Progress in Physical Geography
2023, Vol. 0(0) 1–16

DOI: 10.1177/03091333231156362
journals.sagepub.com/home/ppg
SAGE

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

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Abstract
There is a lack of guidance on the choice of the spatial grain of predictor and response variables in species distribution models (SDM). This review summarizes the current state of the art with regard to the following points: (i) the effects of changing the resolution of predictor and response variables on model performance; (ii) the effect of conducting multi-grain versus single-grain analysis on model performance; and (iii) the role of land cover type and spatial autocorrelation in selecting the appropriate grain size. In the reviewed literature, we found that coarsening the resolution of the response variable typically leads to declining model performance. Therefore, we recommend aiming for finer resolutions unless there is a reason to do otherwise (e.g. expert knowledge of the ecological scale). We also found that so far, the improvements in model performance reported for multi-grain models have been relatively low and that useful predictions can be

generated even from single-scale models. In addition, the use of high-resolution predictors improves model performance; however, there is only limited evidence on whether this applies to models with coarser-resolution response variables (e.g. 100 km^2 and coarser). Low-resolution predictors are usually sufficient for species associated with fairly common environmental conditions but not for species associated with less common ones (e.g. common vs rare land cover category). This is because coarsening the resolution reduces variability within heterogeneous predictors and leads to underrepresentation of rare environments, which can lead to a decrease in model performance. Thus, assessing the spatial autocorrelation of the predictors at multiple grains can provide insights into the impacts of coarsening their resolution on model performance. Overall, we observed a lack of studies examining the simultaneous manipulation of the resolution of predictor and response variables. We stress the need to explicitly report the resolution of all predictor and response variables.

Keywords
Environmental niche modelling, grain, land cover, predictor, resolution, scale, SDM, variable

Introduction

Species distribution models (SDMs) are widely used to assess species–environment relationships and to make predictions of species distributions in both space and time (Elith and Leathwick, 2009; Ferrier et al., 2017; Wiersma et al., 2011). To this end, SDMs relate a biodiversity-related response variable (e.g. the geographic distribution of one or more species) to explanatory variables (i.e. predictors, covariates, or features). The strength of these relationships infere species' niches and can be used to predict a species' occurrence in unsurveyed locations. Although SDMs are a fundamental tool for answering many ecological, evolutionary, and conservation-related questions, some methodological issues remain unresolved (Araújo et al., 2019; Gábor et al., 2020; Moudrý et al., 2017; Rocchini et al., 2011; Santini et al., 2021).

One such issue is the choice of *spatial resolution*, or *grain*, of the input data (Dungan et al., 2002). It has been hypothesized that organisms respond to their environment more strongly at some grains than at others; these grains have been referred to as 'ecological scales' (Lecours et al., 2015), 'characteristic scales' (Holland et al., 2004), 'intrinsic scales' (Wu and Li, 2006), and 'response grains' (Mertes and Jetz, 2018). This concept implies that for every species, there are one or more grains that best capture the scales at which organisms most strongly respond to specific environmental variables. For example, it is assumed that climate constrains species distributions at broader spatial scales (e.g. at the extent of a whole continent, with phenomena that can be measured at a coarse resolution like >100 km^2). At successively finer resolutions and over smaller geographic extents, topography or biotic interactions may be the dominant variables in controlling species distribution, whereas at even finer resolutions, microclimate, vegetation structure, or the presence of individual land cover categories such as water bodies might drive local species distribution (Austin and Van Niel, 2011; Field et al., 2009; Pearson and Dawson, 2003; Wiens, 1989). However, previous studies have suggested that some of the above-mentioned variables may shape species distribution across multiple grains (e.g. Alexander et al., 2015; Bütikofer et al., 2020; Wisz et al., 2013). Consequently, the choice of grain adopted in models can strongly influence our ability to detect and measure species' response to the environment (De Knegt et al., 2010; Huston, 2005; Levin, 1992; Soberón, 2007; Cord et al., 2014; Riva et al., 2023).

