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REVIEW

Spatially nested species distribution models (N-SDM): An effective tool to overcome niche truncation for more robust inference and projections

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Abstract

1. Species distribution models (SDMs) relate species observations to mapped environmental variables to estimate the realized niche of species and predict their distribution. SDMs are key tools for projecting the impact of climate change on species and have been used in many biodiversity assessments. However, when fitted within spatial extents that do not encompass the whole species range (i.e. subrange), the estimated realized environmental niche can be truncated, which can lead to wrong or inaccurate predictions.
2. A simple solution to this niche truncation consists in fitting SDMs at a spatial extent that encompasses the whole species range, but this often implies using a spatial resolution too coarse for local conservation assessments. To keep a fine resolution, a solution is to fit spatially nested SDMs (N-SDMs), where a whole range, coarse-grain SDM is combined with a subrange, fine-grain SDM. N-SDMs have demonstrated superior performance to subrange (truncated) SDMs in projecting species distributions under climate change and have accordingly regained considerable interest.
3. Here, we review developments, applications and effectiveness of N-SDMs. We present and discuss existing methods and tools to fit N-SDMs, and assess when N-SDMs are not needed. We highlight strengths and weaknesses of N-SDMs, underline their importance in reducing niche truncation, and identify remaining

challenges and future perspectives. Our review highlights that subrange SDMs most often lead to niche truncation and thus to incorrect spatial projections, a problem that can be overcome by using N-SDMs. We show that the various N-SDM methods come with their strengths and weaknesses and should be selected depending on the intended goal of the study.

4. *Synthesis*. N-SDMs are key tools to develop untruncated regional climate change forecasts of species distributions at fine resolution over restricted extent. While several N-SDM approaches were proposed, there is currently no universal solution suggesting that further developments and testing are crucial if we are to derive robust future projections of species distributions, at least until SDMs can be applied for most species at high resolution over large geographic extents.

KEYWORDS
bias, climate change, ecological niche, geographic restriction, habitat suitability, multiple scales, predictions, response curves

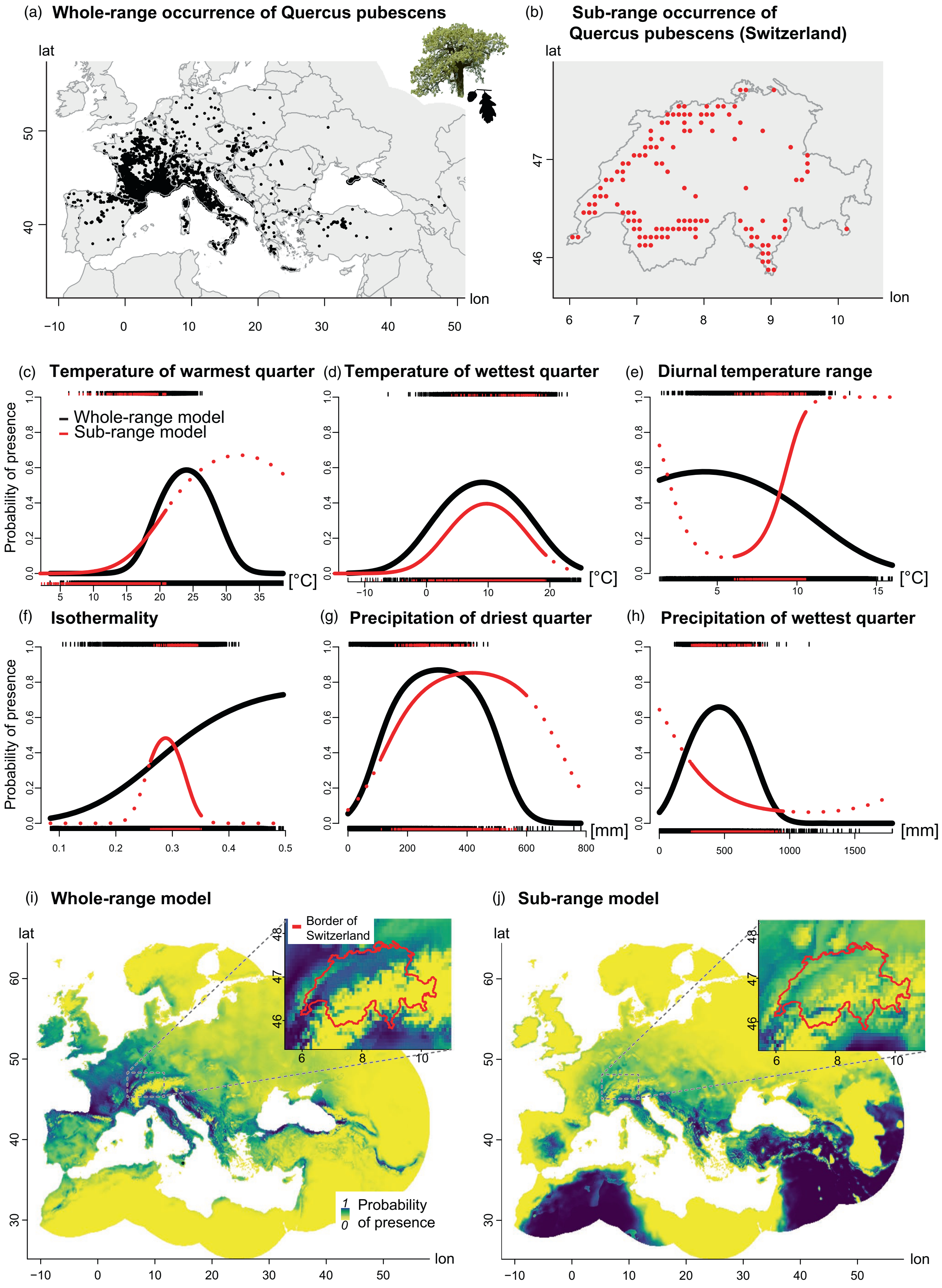
1 | SETTING THE SCENE

Species distribution models (SDMs), also known as ecological niche models (ENMs) or habitat suitability models (HSMs), among other terms (Elith & Leathwick, 2009; Franklin, 2010; Guisan et al., 2017; Peterson et al., 2011), have become major tools in ecology, conservation and biogeography (Araujo et al., 2019; Ferrier et al., 2016; Guisan et al., 2013). SDMs have a wide array of applications, a key one being to derive spatial projections of species distributions across space and time, that is, to predict where suitable locations will be under future (Guisan & Thuiller, 2005; Patiño et al., 2023; Peterson et al., 2018; Petitpierre et al., 2016) or have been under past (Bruni et al., 2024; Maiorano et al., 2013; Nogues-Bravo, 2009; Pearman et al., 2008) climates, and/or in different geographic areas (Gallien et al., 2012; Guisan et al., 2013; Petitpierre et al., 2017).

