multiple grains to estimate the potential impacts of coarsening their resolution on model performance (i.e.
311 to ensure that they preserve enough detail to distinguish environmental features that affect species distribution
312 at a given resolution). Thirdly, (3) studies may benefit from considering multiple grains of the response
313 variable within a single model, even though the improvements reported for multi-grain models have so far
314 been *relatively* low, and we recognize that useful predictions can still be generated from single-scale models.
315 Finally, (4) studies should explicitly report the resolutions of the predictor and response variables, following
316 the standard ODMAP protocol recently proposed by Zurell et al. (2020).

317

318 **7. References**

- 319 Alexander JM, Diez JM and Levine JM (2015) Novel competitors shape species' responses to climate change.
320 Nature 525(7570): 515–518. DOI: 10.1038/nature14952.
- 321 Araújo MB, Anderson RP, Márcia Barbosa A, et al. (2019) Standards for distribution models in biodiversity
322 assessments. Science Advances 5(1): eaat4858. DOI: 10.1126/sciadv.aat4858.
- 323 Austin MP, Van Niel KP (2011) Improving species distribution models for climate change studies: variable
324 selection and scale. Journal of biogeography 38(1):1-8. <https://doi.org/10.1111/j.1365-2699.2010.02416.x>

325 Bahn V and McGill BJ (2007) Can niche-based distribution models outperform spatial interpolation? *Global*
326 *Ecology and Biogeography* 16(6): 733–742. DOI: 10.1111/j.1466-8238.2007.00331.x.

327 Bergman K-O, Jansson N, Claesson K, et al. (2012) How much and at what scale? Multi-scale analyses as
328 decision support for conservation of saproxylic oak beetles. *Forest Ecology and Management* 265: 133–141.
329 DOI: 10.1016/j.foreco.2011.10.030.

330 Boscolo D and Metzger JP (2009) Is bird incidence in Atlantic forest fragments influenced by landscape
331 patterns at multiple scales? *Landscape Ecology* 24(7): 907–918. DOI: 10.1007/s10980-009-9370-8.

332 Bütikofer L, Anderson K, Bebbler DP, et al. (2020) The problem of scale in predicting biological responses to
333 climate. *Global Change Biology* 26(12): 6657–6666. DOI: 10.1111/gcb.15358.

334 Büttner G, Feranec J, Jaffrain G., et al. (2004) The CORINE land cover 2000 project. *EARSeL eProceedings*.
335 3: 331–346.

336 Chauvier Y, Descombes P, Guéguen M, et al. (2022) Resolution in species distribution models shapes spatial
337 patterns of plant multifaceted diversity. *Ecography*. DOI: 10.1111/ecog.05973.

338 Cheng Y, Tjaden NB, Jaeschke A, et al. (2021) Using centroids of spatial units in ecological niche modelling:
339 Effects on model performance in the context of environmental data grain size. *Global Ecology and*
340 *Biogeography* Peres-Neto P (ed.) 30(3): 611–621. DOI: 10.1111/geb.13240.

341 Connor T, Hull V, Viña A, et al. (2018) Effects of grain size and niche breadth on species distribution
342 modeling. *Ecography* 41(8): 1270–1282. DOI: 10.1111/ecog.03416.

343 Cord AF, Klein D, Mora F, Dech S (2014) Comparing the suitability of classified land cover data and remote
344 sensing variables for modeling distribution patterns of plants. *Ecological Modelling* 24(272):129-40.

345 Corsi F, De Leeuw J and Skidmore AK (2000) Modelling species distribution with GIS. *Research techniques*
346 *in animal ecology; controversies and consequences* (Boitani L and Fuller TK, eds). Columbia University
347 Press, New York, USA.

348 de Knecht HJ, van Langevelde F, Coughenour MB, et al. (2010) Spatial autocorrelation and the scaling of
349 species–environment relationships. *Ecology* 91(8): 2455–2465. DOI: 10.1890/09-1359.1.

350 Dungan JL, Perry JN, Dale MRT, et al. (2002) A balanced view of scale in spatial statistical analysis.
351 *Ecography* 25(5): 626–640. DOI: 10.1034/j.1600-0587.2002.250510.x.

352 Elith J, Leathwick JR (2009) Species distribution models: ecological explanation and prediction across space
353 and time. *Annual Review of Ecology, Evolution and Systematics* 40(1): 677-97.