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

It is a common practice to modify the resolution of the input data so that it matches the resolution at which the study is intended, for example, by averaging environmental variables within field plots. Both continuous (e.g. bioclimatic variables, terrain characteristics such as slope) and categorical (e.g. land cover) predictors are 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 between the grain sizes of the response and predictor variables through hierarchical modelling. This allows modelling species distribution using fine-grain species data and coarse-grain environmental data (McInerny and Purves, 2011), coarse-grain species data using fine-grain environmental data (Keil et al., 2013, 2014), or modelling the grain-dependency of the species–environment relationships. The latter can be done using an extra parameter in the model to quantify the relationship across a continuum of spatial scales (Keil and Chase, 2019).

Any end user should know how changing the spatial resolution of predictor and response variables can affect SDM performance and which data characteristics play a role in how profound the effect of changing the resolution will be. Therefore, here we review methodological issues related to the choice of the spatial resolution of predictor and response variables in SDM. In particular, we focus on the following

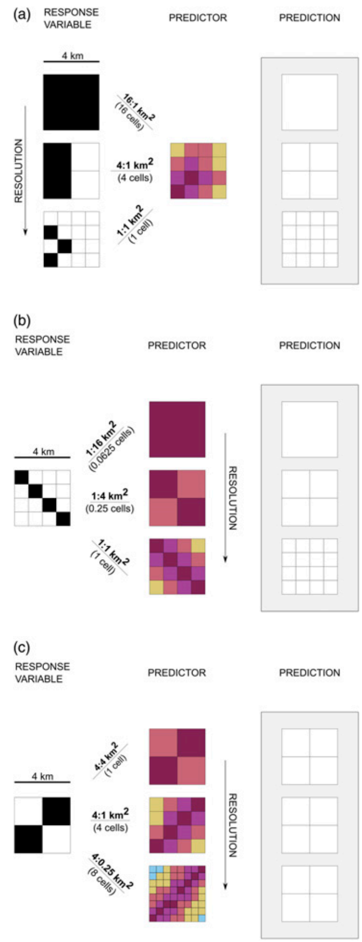

Figure 1. Three approaches typically used for testing the grain dependence of species–environment relationships: (a) manipulation of the resolution of the response variable with a fixed resolution of the predictors, (b) manipulation of the resolution of predictors, so that the resulting predictor was coarser than the response variable, and (c) manipulation of the resolution of predictors, so that the resulting predictor was finer than the response variable. The ratios shown in the figure (i.e. 16:1, 1:16, 4:4) express the resolution ratio that quantifies the magnitude of the difference between the resolution of the species data and that of environmental variables (this ratio quantifies how many cells of a particular predictor lie within a single cell of the response variable – the number shown in brackets). Note that if the fitted relationship is to be used for prediction, it is always limited by the coarsest grain used (either of predictor or response).

issues: (i) the effects of changing the resolution of predictor and response variables on model performance, (ii) the effect of conducting multi-grain versus single-grain analysis on model performance, and (iii) the role of land cover type and spatial autocorrelation in the selection of appropriate grain sizes. Accordingly, we aim at providing recommendations for the critical assessment of the input data.

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 (*The How the resolution of the response variable affects model performance*), others coarsened the resolution of predictor variables so that the resulting predictor was coarser than the response variable (*The How the resolution of the predictor variable (coarser than the response variable) affects model performance?*). Finally, in some studies, the resolution of predictor variables was coarsened so that the resulting predictor was finer than the response variable (*The How the resolution of the predictor variable (finer than the response variable) affects model performance?*). 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).

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

Table 1. Examples of studies focussed on resolution of the response variable. The resolution of the predictors may vary depending on the predictor.

Study	Species	Resolution of response	Predictors	Resolution of predictors
Tobalske (2002)	1 bird	1 and 4 km^2	Landcover, elevation, edge density	25 m (50 m)
Heikkinen et al. (2007)	1 butterfly	0.01, 0.25, 1 km^2	Landcover, habitat connectivity	25 m
Kaliontzopoulou et al. (2008)	1 lizard genus	1 and 100 km^2	Climate, topography, land cover	90 m to 1 km
Seo et al. (2009)	9 plants	1 up to 4096 km^2	Climate	1 km
Rengstorf et al. (2012)	Cold water corals	2500 m^2 up to 1 km^2	Bathymetry	50 m
Gábor et al. (2022a)	1 virtual species	25 m^2 to 0.25 km^2	Topography, canopy height	5 m
Zarzo-Arias et al. (2022)	1 mammal	0.25, 1, 25 km^2	Landcover, topography, human activity	100 m (25 m)
Chauvier et al. (2022)	1180 plants	0.01 up to 1600 km^2	Climate, soil	100 m