SDMs are based on the concept of Hutchinson (1957) realized environmental niche (also known as ecological niche; Austin & Smith, 1989; Guisan et al., 2017; Peterson et al., 2011). The realized niche was formalized as a hypervolume of species requirements in a multidimensional environmental space (Austin et al., 1990; Guisan & Zimmermann, 2000) and is a subset of the fundamental environmental niche constrained by biotic interactions and dispersal limitations (historic factors in Hutchinson's terms; or accessibility in Soberon, 2007). An SDM fitted with empirical observations (e.g. presence–absence, presence-only or abundance data) therefore captures the *realized* environmental niche—hereafter ecological niche—of the modelled species (Araujo & Guisan, 2006; Guisan & Zimmermann, 2000; Pearman et al., 2008; Pearson & Dawson, 2003; Soberon, 2007).

The validity of SDMs is based on several important assumptions (Anderson, 2013; Franklin, 2010; Guisan et al., 2017; Peterson et al., 2011; Zurell et al., 2020). Among these, a critical one is that the model must capture the entire ecological niche to be appropriately projected to other spatiotemporal contexts (Guisan et al., 2017). When this is not the case, there is a risk that the modelled response curves of the species along environmental gradients are truncated, resulting in biased and often incorrect predictions of species distributions (Chevalier et al., 2021; Figure 1). This phenomenon is known as 'niche truncation' and can occur when the geographic extent used to fit the model does not include all possible conditions that compose the ecological niche of a species (Figure 1; Anderson, 2013; Bazzichetto et al., 2023; Pearson et al., 2004; Thuiller, Brotons, et al., 2004). However, not all cases of geographic restriction result in niche truncation because a subset of the species range could cover the entire range of environmental conditions experienced by a species. This problem has been largely overlooked in the extensive SDM literature of the last three decades, despite early studies

FIGURE 1 Illustrating the problem of niche truncation by using a training area (Switzerland, CH) smaller than the species geographic range in Europe (EU). Black dots (a) and black curves (c–h) correspond to the full range of species (IUCN range map). Red dots (b) and red curves (c–h) correspond to the restricted training area (CH), and associated SDM predictions. The maps (i and j) show predictions along a gradient from suitable in blue to unsuitable environments in yellow (through green, intermediate suitability), obtained from a model fitted at the EU scale, and thus encompassing the whole species range (i) versus a model fitted on the restricted range only (j). The distribution of unsuitable yellow areas in the two maps (compared to the actual distribution in a) shows that the global model (i) captures much better the distribution of this species than the regional model (j). Graphs (c–h) show, for six environmental predictors in the models, how the response curves fitted with the full range (black dots in a) and restricted range (red dots in b) diverge. Inspired by Chevalier et al. (2021).


(a) Whole-range occurrence of Quercus pubescens
lat
50
40
lon
−10
0
10
20
30
40
50
(b) Sub-range occurrence of Quercus pubescens (Switzerland)
lat
47
46
lon
6
7
8
9
10
(c) Temperature of warmest quarter
Probability of presence
Whole-range model
Sub-range model
[°C]
5
10
15
20
25
30
35
(d) Temperature of wettest quarter
[°C]
−10
0
10
20
(e) Diurnal temperature range
[°C]
5
10
15
(f) Isothermality
Probability of presence
0.1
0.2
0.3
0.4
0.5
(g) Precipitation of driest quarter
[mm]
0
200
400
600
800
(h) Precipitation of wettest quarter
[mm]
0
500
1000
1500
0.0
0.2
0.4
0.6
0.8
1.0
(i) Whole-range model
lat
60
50
40
30
Border of Switzerland
48
47
46
6
8
10
1 Probability 0 of presence
lon
−10
0
10
20
30
40
50
(j) Sub-range model
lat
60
50
40
30
lon

BOX 1 A short history on the problem of niche truncation by geographic restriction

The challenge of niche truncation due to geographic restriction has been acknowledged in the scientific community for more than two decades, yet it has not been thoroughly examined until recently. The importance of capturing the entire environmental range of species in SDMs to generate meaningful spatial predictions was first emphasized two decades ago (Pearson et al., 2004; Pearson & Dawson, 2003; Thuiller, Brotons, et al., 2004). Using generalized additive models with varying sizes of nested training ranges for three tree species, Thuiller, Brotons, et al. (2004) showed that models based on restricted ranges produced significantly altered response curves and spatial overpredictions compared to full range models (e.g. erroneously predicting a mediterranean oak species in Scandinavia), leading to an underestimation of species extinction risk under climate change (see also Barbet-Massin et al., 2010 for birds in Europe). The same year, Pearson and co-authors proposed a methodological solution to this problem by fitting SDMs at two nested spatial scales, continental (Europe) to fit the entire climatic niche, and national (Britain) to include more specific land cover habitat preferences (Pearson et al., 2004). Although the original intent of the latter study was to illustrate the effects of distinct environmental variables at different spatial scales (i.e. climate in Europe, land use in the United Kingdom), it also provided a solution to the problem of niche truncation.

In a more theoretical article delving into the factors influencing climate change projections based on SDMs, Anderson (2013) underscored the critical significance of the study region that encompasses the entire spectrum of abiotic conditions a species can inhabit. This is crucial for the abiotic variables considered, as failing to do so means that SDMs can only estimate a portion of the environmental niche of the species. Anderson's work highlighted the issues that arise when using such a restricted model, particularly in terms of the inaccuracies in the environmental response curves of the species when making future projections (Fig. 3 in Anderson, 2013). Owens et al. (2013) addressed the same problem, while expanding on the associated problem of model transferability and extrapolation to novel conditions.

Hannemann et al. (2016) further explored the potential causes of prediction errors in SDMs fitted with truncated training datasets (here Germany only) for seven tree species in Europe, revealing several issues with truncated SDMs, including spurious response curves, inconsistent variable selection and large overprediction of the species across Europe. More recently, Scherrer et al. (2021) compared three scales—global, national and local—to fit SDMs for three Mexican tree species, to assess the effects of a geographic restriction of training data on the estimated environmental niche and on its projection in space and time, also assessing how it can affect the potential vulnerability of species to climate change. The results showed that the effects were species-specific and strongly dependent on the extent to which the geographic truncation affected estimations of environmental niches, with cases of strong niche underestimation leading to more vulnerability to climate change (Scherrer et al., 2021). The same year, Chevalier et al. (2021) illustrated the niche truncation problem using virtual simulations and one real plant species, proposing multiscale data fusion methods as solutions.

Since then, other studies have further discussed this niche truncation issue and its impact on species distribution models (e.g. Adde et al., 2023; Carrillo-García et al., 2023; Chevalier et al., 2022; Goicolea et al., 2024), a topic increasingly attracting attention.

showing that truncated SDM can lead to biased projections of species distributions under climate change (Box 1).