354 Feng X, Park DS, Walker C, et al. (2019) A checklist for maximizing reproducibility of ecological niche
355 models. *Nature Ecology & Evolution* 3(10): 1382–1395. DOI: 10.1038/s41559-019-0972-5.

356 Ferrier S and Watson G (1997) An Evaluation of the Effectiveness of Environmental Surrogates and
357 Modelling Techniques in Predicting the Distribution of Biological Diversity. Environment Australia.

358 Ferrier S, Jetz W and Scharlemann, J (2017) Biodiversity modelling as part of an observation system. In *The*
359 *GEO handbook on biodiversity observation networks*. (239-257). Springer, Cham.

360 Field R, Hawkins BA, Cornell HV, et al. (2009) Spatial species-richness gradients across scales: a meta-
361 analysis. *Journal of Biogeography* 36(1): 132–147. DOI: 10.1111/j.1365-2699.2008.01963.x

362 Flousek J, Gramsz B and Telenský T (2015). Ptáci Krkonoš – atlas hnízdního rozšíření 2012–2014 / Ptáci
363 Karkonoszy – atlas ptaków lęgowych 2012–2014. Správa KRNAP Vrchlabí, Dyrekcja KPN Jelenia Góra: 480.
364 <http://ptacikrkonos.krnep.cz/files/PTACI-KRKONOS.pdf>

365 Fourcade Y, Besnard AG and Secondi J (2018) Paintings predict the distribution of species, or the challenge
366 of selecting environmental predictors and evaluation statistics. *Global Ecology and Biogeography* 27(2): 245–
367 256. DOI: 10.1111/geb.12684

368 Gábor L, Jetz W, Lu M, et al. (2022a) Positional errors in species distribution modelling are not overcome by
369 the coarser grains of analysis. *Methods in Ecology and Evolution*: 2041–210X.13956. DOI: 10.1111/2041-
370 210X.13956.

371 Gábor L, Šímová P, Keil P, et al. (2022b) Habitats as predictors in species distribution models: Shall we use
372 continuous or binary data? *Ecography* 2022(7). DOI: 10.1111/ecog.06022.

373 Gottschalk TK, Aue B, Hotes S, et al. (2011) Influence of grain size on species–habitat models. *Ecological*
374 *Modelling* 222(18): 3403–3412. DOI: 10.1016/j.ecolmodel.2011.07.008.

375 Graf RF, Bollmann K, Suter W, et al. (2005) The Importance of Spatial Scale in Habitat Models: Capercaillie
376 in the Swiss Alps. *Landscape Ecology* 20(6): 703–717. DOI: 10.1007/s10980-005-0063-7.

377

378 Graham LJ, Spake R, Gillings S, et al. (2019) Incorporating fine-scale environmental heterogeneity into
379 broad-extent models. *Methods in Ecology and Evolution* Isaac N (ed.) 10(6): 767–778. DOI: 10.1111/2041-
380 210X.13177.

381 Grohmann CH (2015) Effects of spatial resolution on slope and aspect derivation for regional-scale analysis.
382 *Computers & Geosciences* 77. Elsevier: 111–117.

383 Guisan A, Graham CH, Elith J, et al. (2007) Sensitivity of predictive species distribution models to change in
384 grain size. *Diversity and Distributions* 13(3): 332–340. DOI: 10.1111/j.1472-4642.2007.00342.x.

385 Hanberry BB (2013) Finer grain size increases effects of error and changes influence of environmental
386 predictors on species distribution models. *Ecological Informatics* : 15: 8-13.

387 Heikkinen RK, Luoto M, Kuussaari M, et al. (2007) Modelling the spatial distribution of a threatened
388 butterfly: Impacts of scale and statistical technique. *Landscape and Urban Planning* 79(3–4): 347–357. DOI:
389 10.1016/j.landurbplan.2006.04.002.

390 Holland JD, Bert DG and Fahrig L (2004) Determining the Spatial Scale of Species' Response to Habitat.
391 *BioScience* 54(3): 227. DOI: 10.1641/0006-3568(2004)054[0227:DTSSOS]2.0.CO;2.

392 Hu J and Jiang Z (2010) Predicting the potential distribution of the endangered Przewalski's gazelle. *Journal*
393 *of Zoology* 282(1): 54–63. DOI: 10.1111/j.1469-7998.2010.00715.x.

