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A theoretical framework for upscaling species distribution models

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Abstract

1. Species distribution models (SDM) have become one of the most popular predictive tools in ecology. With the advent of new computation and remote sensing technology, high-resolution environmental data sets are becoming more and more common predictors in these modelling efforts. Understanding how scaling affects their outputs is therefore fundamental to understand their applicability.
2. Here, we develop a theoretical basis to understand the consequences of aggregating occurrence and environmental data at different resolutions. We provide a theoretical framework, along with numerical simulations and a real-world case study, to show how these scaling rules influence predictive outputs.
3. We show that the properties of the environment–occurrence relationships change when the data are aggregated: the mean probability of occurrence and species prevalence increases, the optimal environmental values shift and classification rates increase at coarser resolutions up to a certain level. Furthermore, and contrary to the widespread expectation that high-resolution data would produce better predictions, we show here that model performance may increase using coarser resolution data sets rather than the inverse. Finally, we also show that model performance depends not only on the environment–occurrence relationship but also on the interaction between this and the geography and distribution of the available environment.
4. This theoretical framework helps understanding previously incoherent results regarding SDM upscaling and model performance, and illustrates how theoretical and empirical results can provide important feedbacks to advance in understanding scaling issues in macroecology. The interaction between the shape of the environment–occurrence relationship and the rates of change of the environment is fundamental to understand the effects of upscaling in model performance, and may explain why some models are more difficult to transfer to different regions. Most importantly, we argue that there are conceptual choices related to scaling and SDM fitting that require expert knowledge and further explorations between theory and practice in macroecology.

KEYWORDS
AUC, ENM, prediction, resolution, scaling, SDM, spatial scale

1 | INTRODUCTION

Preparing for global change will require integrating phenomena that occur at different temporal and spatial scales (Levin, 1992). Scaling issues are therefore central to face such challenges. In the last decades, technological advances in a variety of disciplines have permitted integration of ecological and evolutionary processes at small and large scales (Chave, 2013). Alongside these advances, species distribution models (SDM) have become a widespread ecological tool with multiple applications (Araujo et al., 2019; Guisan et al., 2017; Guisan & Thuiller, 2005), arguably the most important predictive tool to anticipate climate change effects on biodiversity (Araújo & Guisan, 2006; Bellard et al., 2012; Dawson et al., 2011).

SDMs have been used to make predictions across different time periods. For example, to identify potential habitat for conservation purposes, current environmental conditions where the species is known to occur are used to identify potential habitat where sampling has been limited or non-existent (Guisan et al., 2013). In such situations, the resolution of the environmental predictors in the calibration and the prediction data sets is likely similar. In other situations however, one might be interested in using the current occurrence–environment relationships to predict the species past (hindcasting) or future (forecasting) distributions (Araujo et al., 2019; Varela et al., 2011). In such situations, palaeoclimate, climate change and land use scenarios are sometimes difficult to find for the desired time periods at the same high resolutions. On top of that, the resolution of environmental and physical predictors has improved considerably over time (Pradervand et al., 2014). At the onset of macroecology as a discipline (Brown, 1995), the most common continental or global data sets could go from 1° (~110 km at the equator) to 10° (~1100 km) resolution (e.g. see Rahbek, 2005). In contrast, global climate data sets such as Worldclim (Fick & Hijmans, 2017) or CHELSA (Karger et al., 2017) are now available at ~1 km resolution. Moreover, sensors flown on drones or planes can generate environmental data that amount to a few metre resolution over large regional extents (e.g. de Vries et al., 2021; Randin et al., 2020). Therefore, knowing how SDMs will behave when changing the resolution of the data sets and the scale of prediction is key to understanding how reliable they might be for different applications.

In general, the intuitive expectation dominating the SDM literature in this respect has been that using higher resolution data (i.e. fine grain) would result in better predictive ability (de Vries et al., 2021; Deblauwe et al., 2016; Pradervand et al., 2014; Wunderlich et al., 2022). However, many empirical studies have found the opposite result (Moudrý & Šímová, 2012; Trivedi et al., 2008; Wunderlich et al., 2022). Resolution also interacts with other factors, and may produce increases, decreases or no significant changes in terms of predictive ability (Franklin et al., 2013; Guisan et al., 2007; Moudrý et al., 2023; Suarez-Seoane et al., 2014). High-resolution environmental data sets are often available for smaller regional extents than the national or global coarser data sets. Since the extent of the study area can also influence model performance (Betts et al., 2006; Suarez-Seoane et al., 2014), varying extent and resolution at the same time makes it difficult to isolate the effects of resolution in empirical studies. Similarly, regional biological surveys may sometimes be very detailed at small extents, but they are only available in the form of Atlases with coarse resolutions at national or larger extents (Moudrý et al., 2023). Adding to this, many empirical studies have left the occurrence data intact, while varying the resolution of the environmental layers, raising the question of the interaction between resolution of predictors and response variables; yet others do not explicitly specify what actions were taken, if any, to match the predictors' resolution to that of the occurrence data. To help remedy these issues, Zurell et al. (2020) proposed a reporting protocol that includes predictor and occurrence resolution, while Moudrý et al. (2023) suggested that SDM studies should also report the ratio between occurrence and predictor resolutions. Simulations to study the effects of resolution while avoiding the caveats of empirical studies have concluded that SDM performance is better when modelling is carried out at the resolution at which the species occurrences were originally simulated (Connor et al., 2018; Mertes & Jetz, 2018). Lacking from these SDM scaling studies is a theoretical basis on which to support expectations of SDM behaviour with respect to resolution and upscaling.

When we model large-scale species ranges using fine-resolution data sets such as the ones we see today (i.e. 20 km or finer grain), we may be crossing a line towards a spatial domain where processes differ in a fundamental way that demands additional considerations that are not necessarily immediately intuitive. For example, ingrained in the broader ecological literature is the idea that, while large-scale species distributions are more or less stable over climatically homogeneous periods (Brown & Lomolino, 1998; Gaston, 2003), patterns at finer temporal and spatial grains are highly dynamic and stochastic (Hanski, 1999). It is often assumed that large-scale pedoclimatic gradients determine the broad species ranges setting physiological tolerance limits to species' long-term survival, whereas local occupancy is determined by dispersal, colonization and extinction dynamics that can have deterministic as well as stochastic components (Gaston, 2003; MacKenzie et al., 2006; Mackey & Lindenmayer, 2001). This results in suitable habitat that may be empty at any given point in time locally. The rules that apply across scales from species ranges to local occupancy may therefore be different, and the environment–occurrence relationships may vary, both mechanistically and conceptually, as a function of scale (Gaston, 2003; Mackey & Lindenmayer, 2001). A corollary of this is that presence–absence patterns would be more stable at larger spatial and temporal scales, potentially making them easier to predict. However, in contrast with this ecological hierarchical view of species distributions, the SDM literature has most often assumed that environment–occurrence relationships are constant across scales, without much reference to any theoretical framework. In this context, models fitted using one resolution are sometimes projected into a different resolution (e.g. Araújo et al., 2005; Suarez-Seoane et al., 2014), and measures of model performance have heavily relied on presence–absence classification rates at all scales (Allouche et al., 2006; Lobo et al., 2008; Meynard & Kaplan, 2012).