A promising strategy to address the challenges of niche truncation, that is, capturing the full ecological niche while still predicting species distributions at a fine resolution, is to fit two or more spatially nested SDMs (hereafter N-SDMs, as used in Adde et al., 2023; see dedicated section below) covering different extents and resolutions, and combine their predictions. The N-SDM approach usually includes at least (i) a 'whole range' SDM that spans the entire species range (often at a global or continental scale) to capture the full species' ecological niche, albeit at a coarse resolution and with a limited number of predictors (typically climatic variables that reflect broad-scale climatic requirements), and (ii) a 'subrange' SDM that focuses on a restricted area of interest (e.g. for conservation planning), often containing only a portion of the species range (e.g. at national or regional scale). This subrange model is typically fitted with high-resolution predictors to account for species' detailed, fine-scale requirements, such as habitat or landscape characteristics (Adde et al., 2023; Chevalier et al., 2021, 2022; Goicolea et al., 2024; Mateo et al., 2024; Mateo, Aroca-Fernández, et al., 2019; Riva et al., 2024).

The aim of this review is to present N-SDMs as an effective solution to provide fine-resolution projections at national, regional or local scales while overcoming the problem of niche truncation (Box 1). We review existing developments in this field, synthesize how N-SDMs can combine data at different scales, discuss remaining limitations and challenges, and propose some future perspectives. While doing this, we show that the ongoing development of N-SDMs has the potential to be transformative for biodiversity science. To further clarify our scope, we note that (i) previous studies have used the term 'niche truncation' referring to other issues that must not be confused with the one associated here with geographic

BOX 2 Clarifying the concepts of niche truncation and model transferability

To clarify the scope of this review, there are two important comments to make about niche truncation and model transferability.

First, other studies have used the term 'niche truncation' to refer to other issues, which should not be confused with the one associated with geographic restriction causing niche truncation that is addressed in this review. For example, the term 'truncation' has been used to refer to how much the realized environmental niche is a truncated subset of the fundamental niche (Bush et al., 2018; Chevalier et al., 2024; Vetaas, 2002; Webber et al., 2011), how the realized niche is truncated by the accessible (i.e. dispersal limitations; Peterson et al., 2018) or available environment (Chevalier et al., 2024), or how much humans have caused truncation of current species ranges and niches compared to past ones (Pang et al., 2022; Sales et al., 2022). Although these topics are still related to environmental niche dynamics (Pearman et al., 2008) and can also affect SDM predictions, they are distinct issues that are not addressed in this review.

Second, the implications for climate change projections based on SDMs affected by geographic restriction are closely intertwined with studies on SDM transferability in time and space (Barbosa et al., 2009; Charney et al., 2021; Qiao et al., 2019; Randin et al., 2006; Regos et al., 2019; Yates et al., 2018), where predictions are altered in non-analog conditions (Fitzpatrick & Hargrove, 2009; Petitpierre et al., 2017). Predicting the future distribution of a species from a model affected by niche truncation only makes the transferability issue more complex (Anderson, 2013; Peterson et al., 2018), because (i) such a model does not account for the full conditions actually experienced by the species throughout its entire range and (ii) a larger proportion of non-analog conditions is likely to occur in the future leading to prediction errors also in locations that are included within the training area but where no prediction errors are expected under current conditions (Elith et al., 2010; Velazco et al., 2024). However, this issue embraces a scope far larger than the issue related to niche truncation by geographic restriction (i.e. also touching to other issues around model fitting and evaluation; Peterson et al., 2018; Petitpierre et al., 2017; Yates et al., 2018) and is not addressed in this review.

restriction, and (ii) the implications for climate change projections based on SDMs affected by geographic restriction are closely intertwined with studies on SDM transferability in time and space (Box 2).

2 | NICHE TRUNCATION BY GEOGRAPHIC RESTRICTION

The problem of environmental niche truncation by geographic restriction (Box 1) can affect studies conducted at any extent smaller than the geographic range of the target species, but is particularly prevalent in national conservation assessments (Chevalier et al., 2021; Hannemann et al., 2016; Sanchez-Fernandez et al., 2011; Scherrer et al., 2021). Such national assessments often rely on species occurrence or abundance data retrieved from national biodiversity databases whose extent is limited by the political boundaries of the target countries (e.g. Switzerland in Figure 1, Germany in Hannemann et al., 2016, Mexico in Scherrer et al., 2021, or Iberian peninsula in Sanchez-Fernandez et al., 2011). For most species, the national/regional range used to fit the model is narrower than their entire range, and thus generally captures a subset of their ecological niche. In other terms, a Wallacean shortfall (restricted species range used in the model) often causes a Hutchinsonian shortfall (i.e. niche truncation; Scherrer et al., 2021; see Hortal et al., 2015). A similar truncation effect can occur when following a biased field sampling strategy (Bazzichetto et al., 2023; Rocchini et al., 2023). The problem is that such a Hutchinsonian shortfall can result in significant errors in spatial and/or temporal predictions of species distributions (Barbet-Massin et al., 2010; Chevalier et al., 2021, 2022; Goicolea et al., 2024; Hannemann et al., 2016).

Predictions based on restricted range SDMs can either over- (e.g. Hannemann et al., 2016; Thuiller, Brotons, et al., 2004) or under- (e.g. Sanchez-Fernandez et al., 2011; Scherrer et al., 2021) predict species distributions depending on how the geographic truncation affects species response curves (Chevalier et al., 2021; Figure 1). Such effects of misestimated response curves on spatial predictions exacerbate when projecting the effect of climate change on species distributions (Barbet-Massin et al., 2010; Chevalier et al., 2022; Goicolea et al., 2024), an approach widely used in biodiversity assessments (Araujo et al., 2019) and for conservation decisions (Guisan et al., 2013). For instance, in the study by Thuiller, Brotons, et al. (2004), truncating species response curves resulted in overpredicting the distribution of the species in future climates, leading to an underestimation of species extinction risk. Conversely, in Scherrer et al. (2021), the geographically restricted model tended to overestimate extinction risks compared to a whole-range model. Therefore, the implications of niche truncation for SDM applications are subtle and can be difficult to predict because they depend on how the response curve is truncated (Figure 1). Overall, the impact of niche truncation on SDM predictions is complex and context-dependent, highlighting the need for careful consideration of geographic boundaries and response curve assumptions when projecting species distributions (Anderson, 2013; Chevalier et al., 2021; Thuiller, Brotons, et al., 2004).