studied taxa. As examples of such data, we can name gridded atlases (Jalas and Suominen, 1988; Stastny et al., 2021), the resolutions of which can range from hundreds of metres 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 atlases with maps generated with SDMs (e.g. Flousek et al., 2015; Stastny et al., 2021). As field data may nowadays be gathered with the knowledge that they will also be used for modelling, it is important to know how the resolution of the response affects model performance.

In studies specifically examining the effect of grain size of the response variable on SDM performance, response grain ranges from a few metres to hundreds of kilometres, depending on the predictors tested (Figure 1(a); Table 1; see review by Miguet et al., 2016). These studies typically ask: at what scale(s) is the species distribution most driven or constrained by specific environmental conditions? At finer resolutions, studies typically concentrate on the role of landscape structure (composition and configuration) in driving species distribution (Heikkinen et al., 2007; Holland et al., 2004; Tobalske, 2002). With coarser response grains, studies often include (bio)climatic variables (Chauvier et al., 2022; Kaliontzopoulou et al., 2008; Seo et al., 2009). Typically, such studies report declining model performance with the coarsening of the resolution of the response variable (Chauvier et al., 2022; Gábor et al., 2022a; Heikkinen et al., 2007; Kaliontzopoulou et al., 2008; Seo et al., 2009; Zarzo-Arias et al., 2022), suggesting that modelling species at coarser resolutions is not optimal. However, these studies typically focus on the general performance of the models and do not report the effect of changing the response grain on the variables' importance, which may provide valuable insights into which variables shape species distributions at individual grain sizes (but see Chauvier et al., 2022; Hanberry, 2013).

How the resolution of the predictor variable (coarser than the response variable) affects model performance?

Instead of coarsening the resolution of the response variable, some studies have coarsened the resolution of predictor variables, so that the resulting predictor is coarser than the response variable (Figure 1(b); Table 2). They came to different conclusions. Ferrier and Watson (1997) concluded that coarse environmental data lead to poorer model performance. Graf et al. (2005) found that the predictive power was highest at resolutions of about 1 and 2 km^2. In contrast, Guisan et al. (2007) and Pradervand et al. (2014) concluded that coarsening the predictor variables' resolution did not substantially change

Table 2. Examples of studies that coarsened the resolution of predictors beyond the resolution of the response variable.

Study	Species	Resolution of response	Predictors	Resolution of predictors
Ferrier and Watson (1997)	56 species	20 × 50 m	Climatic, topographic, soil, vegetation	200 m and 5 km
Graf et al. (2005)	1 bird	0.01 km^2	Topographic, climatic, land cover, human disturbance	1 ha up to ~11 km^2
Guisan et al. (2007)	50 species	0.01–1 km^2	Climatic, topographic, soil	0.01–1, 1–100 km^2
Pradervand et al. (2014)	239 plants	4 m^2	Topographic, climatic	4 m^2 up to 0.01 km^2
Vale et al. (2014)	3 vertebrates	Point	Climatic, topographic, habitat	1 km^2 and 100 km^2
Manzoor et al. (2018)	1 plant	Point records	Climatic, topographic, land cover	50 m, 300 m, 1 km

Table 3. Examples of studies focussed on the role of resolution of environmental predictors. Coarsening means that the authors coarser resolution of the original data.

Study	Species	Resolution of response	Predictors	Resolution of predictors	Source of data
Thomas et al. (2002)	Vegetation types	1 km^2	Terrain, landform, rock/ sediment composition	Field measured, 30 m	Various
Tobalske (2002)	1 bird	1 km^2	Landcover, elevation, edge density	25 m, 100 m	Coarsening
Seoane et al. (2004)	54 birds	350 m diameter	Area of shrubs or forests	30, 50, 250 m	Various
Venier et al. (2004)	10 birds	5 km^2	Climate, habitat	200 and 1000 m	Various
Gottschalk et al. (2011)	13 birds	2 km diameter	Terrain, land-use	1 m up to 1 km	Coarsening
Šímová et al. (2019)	7 birds	12 × 11.2 km	Area and perimeter of water bodies	30 m up to 1 km	Various
Connor et al. (2018)	1 mammal	2 km^2	Terrain, land cover, climate, phenology	30 m up to 2 km	Coarsening

model performance, meaning that refining the resolution may not be sufficient to improve the models.