394 Huston MA (2005) Introductory essay: critical issues for improving predictions. *Predicting species*
395 *occurrences: issues of accuracy and scale.* (ed. by J.M. Scott, P.J. Heglund, M.L. Morrison, J.B. Haufler, M.G.
396 Raphael, W.A. Wall and F.B. Samson), pp. 7– 21. Island Press, Covelo, CA.

397 Jackson HB and Fahrig L (2015) Are ecologists conducting research at the optimal scale?: Is research
398 conducted at optimal scales? *Global Ecology and Biogeography* 24(1): 52–63. DOI: 10.1111/geb.12233.

399 Jalas J and Suominen J (Eds.) (1988) *Atlas Florae Europaeae: volume 3: distribution of vascular plants in*
400 *Europe (Vol. 3).* Cambridge University Press.

401 Jetz W, McPherson JM and Guralnick RP (2012) Integrating biodiversity distribution knowledge: toward a
402 global map of life. *Trends in Ecology & Evolution* 27(3): 151–159. DOI: 10.1016/j.tree.2011.09.007.

403 Kaliontzopoulou A, Brito JC, Carretero MA, et al. (2008) Modelling the partially unknown distribution of
404 wall lizards (*Podarcis*) in North Africa: ecological affinities, potential areas of occurrence, and methodological
405 constraints. *Canadian Journal of Zoology* 86(9): 992–1001. DOI: 10.1139/Z08-078.

406 Karl JW, Heglund PJ, Garton EO, et al. (2000) SENSITIVITY OF SPECIES HABITAT-RELATIONSHIP
407 MODEL PERFORMANCE TO FACTORS OF SCALE. *Ecological Applications* 10(6): 1690–1705. DOI:
408 10.1890/1051-0761(2000)010[1690:SOSHRM]2.0.CO;2.

409 Keil P and Chase JM (2019) Global patterns and drivers of tree diversity integrated across a continuum of
410 spatial grains. *Nature Ecology & Evolution* 3(3): 390–399. DOI: 10.1038/s41559-019-0799-0.

411 Keil P, Belmaker J, Wilson AM, et al. (2013) Downscaling of species distribution models: a hierarchical
412 approach. *Methods in Ecology and Evolution* Freckleton R (ed.) 4(1): 82–94. DOI: 10.1111/j.2041-
413 210x.2012.00264.x.

414 Keil P, Wilson AM and Jetz W (2014) Uncertainty, priors, autocorrelation and disparate data in downscaling
415 of species distributions. *Diversity and Distributions* Brotons L (ed.) 20(7): 797–812. DOI: 10.1111/ddi.12199.

416 Kissling WD, Shi Y, Koma Z, Meijer C, Ku O, Nattino F, Seijmonsbergen AC, Grootes MW (2022) Country-
417 wide data of ecosystem structure from the third Dutch airborne laser scanning survey. *Data in Brief*:108798.
418 <https://doi.org/10.1016/j.dib.2022.108798>

419 Kuhn A, Copeland J, Cooley J, et al. (2011) Modeling Habitat Associations for the Common Loon (*Gavia*
420 *immer*) at Multiple Scales in Northeastern North America. *Avian Conservation and Ecology* 6(1): art4. DOI:
421 10.5751/ACE-00451-060104.

422 Kühn I (2006) Incorporating spatial autocorrelation may invert observed patterns. *Diversity & Distributions*
423 0(0): 061117052025001-??? DOI: 10.1111/j.1472-4642.2006.00293.x.

424 Kunin WE (1998) Extrapolating species abundance across spatial scales. *Science* 281(5382). *American*
425 *Association for the Advancement of Science*: 1513–1515.

426 Lauzeral C, Grenouillet G and Brosse S (2013) Spatial range shape drives the grain size effects in species
427 distribution models. *Ecography* 36(7): 778–787. DOI: 10.1111/j.1600-0587.2013.07696.x.

428 Lecours V, Devillers R, Schneider DC, et al. (2015) Spatial scale and geographic context in benthic habitat
429 mapping: review and future directions. *Marine Ecology Progress Series*, 535: 259-284.