3 | LIMITATIONS OF FITTING WHOLE-RANGE MODELS TO AVOID NICHE TRUNCATION

One simple solution to make untruncated future spatial projections for a geographically restricted territory is to calibrate models over the whole species range (e.g. continental or global) and then focus on predictions for the territory of interest (e.g. Thuiller et al., 2005; fitting SDMs at the European scale to infer trends for mountain species). Scherrer et al. (2021) demonstrated the advantage of considering a continental scale whole-range approach to model the distribution of three tree species (*Alnus acuminata* Kunth, *Liquidambar styraciflua* L. and *Quercus xalapensis* Bonpl.) in cloud forest subregions of eastern Mexico, showing that national or regional subrange models overestimated habitat loss under climate change compared to the whole-range model.

However, one key limitation of whole-range—and also of many subrange (see Mod et al., 2016)—SDMs is that they often rely solely on macroclimatic predictors at a coarse resolution, typically ≥1 km grain (e.g. Scherrer et al., 2021; Thuiller et al., 2005) and do not incorporate other categories of predictors (e.g. topography, soil, land use). Climatic data at this resolution may not be sufficient to capture the detailed microclimatic requirements of species (Collart et al., 2024; Franklin et al., 2013; Haesen et al., 2023; Lembrechts, 2023; Randin et al., 2009) or other important biological aspects (e.g. community constraints; Mateo et al., 2017). This limitation is often due to the scarcity of spatially explicit predictors other than climate at the global scale, but also to the difficulty of mapping microclimates at fine resolutions over large extents (Haesen et al., 2023; Lembrechts et al., 2022). Lack of microclimatic data may not be a problem for species with wide distributions and low specialization in terms of microclimatic conditions (e.g. large mammals, dominant large trees). However, it can be very problematic for other species (e.g. species with narrow ecological niches or specific microclimatic needs; Amirkhiz et al., 2021; Carlson et al., 2013) for which whole-range models fail to capture all niche dimensions (i.e. non-climatic ones), in turn significantly influencing predictions of distribution patterns and persistence under climate change (Carrillo-García et al., 2023; Illán et al., 2010; Mateo, Gaston, et al., 2019; Randin et al., 2009). Although whole-range models are instrumental in avoiding niche truncation, they often lack the precision required for fine-scale species mapping at regional or local scales (Guisan et al., 2013; Guisan & Thuiller, 2005; Riva et al., 2023; Sirami et al., 2017). Note importantly that the lack of microclimatic data is not a problem only for whole-range SDMs but likely represents a more pronounced limitation for these models because their global extent exacerbates the probability of missing crucial fine-scale habitat variations that are important for some species (Carlson et al., 2013).

These limitations of whole-range models highlight a critical trade-off between scale and detail in species distribution modelling (Mateo, Gaston, et al., 2019; Riva et al., 2023). N-SDMs can help address these complexities by incorporating fine-resolution environmental predictors at regional or local scales (e.g. topography, soils, land use, habitat features; Mod et al., 2016; Riva et al., 2024).

4 | A PROMISING SOLUTION: SPATIALLY NESTED SDMs

A potential solution to the niche truncation problem by geographic restriction, while still being able to obtain fine-resolution predictions, is to use a spatially nested SDM (N-SDM) approach (Adde et al., 2023; Chevalier et al., 2021). N-SDMs combine a coarse-resolution SDM fitted over the entire species range (often at global or continental scale) with a fine-resolution SDM fitted over the extent desired for the study (often at national, regional or local scales; Figures 2 and 3). In the N-SDM strategy, models are fitted at different extents and resolutions, but are spatially nested within each other (e.g. Araujo et al., 2005; Gastón & García-Viñas, 2010; Keil et al., 2013; Mateo, Aroca-Fernández, et al., 2019). Species with large ranges but complex climatic dependencies, which require the consideration of both macro- and microclimatic conditions and other fine-grained environmental predictors (e.g. alpine species) could be better modelled using the N-SDM approach (e.g. a plant specialist of various habitats—rocky grasslands and meadows—in different European mountains; Chevalier et al., 2021). If the influence of other predictors than climate is expected to be captured at coarse resolution (e.g. land use in Riva et al., 2023), they could also be included in the whole-range model. This multiscale strategy ensures that both the broad scale (e.g. entire niche for the large-scale predictors) and finer ecological requirements are adequately captured (e.g. Amirkhiz et al., 2021). Note that N-SDMs are not necessarily expected to yield improved predictive performance compared to a truncated model if the performance is evaluated within the same region and the same conditions as used for model training (El-Gabbas & Dormann, 2018), because the truncation does not affect predictions inside the training conditions. The N-SDM approach thus matters, especially when untruncated response curves are required to make robust predictions in time or space.

We opted for the term ‘spatially-nested’ SDMs (N-SDMs; as introduced in Adde et al., 2023) here to reflect that this approach combines SDMs fitted at two (or more) nested spatial extents (Figures 2 and 3), but several other terms have also been used in the literature. This includes, for instance, ‘hierarchical models’ (Mateo, Aroca-Fernández, et al., 2019; Mateo, Gaston, et al., 2019; Pearson et al., 2004; Pearson & Dawson, 2003), ‘nested models’ (Adde et al., 2023) or ‘data integration models’ (Chevalier et al., 2021; Isaac et al., 2020; Miller et al., 2019; Table 1). We avoided using the term ‘hierarchical’ because it also has a statistical meaning (Clark & Gelfand, 2006) and has been used for other types of models and applications, such as combining different types of data at the same scale (e.g. data on presence only, presence–absence, abundances, functional traits, species richness; Hefley & Hooten, 2016; Kery & Royle, 2015; Pollock et al., 2012; Talluto et al., 2016). The term