Here, we aim at tackling this lack of theoretical framework for scaling SDMs by building a first theoretical upscaling theory. We will first develop a theoretical framework that will allow us to have clear expectations with respect to the probability of occurrence, the environment–occurrence relationship and model performance in terms of presence–absence classification rates when applying an upscaling strategy. We will exemplify its empirical consequences through numerical simulations and through a real-world case study. We further demonstrate that how model performance changes across scales depends on the interaction between landscape properties, the shape of the environment–occurrence relationship and how it is positioned with respect to the available environmental gradients.

2 | MATERIALS AND METHODS

To understand the effects of upscaling in SDMs, particularly with respect to resolution, we need to distinguish at least three facets of the upscaling process, namely, how the upscaling process affects: (1) the aggregate probability of occurrence, (2) the environment–occurrence relationship and (3) model predictive performance, herein treated in terms of our ability to correctly classify presences and absences.

2.1 | Theoretical and numerical development of the conceptual framework

For simplicity, we summarize the main points of the theoretical development below. A detailed account is available in Appendix S1.

The basic theoretical problem that we wish to explore is how an SDM developed based on environmental and presence–absence data at a given resolution relates to an equivalent model wherein both predictors and occurrence have been aggregated in space across multiple individual grid cells (Figure 1). Following Moudrý et al. (2023)'s terminology, our response-to-predictor resolution ratio will always remain 1:1.

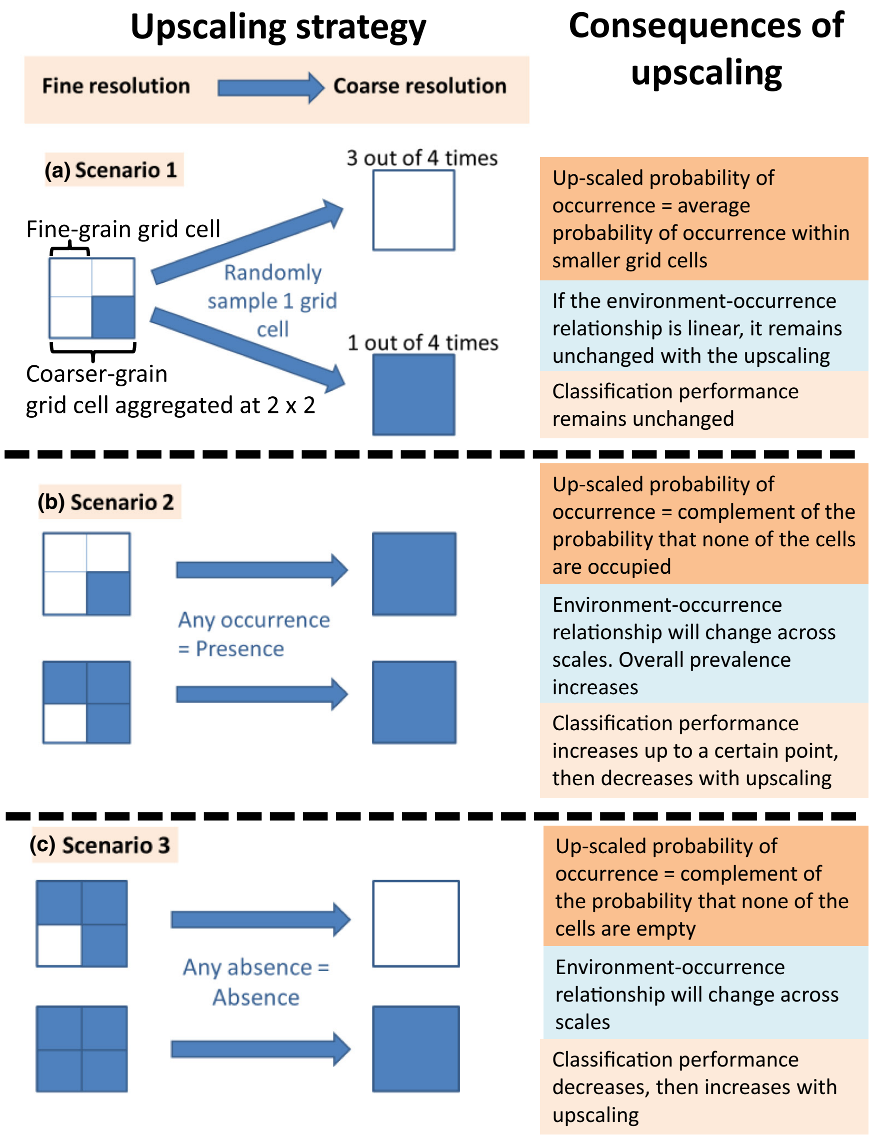
We will start by exploring three simple approaches to aggregating presence–absence data (Figure 1), which will provide a baseline for understanding what happens in situations that are more complex. In each of these, we will initially assume that environmental conditions within the aggregate are homogeneous (the effects of heterogeneity within the aggregates are treated in Appendix S1 and are discussed later).

Theoretical expectations will then be illustrated through numerical simulations using virtual species over different virtual temperature gradients. Simulations focused on the second aggregation scenario (Figure 1b), since this is the more realistic and most common aggregation strategy found in real SDM studies; temperature of the aggregated resolutions was calculated as the average of the corresponding finer resolution data sets. The environment–occurrence relationships, as well as the structure of the virtual landscapes, were tailored to tackle predictions made during the theoretical demonstration. The simulation framework followed virtual species guidelines provided in Meynard et al. (2019) and were implemented using the virtual species package (Leroy et al., 2016) in R v4.2.2 (R Core Team, 2022). The simulated presence–absence patterns were then upscaled following the second aggregation scenario, that is, a fine grain occurrence is translated into a coarse grain occurrence, regardless of whether there is one or multiple occurrences within the focal grid cell. Notice that presence–absence patterns here are perfect, that is, there is no detection, positional or misclassification errors associated with the data set. We used the area under the ROC curve (AUC; Fielding & Bell, 1997) to illustrate the changes of model performance across different scales.