How the resolution of the predictor variable (finer than the response variable) affects model performance?

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

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

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

However, it is essential to know if a given spatial resolution of a predictor variable captures the details that are important for explaining the distribution of the species of interest. Gottschalk et al. (2011) concluded that a higher spatial resolution of predictors could be essential for accurate predictions. In addition, they attributed the improvement in models using detailed land cover maps to the high level of detail in the species response variable (2 km diameter around survey points). This contrasts with results by Šímová et al. (2019) that demonstrated improvement in model performance when using high-resolution land cover data despite the coarse resolution of species data (12 × 11.2 km). They showed that the area and perimeter of water bodies derived from high-resolution land cover datasets (raster data at 30 m resolution) explain distributions of waterbirds better than predictors derived from coarser 1 km data. In line with these findings, it has been recently recommended to first coarsen the resolution of the predictors to match the resolution of the assumed ecological scale before calculating prediction metrics (e.g. standard deviation, Shannon–Wiener diversity index, or Rao's Q) at the resolution of a response variable (Graham et al., 2019). In this context, the recent finding by Gábor et al. (2022b), who showed that in the case of species inhabiting rare habitats, using simple binary predictors (i.e. presence/absence of the habitat) might be sufficient, is of particular interest.

In conclusion, coarse-resolution land cover or terrain predictors may lack details to capture potentially suitable habitats such as wetlands or cliffs. Thus, using high-resolution data could benefit models utilizing coarser-resolution species data (e.g. from gridded atlases). The question of whether the need for fine-scale predictors is somehow related to the resolution of the response variable or whether it can be generalized should be further explored for different taxa and sets of predictors.

Single-grain versus multi-grain analysis

Up to this point, we have neglected discussing the possibility of considering species–environment relationships at multiple grains in a single model. Typically, experimental studies use a single grain for the response variable. Therefore, they implicitly assume the existence of a common ecological scale for all predictor variables. However, it has been shown that the ecological scale is variable-specific since species often respond to different environmental variables at different spatial scales and sometimes even respond differently to a single environmental variable at multiple grains (Leitão et al., 2010; Lecours et al., 2020; Miguet et al., 2016; Roilo et al., 2022). However, despite theoretical concepts and extensive empirical evidence that species respond to their environment at different spatial grains (e.g. Bergman et al., 2012; Graf et al., 2005; Holland et al., 2004; Stuber and Fontaine, 2019; Zweifel-Schielly et al., 2009), the appropriate approach to select the grain of response variable remains unclear (Jackson and Fahrig, 2015; Martin and Fahrig, 2012; Stuber and Gruber, 2020). For example, Mertes et al. (2020) recognized two primary spatial grains at which species typically respond to their environment: they denoted the term 'occupancy grain' for the grain equivalent to a species' typical home range and the term 'response grain' for the grain at which an individual uses an environmental resource. They also developed an optimization procedure for their identification. However, studies usually use grains of response variables coarser than the assumed occupancy and response grain, and it is unclear how to incorporate occupancy and response grains in such studies (but see Graham et al., 2019).

In theory, species distributions are driven by environmental variables at a range of scales (Levin, 1992), and there is no single 'correct' spatial grain at which to characterize species–environment associations (Mitchell et al., 2001; Wiens, 1989). Therefore, models using multiple grains should, in theory, outperform models that assume a common ecological scale for all variables. However, scale-sensitive applications that aim to align the grain of the response variable (or predictor variables; see Graham et al.,

2019) with the ecological scale are rare (McGarigal et al., 2016). In addition, studies have come up with different conclusions. Some have suggested that the performance of models using multiple response variable grains is better than that of single-grain models (Mertes et al., 2020), while others have not drawn similar conclusions (Martin and Fahrig, 2012). Of note is that the improvements reported for multi-grain models were often relatively low, in the order of hundredths of the area under the receiver operating characteristic curve (AUC) values (Boscolo and Metzger, 2009; Graf et al., 2005; Kuhn et al., 2011; Mateo Sánchez et al., 2014). In other words, valuable predictions can still be generated from models using a single arbitrarily selected scale. Hence, it remains unclear whether the increased complexity caused by the use of multiple grains is beneficial, particularly in the case of SDMs used for the projection of species distributions under future climate conditions, which are generally uncertain (e.g. Sinclair et al., 2010).