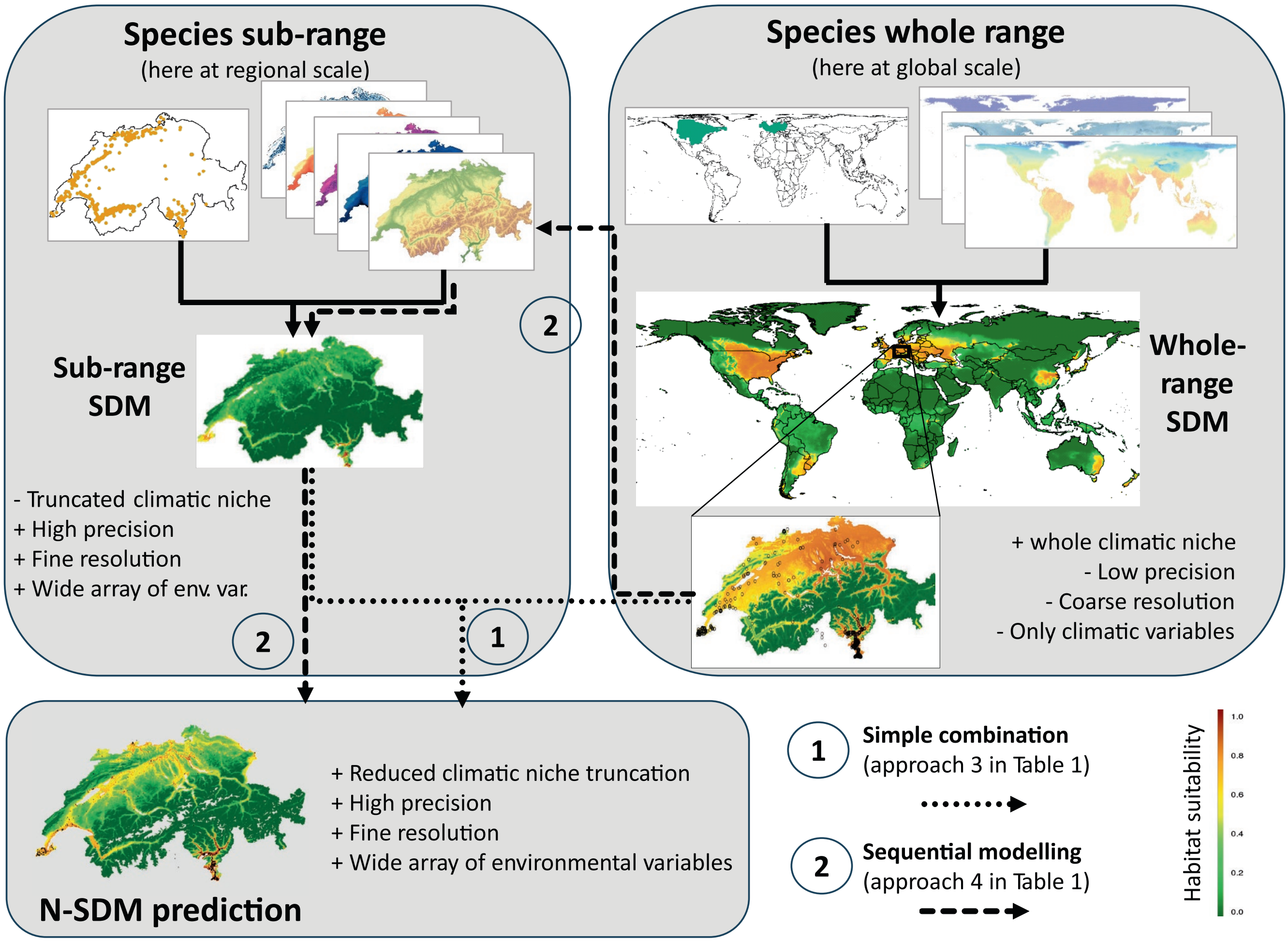


FIGURE 2 Illustration of two approaches to implement the spatially nested SDMs (N-SDM) framework to avoid niche truncation, based on a subrange and a whole-range models, each fitted from species observations and environmental maps: (1) Simple combination (number 3 in Table 1), which combines a global model including only bioclimatic predictors at coarse resolution with a regional model including also non-bioclimatic variables at finer resolution, using an average or multiplication (e.g. geometric mean) of the two predictions. (2) Sequential modelling (number 4 in Table 1), which use the prediction from the whole-range model as forced input in the regional model. Several other N-SDM approaches can be used (Chevalier et al., 2021; Mateo, Aroca-Fernández, et al., 2019) which are described in Table 1 and formalized in Figure 3.

'spatially nested SDM' has the merit of being explicit about what the approach does.

5 | DIFFERENT N-SDM APPROACHES

There are many different ways to fit N-SDMs (Chevalier et al., 2021), which we regrouped here as (Table 1, Figure 3): (1) Simple downscaling; (2) Data fusion (from the two scales, then feeding a single model); (3) Simple combination (combined model predictions, e.g. Average or Multiply options); (4) Sequential modelling (whole-range predictions feeding the subrange model, e.g. as a forced predictor (Covariate option) or through other information (e.g. prior, weight) used to parameterize the subrange model; that is. two-step approach), (5) Hierarchical downscaling, and (6) Advanced hierarchical modelling. Approaches 1 and 2 are simpler and rely on a single model that makes differential use of the data at the two scales: Approach 1 fits a whole-range model and uses it to make projections at finer resolution over a region of interest (Araujo et al., 2005), while approach 2 merges the data before fitting the model (Mateo, Aroca-Fernández, et al., 2019). The four other approaches combine two separate models but in ways of increasing complexity (Merow et al., 2014), from simple (approaches 3 and 4; Amirkhiz et al., 2021; Lomba et al., 2010), to intermediate (approach 5; Adde et al., 2023; Goicolea et al., 2024), to more advanced (approach 6; Diez & Pulliam, 2007; Keil et al., 2013) statistical methods (Table 1). An approach that is not presented in Table 1 but that could belong to Approach 4 relies on the use of whole-range model predictions to inversely weight pseudo-absences in the subrange model (Gallien et al., 2012; Petitpierre et al., 2016). However, how pseudo-absence weighting helps to account for the niche truncation problem is still conceptually and statistically unclear.

Recently, end-to-end SDM software has started to incorporate simple to intermediate N-SDM approaches. For example,