2.2 | A real-world SDM case study: The desert locust in north-western Africa

Desert Locust surveys were extracted from the UN-FAO Locust Information data set (FAO, 2022). We used data over a period of 20 years (2000–2020), where the observers recorded presences and absences of desert locusts (*Schistocerca gregaria*) on several point intervals along recurrent survey routes. Other relevant biological information recorded, such as stage of development (i.e. hoppers vs. adults) and phase (i.e. gregarious vs. solitary phase), allowed us to focus on recession periods (i.e. when no adult swarms and hopper bands are found damaging crops). We limited the extent of the study area to Mauritania, Senegal and Morocco, since this area includes a marked environmental gradient and is currently one of the best surveyed over the desert locust range (Piou et al., 2017). We also limited model calibration and validation data sets to the 95% central values of environmental gradients surveyed, to avoid outliers in the calibration range. We eliminated surveys during periods of outbreaks, when individuals have a gregarious behaviour that form hopper bands or adult swarms that can disperse long distances and during which they can be found in areas outside of their long-term persistence range (similar to Meynard et al., 2017). We aggregated temporal data at the finest spatial resolution of the original climatic data set (30 arc-seconds), that is, each grid cell was recorded as present if any of the surveys in the 20-year period found hoppers or adults during remission periods, and absent if all surveys recorded absences; non-surveyed areas were therefore left out of the calibration set. This results in 43,694 surveyed grid cells (roughly 0.1% of the study area) at the finest resolution, of which 20,002 represent presence records (46%). This data set was divided into an 80% used for model calibration and the remaining 20% used for model evaluation, a procedure that was repeated 10 times.

The finest resolution in our analyses corresponds to the ~1 km resolution (30 arc-seconds) of the CHELSA v2.1 climatic data set (Karger et al., 2017). As with the numerical simulations, environmental and occurrence data were subsequently upscaled (i.e. aggregated) using the second method described above (Figure 1b). We aggregated cells at 10 different resolutions, from the 1 × 1 finer



Up-scaled probability of occurrence = average probability of occurrence within smaller grid cells

If the environment-occurrence relationship is linear, it remains unchanged with the upscaling

Classification performance remains unchanged

Up-scaled probability of occurrence = complement of the probability that none of the cells are occupied

Environment-occurrence relationship will change across scales. Overall prevalence increases

Classification performance increases up to a certain point, then decreases with upscaling

Up-scaled probability of occurrence = complement of the probability that none of the cells are empty

Environment-occurrence relationship will change across scales

Classification performance decreases, then increases with upscaling

FIGURE 1 A schematic figure representing the three upscaling strategies studied in the theoretical section.

resolution to the largest 19 × 19 resolution, in intervals of two grid cells (1 × 1, 3 × 3, 5 × 5 etc.). CHELSA contains 40+ variables (Karger et al., 2017), many of which are irrelevant for this area. We therefore reduced to 19 bioclim variables (mean, minimum, maximum and variance of annual and seasonal rainfall and temperature), plus net primary productivity, degree-days above 10°C and growing season length. We carried out a principal component analysis with standardized environmental variables at the original data resolution, and extracted the first two principal components, which explained 72% of the variance. We used these two principal component axes (named PC1 and PC2, respectively) as the main predictors in our SDM exercises. When aggregating data, we used mean PC1 and PC2 values at coarser resolutions.

We combined five modelling techniques that are among the best-performing SDMs currently used (Norberg et al., 2019; Valavi et al., 2022): GAM (mgcv), GLM-Lasso (glmnet), RandomForest-downsampled (randomForest), Maxent (dismo) and BRT (gbm); the ensemble was calculated as the average across models. All SDMs were carried out at the 1:1 predictor-to-response ratio for each scale. The 20% left out as testing set (see above) was used to calculate performance metrics based on presence–absence classification rates at each of the 10 iterations. Notice that absences represent grid cells that were visited, but where the species was never recorded as present throughout the 20-year period. Scripts and data can be found in our GitHub—Zenodo repository (Meynard et al., 2023) and are presented in Appendix S2.

3 | RESULTS

3.1 | Theoretical and numerical results

In the first aggregation scenario (Figure 1a), only one grid cell is sampled to register the presence or absence of the species in the larger aggregate. The aggregate receives the value of that one random sample, whether it is a presence or an absence. If this is done over a large landscape and with many well-spread samples that include presences and absences, the probability of occurrence of the species in the aggregate will reflect the average probability of occurrence of the smaller grid cells within the aggregate. To answer our three initial questions then: (1) the correct theoretical probability of occurrence of the larger aggregate corresponds to the mean probability of occurrence of the smaller units; (2) the environment–occurrence relationship remains unchanged during the upscaling process; and (3) the predictive ability of the models remains unchanged regardless of the resolution of the environmental and occurrence data set. Notice, however, that if one were to apply this aggregation strategy in a real setting, it would require randomly sampling presence and absence data within larger aggregates, meaning that some presence records (e.g. well-known habitat) would be ignored. This is an unlikely scenario, both because random sampling is rare, and because if some well-known habitat falls within an area of survey, it is unlikely to be dismissed.

In the second aggregation scenario (Figure 1b), the aggregate will be recorded as a presence if any of the smaller grid cells is occupied, regardless of whether it is only one or many grid cells that are occupied. This is what would happen with relatively dense (and homogeneously distributed) sampling data aggregated at a given coarser scale either to match the resolution of the predictors or to meet some other modelling objective (e.g. to meet spatial scales of management). Notice that this is the most common procedure in SDM practice, where it is often recommended to trim the occurrences (but not the absences) to a single presence at the resolution of the environmental data sets (e.g. Aiello-Lammens et al., 2015).

In this case, the correct theoretical probability of occurrence of the aggregate is the complement of the probability that none of the grid cells is occupied, ultimately leading to higher perceived probability of presence in the aggregate than in the unaggregated system, as within each aggregate one has multiple chances to observe a species. In this scenario, the relationship between the environmental gradients and the probability of occurrence will not be the same at the aggregate level than at the smaller grid level, meaning that the shape of the occurrence–environment relationship is resolution dependent.