430 Lecours V, Gábor L, Edinger E, et al. (2020) Fine-scale habitat characterization of The Gully, the Flemish
431 Cap, and the Orphan Knoll, Northwest Atlantic, with a focus on cold-water corals. In: *Seafloor*
432 *Geomorphology as Benthic Habitat*. Elsevier, pp. 735–751.

433 Legendre P (1993) Spatial autocorrelation: trouble or new paradigm? *Ecology* 74(6). Wiley Online Library:
434 1659–1673.

435 Leitao PJ, Moreira F, and Osborne PE (2010) Breeding habitat selection of steppe birds in Castro Verde: A
436 remote sensing and advanced statistics approach. *Ardeola*, 57, 93-116.

437 Leitão PJ, Santos MJ. Improving models of species ecological niches: a remote sensing overview. *Frontiers in*
438 *Ecology and Evolution*. 2019 Jan 29;7:9.

439 Levin SA (1992) The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture.
440 *Ecology* 73(6): 1943–1967. DOI: 10.2307/1941447.

441 Manzoor SA, Griffiths G and Lukac M (2018) Species distribution model transferability and model grain size
442 – finer may not always be better. *Scientific Reports* 8(1): 7168. DOI: 10.1038/s41598-018-25437-1.

443 Martin AE and Fahrig L (2012) Measuring and selecting scales of effect for landscape predictors in species–
444 habitat models. *Ecological Applications* 22(8): 2277–2292. DOI: 10.1890/11-2224.1.

445 Mateo Sánchez MC, Cushman SA and Saura S (2014) Scale dependence in habitat selection: the case of the
446 endangered brown bear (*Ursus arctos*) in the Cantabrian Range (NW Spain). *International Journal of*
447 *Geographical Information Science* 28(8): 1531–1546. DOI: 10.1080/13658816.2013.776684.

448 McGarigal K, Wan HY, Zeller KA, et al. (2016) Multi-scale habitat selection modeling: a review and outlook.
449 *Landscape Ecology* 31(6): 1161–1175. DOI: 10.1007/s10980-016-0374-x.

450 McNerny GJ and Purves DW (2011) Fine-scale environmental variation in species distribution modelling:
451 regression dilution, latent variables and neighbourly advice: Regression dilution in species distribution
452 models. *Methods in Ecology and Evolution* 2(3): 248–257. DOI: 10.1111/j.2041-210X.2010.00077.x.

453 Mertes K and Jetz W (2018) Disentangling scale dependencies in species environmental niches and
454 distributions. *Ecography* 41(10): 1604–1615. DOI: 10.1111/ecog.02871.

455 Mertes K, Jarzyna MA and Jetz W (2020) Hierarchical multi-grain models improve descriptions of species’
456 environmental associations, distribution, and abundance. *Ecological Applications* 30(6). DOI:
457 10.1002/eap.2117.

458 Michener WK and Jones MB (2012) Ecoinformatics: supporting ecology as a data-intensive science. *Trends*
459 *in Ecology & Evolution* 27(2): 85–93. DOI: 10.1016/j.tree.2011.11.016.

460 Miguet P, Jackson HB, Jackson ND, et al. (2016) What determines the spatial extent of landscape effects on
461 species? *Landscape Ecology* 31(6): 1177–1194. DOI: 10.1007/s10980-015-0314-1.

462 Miller JA (2012) Species distribution models: Spatial autocorrelation and non-stationarity. *Progress in*
463 *Physical Geography: Earth and Environment* 36(5): 681–692. DOI: 10.1177/0309133312442522.

464 Mitchell MS, Lancia RA, Gerwin JA (2001) Using landscape-level data to predict the distribution of birds on
465 a managed forest: effects of scale. *Ecological Applications*: 11(6):1692-708.

466 Moudrý V and Šímová P (2012) Influence of positional accuracy, sample size and scale on modelling species
467 distributions: a review. *International Journal of Geographical Information Science* 26(11): 2083–2095. DOI:
468 10.1080/13658816.2012.721553.

469 Moudrý V, Komárek J and Šímová P (2017) Which breeding bird categories should we use in models of
470 species distribution? *Ecological Indicators* 74: 526–529. DOI: 10.1016/j.ecolind.2016.11.006.

471 Moudrý V, Lecours V, Malavasi M, et al. (2019) Potential pitfalls in rescaling digital terrain model-derived
472 attributes for ecological studies. *Ecological Informatics* 54: 100987. DOI: 10.1016/j.ecoinf.2019.100987.