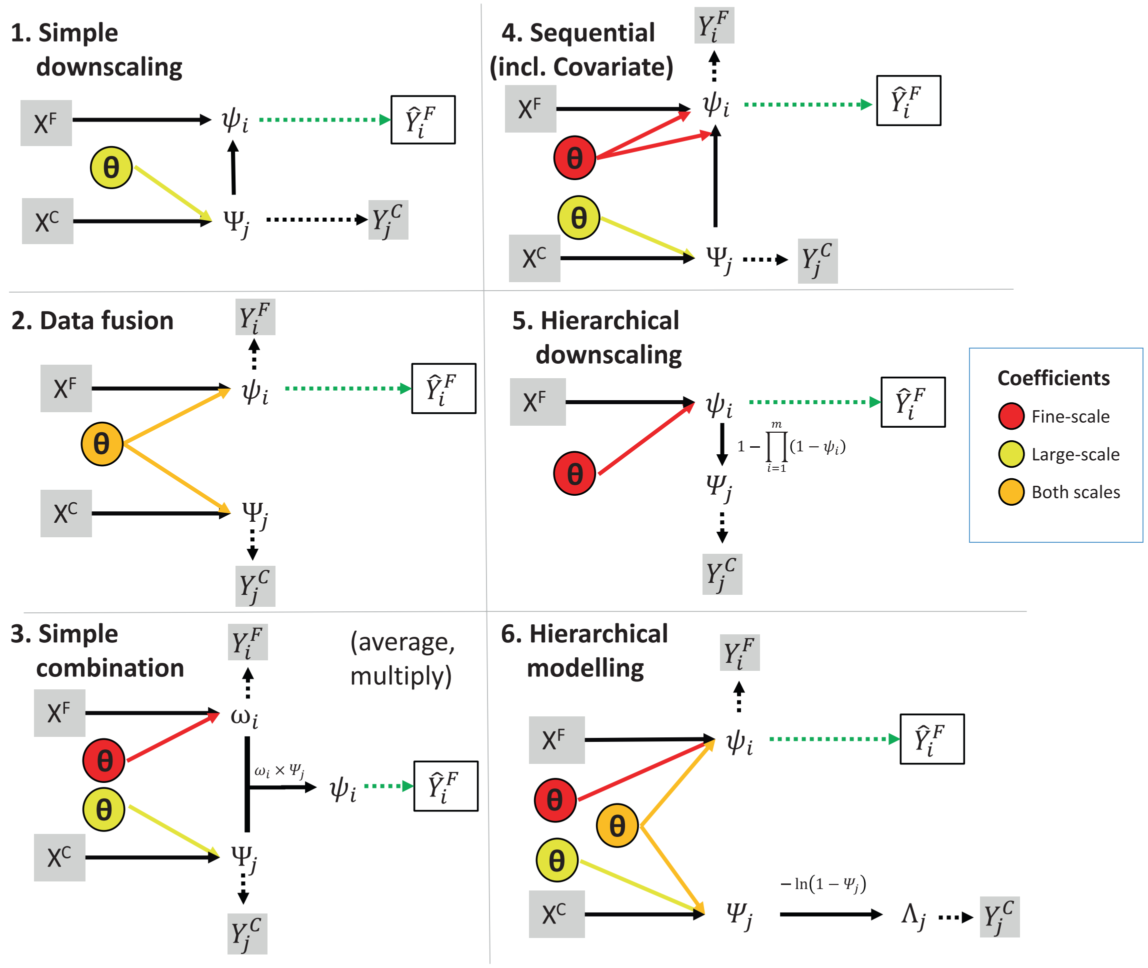


FIGURE 3 Structure of the six N-SDMs strategies described in Table 1 and represented as Bayesian networks. The aim of all strategies is to overcome the problem of niche truncation while providing predictions at high resolution. Red dots represent subrange model parameters (θ) usually associated with fine-grain predictors (e.g. land use, land cover), while yellow dots represent whole-range model parameters usually associated with coarse-grain predictors (e.g. climate). Orange dots indicate coefficients that are influenced by both data sets through joint likelihood. Grey squares are observed data (*X* denotes predictors whereas *Y* denotes distribution data such as presence–absence or presence-only) with superscript F pointing to the fine-scale data and superscript C pointing to the coarse-scale data. The open squares point to the presence–absence predictions against which model performance can be assessed, while the parameter ψ points to estimated suitability. Superscript PO indicates presence-only data. The dashed and solid arrows represent stochastic and deterministic relationships, respectively. For mathematical details, see (Chevalier et al., 2021; Isaac et al., 2020; Keil et al., 2013; Koshkina et al., 2017; Miller et al., 2019).

approaches 3 and 4 were implemented in a new N-SDM pipeline designed for high-performance computing (HPC) platforms (N-SDM package in R; Adde et al., 2023). This pipeline has already been used to compare regional predictions of tree distributions between Spain and Switzerland (Goicolea et al., 2024) and to generate 'untruncated' projections for more than 7000 species distributions in Switzerland under various climate change scenarios (Adde et al., 2024). Another R package has recently been developed to implement the same two N-SDM approaches on standard computers (i.e. non-HPC; sabinaNSDM R package; Mateo et al., 2024).

Some N-SDMs were developed under Bayesian frameworks (Chevalier et al., 2021; Hefley & Hooten, 2016; Keil et al., 2013; Mateo, Aroca-Fernández, et al., 2019), which usually better manage the propagation of uncertainty across models and scales (Gelman et al., 2013). These are often applied to simple or artificial datasets of small/moderate size but can be challenging to apply at larger scales with hundreds of observations and millions of pixels for the projections. For instance, Chevalier et al. (2021) found that some Bayesian modelling approaches (e.g. hierarchical downscaling; Keil et al., 2013) that they tested on artificial data were too computationally intensive to be scaled up for application to hundreds of species across Europe and Switzerland (Chevalier et al., 2022; Goicolea et al., 2024). However, recent developments using spatial random effects (e.g. Mateo, Aroca-Fernández, et al., 2019), together with latent terms to account for the dependence between data sources and automatic differentiation, show promise for reducing the computational burden of these models, broadening their use to many case studies including those with a large number of observations (Dovers et al., 2024). Inferences based on integrated nested Laplace approximations (INLA) have also been shown to be effective in reducing

TABLE 1 Approaches used to fit spatially nested models of species distributions (N-SDMs) grouped in six main categories, adapted from Chevalier et al. (2021) and Mateo, Aroca-Fernández, et al. (2019).

	Approach	Description	Reference	Strength	Weakness
1	Simple downscaling	A whole-range model fitted with coarse predictors. Predictions are then made over a subregion of interest, using the same predictors but at finer resolution or through recalibration	Araujo et al. (2005) *GEB*; Araujo et al. (2005); Barbosa et al. (2010) *Conserv. Biol.*; Bombi and D'Amen (2012) *J. Biogeogr.*; Gastón and García-Viñas (2010) *Ecol. Mod.*	Very simple. Only one model	Using the same predictors at the two scale (usually only climatic). Assume values of the environmental predictors at the two grain size to be equivalent. Does not account for microclimatic requirements
2	Data fusion (or data Pooling)	Merging coarse and highly resolved data at the two scales and fitting a single model	Fletcher et al. (2016) *Landsc. Ecol.*	Very simple. Only one model	Using the same predictors at the two scale (usually only climatic). Estimated response curves possibly biased by the dataset with the largest number of occurrences
3	Simple combinations (incl. average and multiply)	Whole-range model and subrange model predictions are kept separate (i.e. providing the whole information), or combined in a simple way into a final prediction, for example, through averaging (Average) or geometric mean (Multiply)	Pearson et al. (2004) *Ecography*; del Barrio et al. (2006) *Environm.Science & Policy*; Lomba et al. (2010) *Biol. Cons*; Fournier et al. (2017) *Global Ecol. Conserv*; Adde et al. (2023) *Ecography*; Mateo, Aroca-Fernández, et al. (2019) *Ecol. Mod.*; Goicolea et al. (2024), *Ecography*	Allows keeping the predictions by the models at the two scales separate, thus full information available. Different predictors can be considered in each model	Same weight usually given to the models at the two scales. In the average or multiply, a similar final prediction can be obtained from distinct combinations of suitability values of the two models
4	Sequential modelling (incl. Covariate)	Predictions of the whole-range model used as input in the subrange model as a 'forced' covariate or through other information (e.g. prior, weight) used to parameterize the subrange model (i.e. two-steps approach)	El-Gabbas and Dormann (2018) *Ecol. Evol.*, Adde et al. (2023) *Ecography*, Bellamy et al. (2020) *Landscape Ecol.*	Predictions of both whole-range and subrange suitability separate. Different predictors can be considered in each model	If climatic effects are only accounted for in the subrange model through the whole-range prediction covariate, the former may lose some accuracy to capture microclimatic requirements
5	Hierarchical downscaling	Treats subrange fine-grain presences/absences as latent variables (i.e. unobserved) which are modelled as a function of fine-grain environmental variables and constrained by whole-range coarse-grain presences/absences	Keil et al. (2013) *MEE*; Chevalier et al. (2021) *Ecol. Appl.*	Can be used without fine-scale distribution data (i.e. only relies on coarse-grain distribution data) but the model could also include fine-scale distribution data	Computationally intensive. Subject to numerical underflow when the difference in resolution between the two scales is very large. Needs fine-grain predictors over the whole-range
6	Hierarchical modelling (model fusion through joint likelihood)	Separate models at the two scales but with some parameters (typically the ones describing response curves along climatic gradients) common between the two models	Miller et al. (2019) *Methods Ecol. Evol.*; Fletcher et al. (2016) *Ecology*; Koshkina et al. (2017) *Methods Ecol. Evol*; Mateo, Gaston, et al. (2019) *Ecol. Mod.*	Strong statistical framework. Can accommodate different data types (e.g. large-scale presence-only data modelled through a spatial point process and regional presence-absence data fitted through a binomial GLM) and different response curves at the two scales. Different predictors can be considered in each model	Computationally intensive. Predictions are balanced toward the dataset that has the more influence on the likelihood (i.e. the dataset with more occurrence): thus may not solve the problem of truncation in very unbalanced datasets