A first example is given assuming a single environmental gradient with a logistic relationship to the probability of occurrence (Figure 2a). In this simple case, even if the relationship is still approximately logistic at the aggregate level, the inflexion point is displaced towards the right with respect to the environmental gradient, and the slope of the logistic becomes steeper the larger the aggregate. However, the slope of the logistic curve at higher aggregation levels never reaches a threshold-like relationship, converging instead towards a finite maximum inflexion-point slope (Figure 2a). A second example comes from assuming a normal distribution of the probability of occurrence with respect to a unique environmental gradient. In this case, the results are similar to a double-sided logistic distribution (Figure 2b): As we increase the level of aggregation, the core area of species presence becomes fatter towards the sides and taller, but never reaches a two-sided threshold relationship. This demonstrates that the shape and

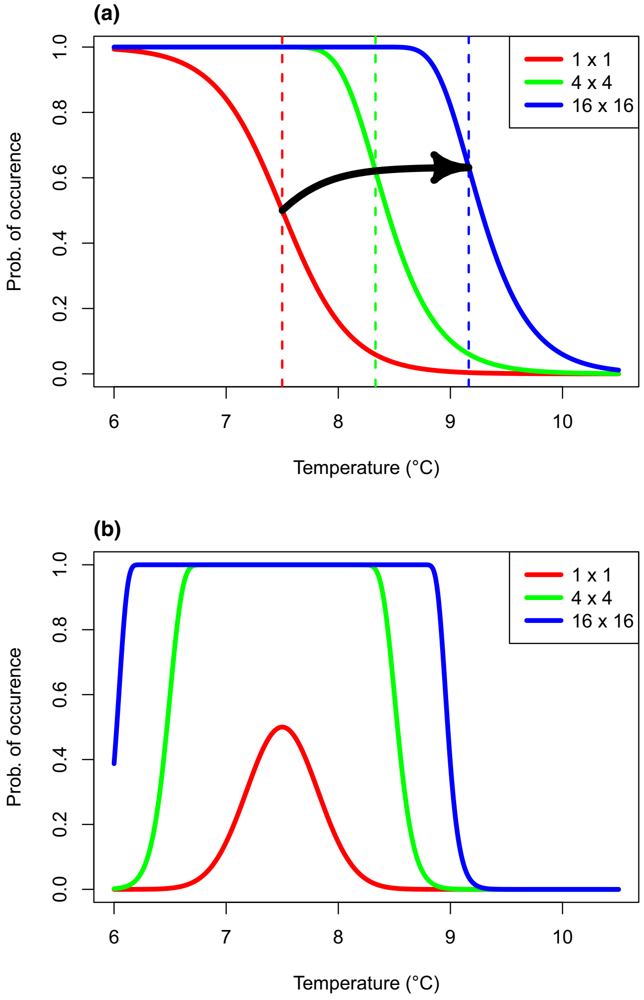


FIGURE 2 Effects of upscaling on the shape of the environment–occurrence relationships: (a) for a sigmoidal environment–occurrence relationship, aggregation will move the inflexion point following the black arrow, that is, to a higher mean probability of occurrence and along the environmental gradient (in this case towards higher temperatures); the slope of the curve at the inflexion point also increases; (b) for a Gaussian response curve, the result is similar (overall higher mean probability of occurrence, steeper slope at inflexion point and change in the position of the inflexion points along the environmental gradient).

parameter values associated with the environment–occurrence relationship change when the same data set is scaled up. A side effect of this is that the overall prevalence of the species is higher at coarser resolutions, the probability of occurrence being displaced globally upwards (Figure 2).

How scale of aggregation will impact SDM presence–absence classification performance indices (e.g. AUC and true skill statistic [TSS] among others, see Allouche et al., 2006; Fielding & Bell, 1997) depends not only on the environment–occurrence relationship but also on the relationship between space and environmental conditions. Likely, the most important effect is the shape of the environment–occurrence relationship itself, and its position with respect to the available environmental gradients.

Model performance is essentially determined by areas for which environmental conditions lead to probabilities of occupancy that are far from zero or one. As aggregation initially increases the slope of the environment–occupancy relationship (Figure 2), this will have a tendency to reduce the area over which probabilities of occupancy are intermediate, thereby increasing model performance as level of aggregation is increased. However, because the slope in the logistic curve (or the slopes of the Gaussian bell) reaches an asymptote at the highest aggregation levels, the position of this inflexion point with respect to the environmental conditions available in the landscape will be key to determine model performance at higher aggregation scales (Figure 3). Of particular relevance is how common or rare the environmental conditions that are favourable to a species' occurrence are in the landscape, especially for intermediate probabilities of occurrence. As aggregation is increased, the mean environmental conditions over which the probability of occurrence is intermediate-to-high will be shifting in the environmental axis. Depending on the relative prevalence of environmental conditions producing intermediate probabilities of occupancy for the unaggregated and aggregated landscapes, aggregation could lead to increases or decreases in model performance.