Land cover types and spatial autocorrelation

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 environment. The difference in land cover types used in different analyses might, therefore, explain some contrasting findings. For example, Seoane et al. (2004) and Venier et al. (2004) observed no improvement in models when using finer-grain land cover data, while Gottschalk et al. (2011) and Šímová et al. (2019) observed a significant improvement. Both Seoane et al. (2004) and Venier et al. (2004) used data on common land cover types, such as the proportion of forests within mapping units. For homogeneous landscapes displaying strong spatial autocorrelation (e.g. large blocks of forests), land cover information does not change much when spatially aggregated to coarser resolutions. In contrast, Šímová et al. (2019) focussed on water bodies, a land cover category that can become virtually invisible at coarser resolutions; coarsening the resolution often leads to a bias and underrepresentation of rare environments such as (especially linear) water bodies in certain landscapes. Similarly, Seoane et al. (2004) observed considerable improvement in models for riparian species when finer-resolutions predictors were used. This may be one of the reasons why Tuanmu and Jetz (2014) found that the Global Consensus Land Cover that has a spatial resolution of 1 km^2 (https://www.earthenv.org/landcover; see Table 2) performed worse for predicting aquatic species than species inhabiting other environments. Similarly, Cord et al. (2014) showed for 30 tree species that SDM performance was significantly positively correlated with the species-specific degree of association between the focal species and different land cover types.

Environmental variables are typically spatially autocorrelated (i.e. values between two locations are more similar the closer the locations are in space; Legendre, 1993). This spatial autocorrelation can be quantified using an empirical variogram that can be used to calculate the characteristic distance within which spatial autocorrelation operates (i.e. the ‘range’ of an empirical variogram). Recently, Mertes and Jetz (2018) highlighted the importance of considering environmental autocorrelation for the ability of SDMs to estimate species–environment associations. Similar results were obtained by Kühn (2006) for species richness. More recently, Smith and Santos (2020) explored the effect of the resolution of predictor variables and their autocorrelation on estimates of their importance. This body of literature shows that using coarser environmental data in SDMs without consideration of the autocorrelation can mischaracterize species–environment relationships (see Miller, 2012, for review). This is particularly true for variables that vary rapidly over space, that is, heterogeneous landscapes characterized by spatial autocorrelation with relatively small range values (Mertes and Jetz, 2018). Aggregating heterogeneous landscapes to a coarser resolution results in the loss of a portion of that heterogeneity (Graham et al., 2019; Karl et al., 2000; Mertes and Jetz, 2018). Lower autocorrelation means higher randomness; hence, very distinct values are aggregated together. In contrast, if there is strong autocorrelation, aggregating over a larger area does not change the value

Table 4. Resolutions adopted in studies evaluating the importance of fine-resolution predictors. The resolution ratio quantifies how many cells of the predictor lie within a single cell of the response variable.

Study	Resolution of response	Resolution of predictors	Resolution ratios
Seoane et al. (2004)	96,000 m^2	900 m^2; 2500 m^2, 62,500 m^2	96,000: 900 m^2 (~107 cells) 96,000: 2500 m^2 (~38 cells) 96,000: 62,500 m^2 (~1.5 cells)
Venier et al. (2004)	5 km^2	0.04 km^2 and 1 km^2	5: 0.04 km^2 (125 cells) 5:1 km^2 (5 cells)
Gottschalk et al. (2011)	3.14 km^2	1 m^2 up to 1 km^2	3.14: 1×10^{-6} km^2 (3,140,000 cells) 3.14: $1x10^{-5}$ km^2 (314,000 cells) 3.14: $1x10^{-4}$ km^2 (31,400 cells) 3.14: 1×10^{-3} km^2 (3,140 cells) 3.14: 0.01 km^2 (314 cells) 3.14: 0.1 km^2 (31.4 cells) 3.14: 1 km^2 (3.14 cells)
Šímová et al. (2019)	134 km^2	900 m^2 up to 1 km^2	134: 0.0009 km^2 (~150,000 cells) 134: 0.01 km^2 (13,400 cells) 134: 1 km^2 (134 cells)

much because the values were similar even in the finer resolutions.