the computational time in some cases (Foster et al., 2024). These approaches are now implemented in R packages (Dovers et al., 2024; Foster et al., 2024) but have not yet been applied to the N-SDM framework.

6 | USES AND APPLICATIONS OF N-SDMs

N-SDMs proved essential in national and regional studies where projections in space and/or time are needed at fine resolution, such as anticipating biological invasions (Gallien et al., 2012; Jones et al., 2010; Petitpierre et al., 2016; Vicente et al., 2019), for downscaling large-scale SDMs (Bombi & D'Amen, 2012; Keil et al., 2013; McPherson et al., 2006) or for assessing the potential effects of climate change on species distributions (Adde et al., 2024; Chevalier et al., 2021, 2022; Pearson et al., 2004). For example, Pearson et al. (2004) applied this approach to account for the large-scale effect of climate while considering the fine-scale effect of land use on the distribution of four plant species in Britain under climate change. Gallien et al. (2012) showed the importance of N-SDMs to predict invasions, as it allows including the native climatic niche in the model. Chevalier et al. (2022) showed the strength of using N-SDMs to predict the future distribution of 89 bird species in Switzerland under climate change, with larger differences in projections between subrange SDMs and N-SDMs for species whose future conditions were non-analog to the national dataset (Chevalier et al., 2022). Altogether, these studies demonstrate that N-SDMs are valuable tools for addressing niche truncation by providing a robust framework that combines the information of both coarse-grain whole-range and fine-grain subrange models to support biodiversity conservation assessments.

Beyond mitigating the effect of niche truncation on spatial and temporal predictions, another key use of N-SDMs is to quantify the effect of environmental predictors at different spatial scales (Diez & Pulliam, 2007; Lomba et al., 2010; McGill, 2010; Vicente et al., 2019). This can already be achieved within a single model (i.e. without N-SDM), for instance, through the use of spatial autocorrelation structures (Vicente et al., 2014), multigrain analyses (Riva et al., 2023) or by conducting focal analyses using moving windows of varying sizes (Adde et al., 2023; Riva et al., 2024; Scherrer et al., 2019). However, N-SDMs constitute a particularly efficient tool to decipher the effect of different predictors at different scales (i.e. resolutions and extents; McGill, 2010; Riva et al., 2023; Vicente et al., 2014), thereby offering more nuanced and actionable insights for preservation efforts (Amirkhiz et al., 2021; Carroll et al., 2010; Lomba et al., 2010; Mateo, Gaston, et al., 2019). A notable example is the advanced hierarchical three-scale SDM utilized by Diez and Pulliam (2007) to model the distribution of two orchid species in the forests of eastern North America. Using data from a hierarchical field sampling design, they discovered that understory light availability and soil moisture were key factors in explaining the presence and abundance patterns on a microsite scale (<4 m^2), while soil organic content had an effect on a population scale (<400 m^2).

N-SDMs also already proved useful in guiding various fine-resolution conservation decisions (Araujo et al., 2005; Barbosa et al., 2010; Carroll et al., 2010; Guisan et al., 2013; Maréchaux et al., 2017; Mateo, Gaston, et al., 2019). The importance of fine-scale species mapping in regional biodiversity conservation has been evidenced in several regional and national N-SDM applications (Box 1), including identifying critical habitats for sensitive species (Guisan et al., 2013), informing landscape-level species conservation (Lomba et al., 2010; Mateo, Gaston, et al., 2019), ecological restoration programmes (Carrillo-García et al., 2023), or improving the design and mapping of current and future ecological infrastructures and priority conservation areas (Honeck et al., 2020; Sanguet et al., 2023; Vincent et al., 2019), but examples of these involving N-SDMs are still rare. Some N-SDMs were also further combined with dispersal and connectivity models (del Barrio et al., 2006).

Overall, N-SDMs can thus help better understand species' ecology (Amirkhiz et al., 2021; Lomba et al., 2010; Mateo, Aroca-Fernández, et al., 2019), the role of landscape configuration (Adde et al., 2023; Austin & Meyers, 1996; Gastón et al., 2017; Girvetz & Greco, 2009; Riva et al., 2024; Scherrer et al., 2019), the drivers of local assembly of communities (Guisan & Rahbek, 2011; Hortal et al., 2012; Riva et al., 2023) and support various fine-grain conservation applications.

7 | CASE STUDIES COMPARING DIFFERENT N-SDM FRAMEWORKS

There are still relatively few studies that compare different N-SDM frameworks. Mateo, Aroca-Fernández, et al. (2019) evaluated the predictive performance of six N-SDM frameworks (encompassing approaches 1, 3, 4 and 6 in Table 1), in producing high-resolution predictions for five tree species in Central Spain. Combining data from regional (Mainland Spain) and landscape (a Biosphere Reserve) scales, the N-SDM approaches generated reliable predictions at a resolution of 25 m. Simpler N-SDM approaches, like multiplying the subrange and whole-range predictions, or including the whole-range predictions as a covariate in the subrange model (i.e. 'multiply' and 'covariate', respectively; see approaches 3 and 4 in Table 1) performed well, particularly when sample size was not a limiting factor, while Bayesian hierarchical modelling with spatially correlated random effects (approach 6 in Table 1) excelled for species with low sample size. Overall, the authors found that N-SDM approaches outperformed subrange SDMs and provided more precise projections.