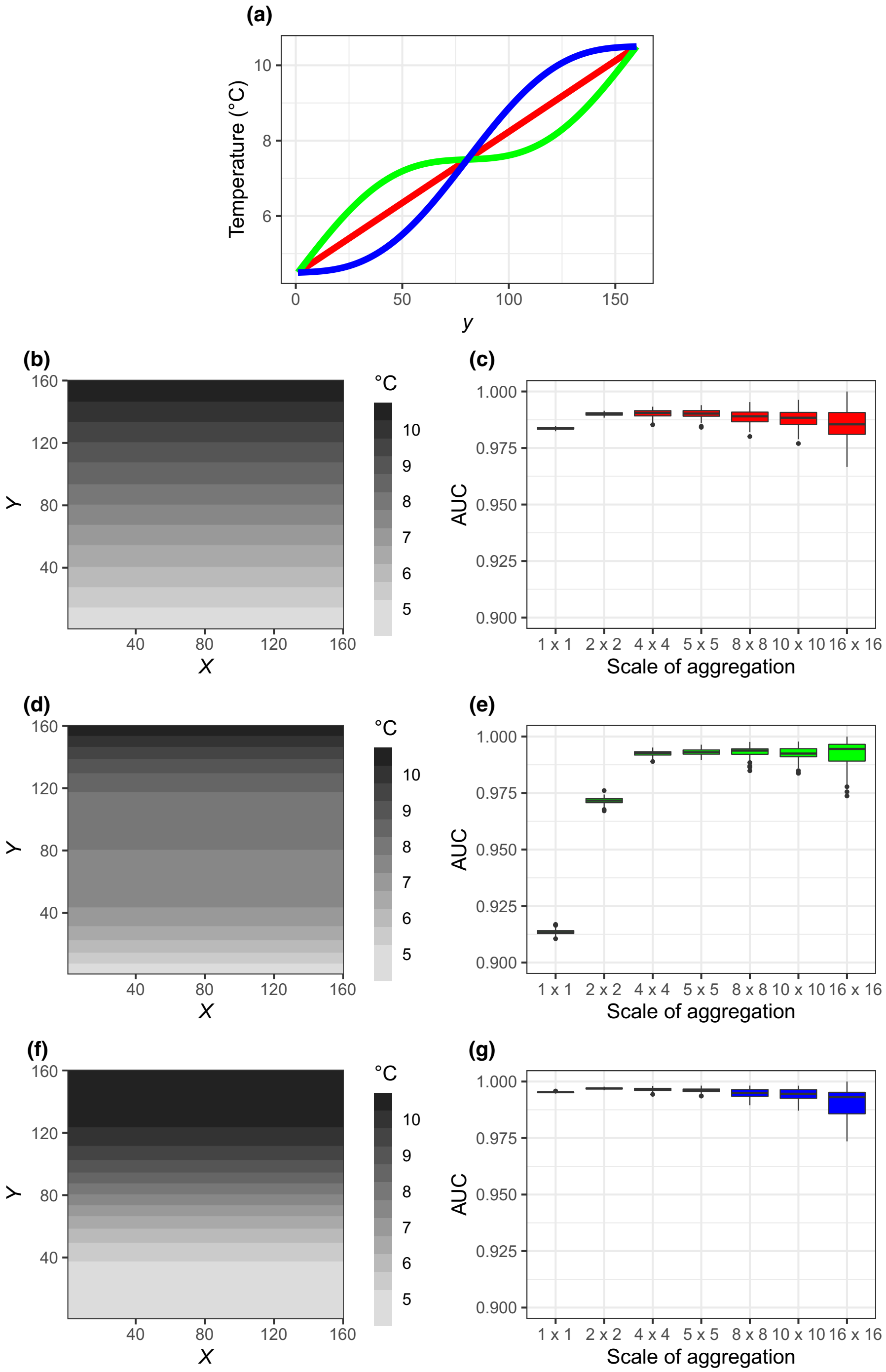


FIGURE 3 Interaction between environment–occurrence relationships, distribution of environmental drivers and AUC (area under the ROC curve), as illustrated by a virtual species simulation. In all simulations, the virtual species is the same and has a logistic response to the temperature gradient, and there were 80 replicates for each particular aggregation scale. The response curve therefore behaves as in Figure 2a during the upscaling process. Here, (a) we generated three types of virtual temperature landscapes, depending on how temperatures are changing along the *y*-spatial axis: in the red curve, temperature increases linearly (i.e. at a fixed rate) along the *y*-axis, as shown in the landscape (b); in the green line, intermediate values of temperature are prevalent, since temperature is changing slowly exactly where the inflexion point is for the virtual species (and remember that the upscaling process is moving this inflexion point towards higher temperatures at coarser resolutions), as shown in landscape (d); finally, the blue line indicates a landscape for which intermediate values of temperature are changing quickly, therefore making them less prevalent than extreme values, as shown in landscape (f). Panels (c, e, g) show the behaviour of the ensemble model performance in terms of presence–absence classification rates, as measured by the AUC, during the aggregation process, for each of the landscape types they face (b, d and f respectively).

To illustrate this, we projected the same environment–occurrence relationship into three different types of landscapes (Figure 3). In the first one, temperature is increasing at a regular pace (linearly increasing along the *y*-axis, red line in Figure 3a, example landscape in Figure 3b); in the second case, temperature is following a sigmoidal increase, where intermediate temperature values are prevalent (green line, Figure 3a, example landscape in Figure 3d); and in the final landscape, temperature is also increasing in the *y*-axis following a sigmoidal, but where intermediate values of temperature change quickly (blue line in Figure 3a, example landscape in Figure 3f). In the aggregation process, the virtual species is shifting its mean probability of occurrence upwards and towards higher temperatures (following Figure 2a), as the upscaling is taking effect. This means that the available favourable environment is becoming more common, albeit at different rates between landscapes (Figure 3b,d,f). This translates into classification rate performances that are increasing and then stabilizing around a maximum value past the 4 × 4 aggregation scale for the linear case, whereas the AUC decreases and becomes more erratic after the 8 × 8 aggregation scale for the nonlinear cases, but especially so for the blue case, which corresponds to fast rates of change in the environmental gradient right where the intermediate probabilities of occurrence (i.e. inflexion point) occur.

To answer our three initial questions for this aggregation scenario then: (1) the correct theoretical probability of occurrence of the larger aggregate will be shifted to higher values; (2) the environment–occurrence relationship changes during the upscaling process, overall increasing the mean probability of occurrence of the species when using coarser resolutions, and shifting the position of the inflexion point (i.e. where intermediate probabilities of occurrence can be found) over the environmental gradient; and (3) the predictive ability of the models will depend on the interactions between environment and occurrence relationships, as well as the relative prevalence and rate of change of environmental conditions available to the species of interest. There is usually an increase of classification performance up to a level, where model performance stabilizes around a maximum classification rate, or decreases, depending on the frequency distribution of favourable environments in the landscape with respect to the environment–occurrence relationship (Figure 3).

The third and final theoretical aggregation scenario (Figure 1c) is the complement of the second one in that here we will require all the composing grid cells to be occupied before we declare the aggregate to be occupied. In this rather unlikely case, the probability of occurrence of the aggregate will be equivalent to the probability that none of the grid cells are empty, and the implications for the probability of occurrence and its relationship to the environmental gradients mirror those of the second scenario and will not be discussed further.

The main point to draw from this theoretical framework is that spatial aggregation, at least in the most realistic aggregation scenario, fundamentally changes the parameters in the environment–occurrence relationship in a predictable way. In other words, there is no reason to expect that upscaling will preserve the same environment–occurrence relationships as in the original fine grain data set. Moreover, contrary to the prevalent intuitive expectation, aggregation may increase our predictive ability up to a certain level.