473 Moudrý V, Cord AF, Gábor L, Laurin GV, Barták V, Gdulová K, Malavasi M, Rocchini D, Stereńczak K,
474 Prošek J, Klápště P (2022) Vegetation structure derived from airborne laser scanning to assess species
475 distribution and habitat suitability: The way forward. *Diversity and Distributions*.
476 <https://doi.org/10.1111/ddi.13644>

477 Osborne OG, Fell HG, Atkins H, et al. (2022) Fauxcurrence: simulating multi-species occurrences for null
478 models in species distribution modelling and biogeography. *Ecography* 2022(7). DOI: 10.1111/ecog.05880.

479 Pearson RG and Dawson TP (2003) Predicting the impacts of climate change on the distribution of species:
480 are bioclimate envelope models useful?: Evaluating bioclimate envelope models. *Global Ecology and*
481 *Biogeography* 12(5): 361–371. DOI: 10.1046/j.1466-822X.2003.00042.x.

482 Pradervand J-N, Dubuis A, Pellissier L, et al. (2014) Very high resolution environmental predictors in species
483 distribution models: Moving beyond topography? *Progress in Physical Geography: Earth and Environment*
484 38(1): 79–96. DOI: 10.1177/0309133313512667.

485 Rengstorf AM, Grehan A, Yesson C, et al. (2012) Towards High-Resolution Habitat Suitability Modeling of
486 Vulnerable Marine Ecosystems in the Deep-Sea: Resolving Terrain Attribute Dependencies. *Marine Geodesy*
487 35(4): 343–361. DOI: 10.1080/01490419.2012.699020.

488 Rocchini D and Neteler MG (2012) Let the four freedoms paradigm apply to ecology. GB.

489 Rocchini D, Hortal J, Lengyel S, et al. (2011) Accounting for uncertainty when mapping species distributions:
490 The need for maps of ignorance. *Progress in Physical Geography: Earth and Environment* 35(2): 211–226.
491 DOI: 10.1177/0309133311399491.

492 Roilo S, Engler JO, Václavík T, Cord AF (2022) Landscape-level heterogeneity of agri-environment measures
493 improves habitat suitability for farmland birds. *Ecological Applications*. Aug 6:e2720.

494 Santini L, Benítez-López A, Maiorano L, et al. (2021) Assessing the reliability of species distribution
495 projections in climate change research. *Diversity and Distributions* Fourcade Y (ed.) 27(6): 1035–1050. DOI:
496 10.1111/ddi.13252.

497 Seo C, Thorne JH, Hannah L, et al. (2009) Scale effects in species distribution models: implications for
498 conservation planning under climate change. *Biology letters* 5(1). The Royal Society London: 39–43.

499 Seoane J, Bustamante J and Díaz-Delgado R (2004) Are existing vegetation maps adequate to predict bird
500 distributions? *Ecological Modelling* 175(2): 137–149. DOI: 10.1016/j.ecolmodel.2003.10.011.

501 Sillero N and Barbosa AM (2021) Common mistakes in ecological niche models. *International Journal of*
502 *Geographical Information Science* 35(2): 213–226. DOI: 10.1080/13658816.2020.1798968.

503 Šímová P, Moudrý V, Komárek J, et al. (2019) Fine scale waterbody data improve prediction of waterbird
504 occurrence despite coarse species data. *Ecography* 42(3): 511–520. DOI: 10.1111/ecog.03724.

505 Sinclair SJ, White MD and Newell GR (2010) How useful are species distribution models for managing
506 biodiversity under future climates? *Ecology and Society* 15(1). JSTOR.

507 Smith AB and Santos MJ (2020) Testing the ability of species distribution models to infer variable
508 importance. *Ecography* 43(12): 1801–1813. DOI: 10.1111/ecog.05317.

509 Soberón, J. (2007) Grinnellian and Eltonian niches and geographic distributions of species. *Ecology letters*,
510 10(12), 1115-1123. <https://doi.org/10.1111/j.1461-0248.2007.01107.x>

511 Št'astný K, Bejček V, Mikuláš I. and Telenský T (2021) Atlas Hnízdního Rozšíření Ptáků v České Republice
512 2014-2017 (Aventinum, 2021)

513 Stockwell DRB and Peterson AT (2002) Controlling bias in biodiversity data. *Predicting species occurrences:*
514 *issues of accuracy and scale*. Edited by JM Scott, PJ Heglund, F. Samson, J. Haufler, M. Morrison, M.
515 Raphael, and B. Wall. Island Press, Washington, DC, 537-546.