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

The ratio between the resolution of response and predictor variables

A recently proposed standard protocol (Zurell et al., 2020) recommends reporting information on data, modelling techniques, validation, and underlying questions (Araújo et al., 2019; Michener and Jones, 2012; Rocchini and Neteler, 2012). However, many studies still lack it (see Feng et al., 2019, for a review). When evaluating the effect of changing the resolution of predictor variables, it is also important to consider the resolution of the response variable (i.e. species occurrences). The opposite is also true: when evaluating the role of the resolution of the response variable, one should be aware of the resolution of predictor variables. Although this may seem like a trivial recommendation, it remains infrequent that studies evaluating the effects of changing resolutions discuss their results with respect to the ratio between the resolutions of the response variable and predictor variable (but see Moudrý and Šímová, 2012). The ratio between the resolution of the response and the resolution(s) of the predictor variables differs among studies and might be the reason for reported contradicting results (Figure 1). For example, in studies evaluating the importance of finer-resolution predictors to explain species distributions, response grains can differ considerably (Table 4). It can be expected that for small ratios, coarsening of the resolution of predictor variables will have a minimal effect on model performance (e.g. Seoane et al., 2004; Venier et al., 2004), while for high ratios (indicating a high difference between the resolutions of the response and predictor variables), considerable effects can be expected due to the aggregation of highly different values (e.g. Gottschalk et al., 2011; Šímová et al., 2019). Practices could be improved by reporting the resolution of predictor variables as well as that of the response variable.

Conclusions

Spatial scale is one of the most critical issues in ecology and associated disciplines (Levin, 1992). Species respond to their environment at different scales, and processes controlling species distribution operate at various spatial scales. Unsurprisingly, the studies we reviewed found various optimal resolutions, depending on the species and ecosystems analyzed. Besides, most studies analyzing multiple species usually report only a general trend in models' behaviour with respect to changing resolution, and there are always some models that do not conform to the general pattern (e.g. Guisan et al., 2007; Pradervand et al., 2014). Our review highlights that within the typically used resolutions of response variables (0.01–100 km^2) finer-resolution models generally perform better. Besides, the use of coarse-resolution response variables has implications for the predicted distribution range (Kunin, 1998). When the resolution of the response variable is too coarse, there is a risk of overestimating the occupied area (Connor et al., 2018; Hu and Jiang, 2010; Lauzeral et al., 2013; Seo et al., 2009). Moreover, Gábor et al. (2022a) recently showed that coarsening the resolution does not compensate for positional error in species occurrence data. Therefore, we recommend basing the choice of the resolution of the response variable on practical aspects, such as aiming for finer resolutions unless there is a reason to do otherwise (e.g. expert knowledge of the ecological scale of the species under study).

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

Acknowledgements

VM, JP, and JW were supported by the Czech Science Foundation [No. 20-28119S] and by Czech Academy of Sciences [long-term research development project RVO 67985939]. PK, FG, and FL were supported by a REES (Research Excellence in Environmental Sciences) grant from the Faculty of Environmental Sciences, Czech University of Life Sciences in Prague. AZA was financially supported by a Margarita Salas contract financed by NextGenerationEU, MIU DGPMRR, through the call of the Universidad de Oviedo (Asturias, Spain).

Declaration of conflicting interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Funding

The author(s) disclosed receipt of the following financial support for the research, authorship, and/or publication of this article: This work was supported by the Czech Science Foundation [No. 20-28119S] and by Czech Academy of Sciences [long-term research development project RVO 67985939]. PK, FG, and FL were supported by a REES (Research Excellence in Environmental Sciences) grant from the Faculty of Environmental Sciences, Czech University of Life Sciences in Prague. AZA was financially supported by a Margarita Salas contract financed by NextGenerationEU, MIU DGPMRR, through the call of the Universidad de Oviedo (Asturias, Spain).

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