3.2 | A real case study: Upscaling a desert locust SDM in north-western Africa

This case study shows how the theoretical findings translate into a real-case SDM. First, as expected, the prevalence of the species seems to increase in the landscape as a side effect of the upscaling process (Figure 4). Notice that this change in prevalence is purely an effect of the upscaling strategy which is coarsening the occurrence grain.

Second, this translates into several changes across scales in the environment–occurrence relationship (Figure 5). If we look at the response curves across both environmental gradients produced by the ensemble models, we can see that upscaling from 1 × 1 to 19 × 19 globally increases the probability of occurrence, as the environment–occurrence relationships along PC1 and PC2 shift upwards when we use coarser grains of analysis (Figure 5). Although these curves do not match the more idealistic logistic or Gaussian cases shown in Figure 2, the theoretical predictions that the environment–occurrence relationship changes across resolutions and globally increases the species prevalence at coarser grains remain valid.

Finally, this reflects into the classification rate performance of the models in a predictable way. As expected, classification rates increase as we upscale from a 1 × 1 to a 11 × 11 resolution (Figure 6). Beyond that point, classification rates remain constant and/or decrease past the 15 × 15 aggregation scale.

4 | DISCUSSION

4.1 | Clarifying some previous results regarding resolution in the SDM literature

Our upscaling theoretical framework helps explaining some of the previous results regarding the effects of resolution on model performance. The fact that the environment–occurrence relationship is changing as a side effect of the aggregation process means that, as a general rule, calibrating SDM models using one resolution and projecting at a different resolution (e.g. Araújo et al., 2005) is likely to fail, unless the environment over which the probability of occurrence is intermediate is changing very slowly in the projection landscape (Figure 3d,e). It also means that an upscaling procedure that works in one region might not work in a different one, especially if environmental gradients are steeper in one of them. This may also help explain the fact that some models seem to be perfectly transferable from one region to another, while others are not (Rana & Tolvanen, 2021; Randin et al., 2006), and why the choice of predictors has such a large influence on model transferability (Petitpierre et al., 2017). Studying the rates of change of the

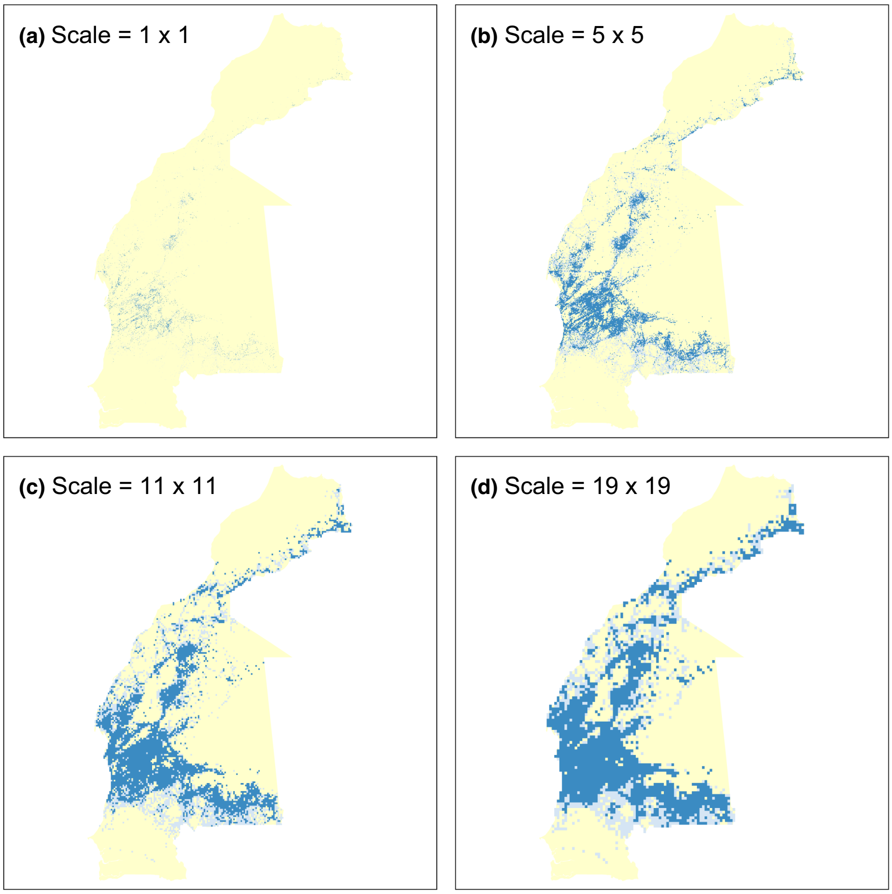


FIGURE 4 Upscaling effects on the perceived species distribution and prevalence. Dark blue indicates presence records, light blue indicates absences; yellow areas are part of the study area but were not surveyed during the period of study. Notice that the data used to draw the maps are always the same; the perceived increased prevalence is therefore a side effect of aggregation using a coarser resolution. Different aggregation scales: (a) 1 × 1 cells (no aggregation); (b) 5 × 5 grid cells; (c) 11 × 11 grid cells; (d) 19 × 19 grid cells.