516 Stuber EF and Fontaine JJ (2019) How characteristic is the species characteristic selection scale? *Global*
517 *Ecology and Biogeography* Issac N (ed.) 28(12): 1839–1854. DOI: 10.1111/geb.12998.

518 Stuber EF and Gruber LF (2020) Recent Methodological Solutions to Identifying Scales of Effect in Multi-
519 scale Modeling. *Current Landscape Ecology Reports* 5(4): 127–139. DOI: 10.1007/s40823-020-00055-8.

520 Thomas K, Keeler-Wolf T and Franklin J (2002) A comparison of fine-and coarse-resolution environmental
521 variables toward predicting vegetation distribution in the Mojave desert. *Predicting species occurrences:*
522 *issues of accuracy and scale.* Edited by JM Scott, PJ Heglund, F Samson, J Haufler, M Morrison, M Raphael,
523 and B Wall. Island Press, Washington, DC, 133-139.

524 Tobalske C (2002) Effects of spatial scale on the predictive ability of habitat models for the green woodpecker
525 in Switzerland. *Predicting species occurrences: issues of accuracy and scale.* Edited by JM Scott, PJ Heglund,
526 F Samson, J Haufler, M Morrison, M Raphael, and B Wall. Island Press, Washington, DC, 197-204.

527 Tuanmu M-N and Jetz W (2014) A global 1-km consensus land-cover product for biodiversity and ecosystem
528 modelling: Consensus land cover. *Global Ecology and Biogeography* 23(9): 1031–1045. DOI:
529 10.1111/geb.12182.

530 Vale CG, Tarroso P and Brito JC (2014) Predicting species distribution at range margins: testing the effects of
531 study area extent, resolution and threshold selection in the Sahara-Sahel transition zone. *Diversity and*
532 *Distributions* Robertson M (ed.) 20(1): 20–33. DOI: 10.1111/ddi.12115.

533 Venier LA, Pearce J, McKee JE, et al. (2004) Climate and satellite-derived land cover for predicting breeding
534 bird distribution in the Great Lakes Basin: Climate and land cover for predicting bird distribution. *Journal of*
535 *Biogeography* 31(2): 315–331. DOI: 10.1046/j.0305-0270.2003.01014.x.

536 Wiens JA (1989) Spatial scaling in ecology. *Functional ecology.* 3: 385-397.

537 Wiersma YF, Huettmann F and Drew CA (2011) Introduction, landscape modeling of species and their
538 habitats: history, uncertainty, and complexity. In: Drew CA, Wiersma YF, Huettmann F (Eds.), *Predictive*
539 *Species and Habitat Modeling in Landscape Ecology.* Springer, New York, pp. 1–6.

540 Wisz MS, Pottier J, Kissling WD, et al. (2013) The role of biotic interactions in shaping distributions and
541 realised assemblages of species: implications for species distribution modelling. *Biological Reviews* 88(1):
542 15–30. DOI: 10.1111/j.1469-185X.2012.00235.x.

543 Wu J and Li H (2006) Concepts of scale and scaling. In: Jianguo Wu, Jones KB, Li H, Louck OL (eds)
544 Scaling and uncertainty analysis in ecology: methods and applications. Springer, Dordrecht, Netherlands, pp
545 3–15

546 Zarzo-Arias A, Penteriani V, Gábor L, Šímová P, Grattarola F, Moudrý V (2022) Importance of data selection
547 and filtering in species distribution models: a case study on the Cantabrian Brown bear. *Ecosphere*.

548 Zurell D, Franklin J, König C, et al. (2020) A standard protocol for reporting species distribution models.
549 *Ecography* 43(9): 1261–1277. DOI: 10.1111/ecog.04960.

550 Zweifel-Schielly B, Kreuzer M, Ewald KC, et al. (2009) Habitat selection by an Alpine ungulate: the
551 significance of forage characteristics varies with scale and season. *Ecography* 32(1): 103–113. DOI:
552 10.1111/j.1600-0587.2008.05178.x.