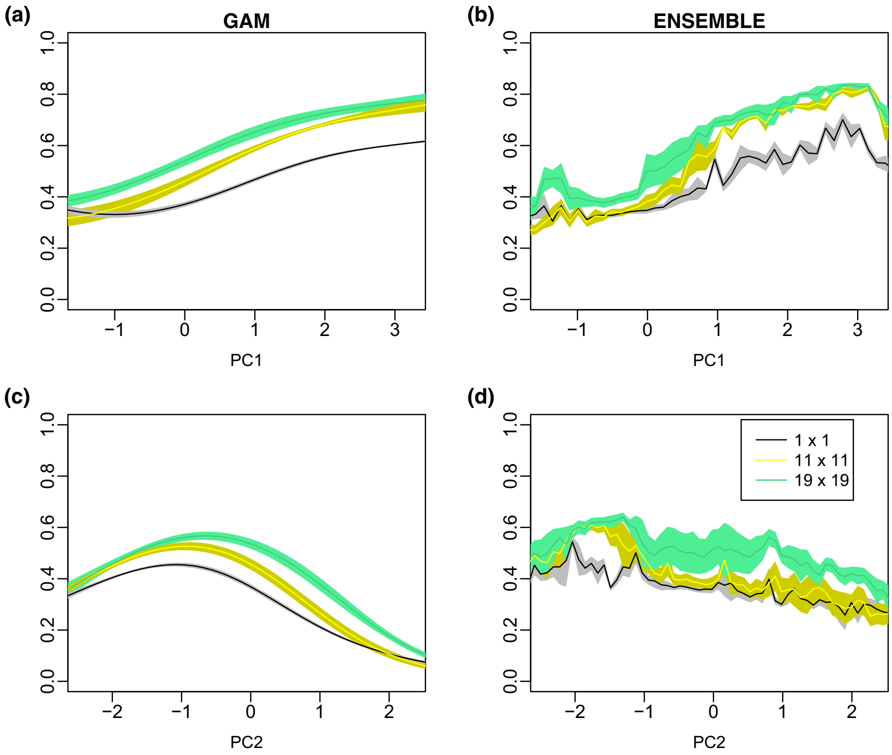


FIGURE 5 Environment–occurrence relationship across scales in the Desert Locust along the environmental gradients used in an species distribution model ensemble modelling effort. Upper row (a, b): response with respect to PC1; lower row (c, d): response with respect to PC2. Left (a, c): GAM functional responses; Right (b, d): ensemble of five different modelling techniques (GAM, random forests, boosted regression, GLM-Lasso and Maxent). The line represents mean predicted probability of occurrence from 10 replicates of the data splitting, and the corresponding coloured areas are the 95% confidence intervals. Notice that the mean probability of occurrence shifts upwards and changes through the aggregation process. Black = finest grain (1 grid cell); yellow = aggregation of 11 × 11 grid cells; green = coarsest grain (aggregation of 19 × 19 grid cells).

environmental gradients driving SDMs of the species of interest, especially at intermediate probability values, might be an interesting venue to predict model transferability between regions.

In reality, however, many factors are covarying with resolution, so it becomes difficult to determine which one is the main culprit in explaining model performance. For example, in Suarez-Seoane

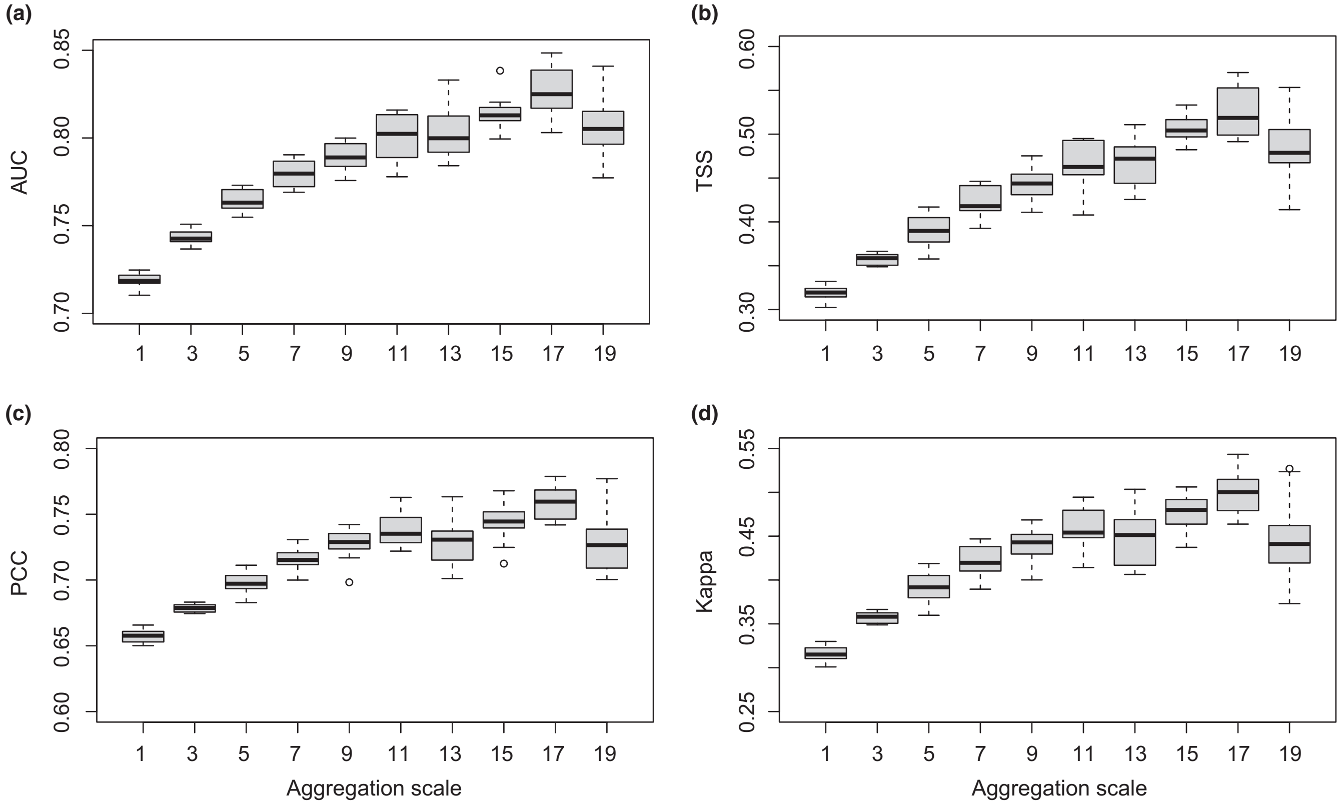


FIGURE 6 Effect of upscaling on presence–absence classification rates using different performance indices applied to a validation set. (a) AUC, area under the ROC curve; (b) TSS, true skill statistic; (c) PCC, proportion of correctly classified; (d) Kappa, Kappa statistic. The *x*-axis denotes the aggregation scale, with 1 = no aggregation with respect to the native resolution, 3 = aggregation of 3 × 3 grid cells, etc. Boxplots indicate median values from 10 data splits in the original Desert Locust data set (80% used for model calibration, 20% for validation).

et al. (2014), some of the regional models (i.e. smaller extent) had poor predictive performances, which the authors explained through the more marginal positions of these regions with respect to the overall biogeographic gradient. In this context, it was difficult to interpret the different directions of variation of the performance index used (AUC), sometimes increasing or decreasing, as the extent, resolution and position on the environmental gradients were all varying at the same time. Our theoretical framework clearly explains why classification success metrics could be improving at coarse resolutions, and why, after a certain point, coarser resolutions could bring a decrease in AUC due to the interaction between environmental gradients and environment–occurrence relationships. So they also help explain the counterintuitive results in Wunderlich et al. (2022) and Trivedi et al. (2008), among others, where AUC values improved at coarser resolutions.

Our theoretical framework also supports the idea that overprediction is an important side effect of the upscaling process (Connor et al., 2018; Franklin et al., 2013). Indeed, we do not need much analysis to understand the effects that this upscaling process has on the perceived species prevalence (Figure 4). However, the corresponding changes in the environment–occurrence relationships (Figure 5) are perhaps less intuitive and equally important: The estimate mean probability of occurrence will be higher just by virtue of using a coarser resolution in the modelling process. This is visible in the numerical simulations (Figure 2), but also in the case study (Figure 5) and in other real-case studies such as de Vries et al. (2021) and Franklin et al. (2013) where species responses are wider at coarser resolutions.

Finally, with respect to previous simulation studies, our framework supports the idea that SDM performance is best when the response grain and the predictor grain are the same (Connor et al., 2018; Mertes & Jetz, 2018), since we showed that upscaling itself will change the shape of the environment–occurrence relationship. Also, upscaling will produce larger areas of overprediction (Connor et al., 2018; Franklin et al., 2013) as an artefact of using larger spatial units. However, our framework goes a step further in providing a clear mechanism, and an explanation to coarser resolution sometimes increasing predictive ability (Trivedi et al., 2008; Wunderlich et al., 2022). Both Connor et al. (2018) and Mertes and Jetz (2018), using simulations, concluded that fine predictor resolution produces higher model performance. However, in their studies, the occurrence data were not degraded in the same way the environmental data were, changing the response-to-predictor ratio (sensu Moudrý et al., 2023) across simulations. This highlights the importance of understanding how far the implicit assumptions of the simulation process might influence general conclusions (Meynard et al., 2019), and the utility of explicitly reporting the resolution of both predictor and response variables (Moudrý et al., 2023; Zurell et al., 2020). Here, we showed that fine-resolution environmental data are better for fine-resolution occurrence data. However, we also showed that increasing both the occurrence and the environmental grain can provide higher classification rates. In reality, there might be a strong trade-off between being more certain about our predictions (i.e. getting a high AUC or TSS) versus generating predictions at a sufficiently fine grain that they are useful for management purposes.

Notice also that the predictor used here (average of temperature in aggregated grid cells) is still representative of the same variable at finer resolutions. This is unlike what might happen with land use or other types of predictors. For example, Šímová et al. (2019) showed that water presence is completely missed when using coarser data sets, which greatly affects the potential occurrence of water birds and therefore SDM performance. The same applies to some topographic variables. For example, altitudinal variance at a 10-km resolution calculated from a 100-m resolution versus a 1-km resolution data set are not equivalent, the finer grain altitude providing much more topographic detail. Land use and topography variables such as these would be better handled by calculating a statistic at the modelling resolution directly from a fine-resolution data set (e.g. percent water cover at coarse resolution).

4.2 | Important caveats: It is never impossible to find a crocodile in the arctic

At least two exceptions to the assumptions in our theoretical framework are worth considering. The first is the idea that the environment–occurrence relationship never gets to be threshold-like as we continue to aggregate small grid cells during the upscaling process. A corollary of this is that the probability of occurrence is never truly identical to 0. This might be unrealistic for most real-case scenarios, as one may argue that at some large scale, there will be legitimately environments where it is impossible to find a species (e.g. a crocodile in the arctic). In more general terms, as we increase the scale of study to continental or global extents, we may more easily identify environments that are unsuitable for a species survival over the long term. The solution to this conundrum seems to be conceptual rather than statistical: If distributions are truly hierarchical, as proposed by Mackey and Lindenmayer (2001), we will have to accept that at some scale, the relevant predictors truly change and the probability of occurrence can be turned off to exactly 0. If we rely on the statistical upscaling process alone, there will always remain an area where the probability remains low but non-null. This theory therefore applies to a resolution range where such a threshold is still not attained.

4.3 | The environment varies at a finer resolution than the aggregate

The second important exception to this theory of upscaling is a situation where the environment within the aggregates is not homogeneous, and especially when it is highly variable. We treat this case with a numerical simulation (Appendix S1): although the theoretical probability of occurrence is not exactly the same as the observed one when there is variability in environmental conditions within the aggregates, the two are very similar. The difference between them is driven by the most extreme values within each aggregate. This means that the environment would need to be extremely heterogeneous within each aggregate for it to cause meaningful differences between the observed and estimated probability of occurrence. In real life, environmental predictors are usually spatially autocorrelated, which will decrease the importance of these local variations and potentially increase model performance (Moudrý et al., 2023). This goes hand in hand with the idea that classification rate can increase with upscaling, but after a certain level, it might decrease. Indeed, the coarser the resolution of the data set, the more likely it is to include areas within each grid cell that are increasingly heterogeneous. New approaches, such as hierarchical modelling, may be an interesting venue to incorporate both the hierarchical nature of species ranges and the intrinsic heterogeneity of dynamics, especially when the range of distribution is large (Lawton et al., 2022). However, there might be an optimal aggregation scale that allows increasing our ability to predict presence and absences, while keeping a reasonably fine resolution that is still useful for management purposes, regardless of the modelling method.

5 | CONCLUSIONS AND PERSPECTIVES

We have demonstrated here that upscaling environmental and occurrence data have predictable consequences. Our results show that upscaling fundamentally changes the environment–occurrence relationships, globally increases species prevalence and the mean probability of occurrence and can increase classification success up to a certain level. However, if distributions are really hierarchical, as suggested by Mackey and Lindenmayer (2001), the upper and lower bound for which this scaling theory applies depends on the scale at which processes change. The decision of the biological expert regarding relevant predictors at different scales cannot be underestimated in this regard. This study also demonstrates how a theoretical framework can greatly contribute to a better understanding of applied SDM results.

AUTHOR CONTRIBUTIONS

Christine N. Meynard and David M. Kaplan developed the conceptual framework, simulation and modelling scenarios; David M. Kaplan developed mathematical demonstrations and much of the numerical implementation; Cyril Piou provided and processed the desert locust data set; all three authors contributed to writing.

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CONFLICT OF INTEREST STATEMENT

The authors do not have any conflict of interests to declare.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data and scripts (in RMarkdown format) associated with this paper are available in our Zenodo repository (Meynard et al., 2023). We did not collect any biological samples for the purposes of this study; therefore, no permits were required.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Mathematical presentation of the theory behind the paper.

Appendix S2. Methods, code and supplementary figures for the case study presented in the paper.

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