In another methodological study, Chevalier et al. (2021) illustrated how and to which extent niche truncation affected SDM performance, while also testing the capacity of data integration methods (fitted with a Bayesian hierarchical approach; Isaac et al., 2020; Miller et al., 2019; approach 6 in Table 1) to solve the problem. Using primarily virtual species, this study confirmed that subrange SDMs provide biased niche estimates and thus incorrect spatial predictions outside the training area or time period considered, whereas data integration methods incorporating larger scale information reduced this bias and generated more accurate projections. However, in their real case study with a plant species (*Potentilla aurea* L.) in Switzerland, Chevalier et al. (2021) also showed that different N-SDMs can yield vastly different future predictions, from strong decrease to slight increase in environmental suitability, although one cannot know in such case which strategy is the closest to the truth.

In a third study, Goicolea et al. (2024) compared the effectiveness of the 'multiply' and 'covariate' strategies implemented in the N-SDM software (Adde et al., 2023; approaches 3 and 4 in Table 1). They focused on 108 tree species in two national-scale study areas, Spain and Switzerland, as the 'subrange' scale, with Eurasia and North Africa as the 'whole range' scale. Comparisons were made between the two N-SDMs and a subrange SDM. They found that the subrange SDM was susceptible to niche truncation and environmental extrapolation issues. In contrast, both N-SDMs, and especially the covariate approach, outperformed the subrange SDM, with significant differences in predicted (present) and projected (future) values. Although in this study the covariate N-SDM strategy demonstrated higher model performance than the multiply one, uncertainties regarding model temporal transferability supported the adoption and further investigations of multiple N-SDM approaches (Goicolea et al., 2024).

Several approaches thus exist to fit N-SDMs, but which one should be used depends primarily on the study objectives, for example whether a simple or more complex approach is required (Table 1), how uncertainty is dealt with (e.g. in a Bayesian framework), whether the two models must remain separate or whether their predictions should be sequentially combined or directly integrated within the same modelling framework (Table 1). When projection is the only aim, a sequential or an integrated approach may be more suited (e.g. Chevalier et al., 2022), but when management decision is the aim, keeping predictions separate may be more informative (Lomba et al., 2010). Yet they are still too few N-SDM studies comparing more than two methods (as, e.g. Chevalier et al., 2021; Keil et al., 2013; Mateo, Aroca-Fernández, et al., 2019), making it difficult to accurately determine which one to use in which context, more research is needed in this context.

8 | A MATTER OF SCALE: WHEN ARE N-SDMs NOT NEEDED?

N-SDMs have thus proven useful in various situations. But when are N-SDMs unnecessary? In other words, when is a single SDM sufficient to model the distribution of a given species? The decision to use an N-SDM or a single SDM fitted at a single extent depends on several factors (Figure 4), including the size of the species range (e.g. Franklin et al., 2013), the species ecology (e.g. Araujo & Pearson, 2005), environmental data availability (e.g. Mod et al., 2016), the required resolution of the environmental predictors (e.g. Moudry et al., 2023) and the intended use and target applications of the SDMs (e.g. whether projecting or not to other conditions, either in time or space; Araujo et al., 2019; Guisan & Thuiller, 2005). We discuss two situations below where either (i) large-extent and coarse-resolution models or (ii) small-extent and fine-resolution models are sufficient.

8.1 | Large-extent and coarse-resolution SDMs

This option is suitable when a relatively coarse resolution (e.g. 1 km and larger) and few predictor types (e.g. only climatic) are sufficient to the target application, and when we can reasonably assume that all populations respond similarly along environmental gradients across the whole species range (e.g. plants in Europe; Thuiller et al., 2005). In such cases, whole-range model predictions can be clipped or extracted regionally for a given study area (e.g. country, mountain range) but represent coarse estimates that likely overlook

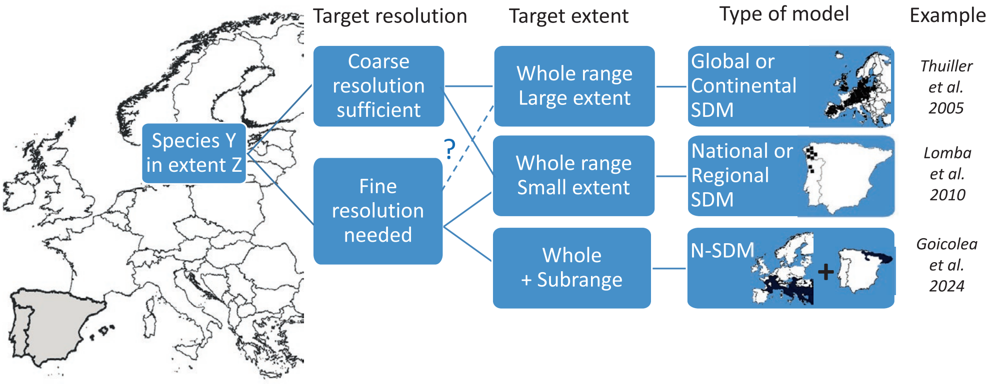


FIGURE 4 The three possible solutions identified to avoid or overcome niche truncation for predicting species *Y* in an extent *Z*, pictured here with the Iberian Peninsula (in grey, with thick contour) in Europe, depending on whether (i) a coarse resolution is sufficient or if a very fine resolution is needed and (ii) the whole species range encompasses a large or small extent, as large extents (e.g. continental, global) are still difficult to model at fine resolution. If the whole range is modelled at coarse-resolution/large extent (e.g. Thuiller et al., 2005) or fine resolution/small extent (e.g. Lomba et al., 2010), a single model accounting for the entire species niche can be used. If a part of the range (i.e. subrange) needs to be modelled at fine resolution and future projections are required, the N-SDM approach (e.g. Goicolea et al., 2024) is best suited.

regional, landscape and/or local environmental peculiarities (e.g. Patiño et al., 2023; Randin et al., 2009). Since the model is trained on the whole species range, it is not affected by niche truncation and can be used to perform predictions to other conditions (which, nevertheless, can still be affected by classical extrapolation issues; Yates et al., 2018). Whole-range SDMs are instrumental in wide-ranging studies that aim to discern large-scale species distribution patterns and their shifts over time, rather than providing detailed predictions for regional or local conservation efforts. Their applications are broad, encompassing global or continental biodiversity conservation assessments (Araujo et al., 2019), assessing species-climate relationships (Araujo & Pearson, 2005), evaluating the impact of climate change on species distributions (Thuiller et al., 2005), facilitating the creation of species distribution atlases (Araujo et al., 2005; Bombi & D'Amen, 2012) and serving as foundational inputs for N-SDMs (Chevalier et al., 2021; Mateo, Aroca-Fernández, et al., 2019; Pearson et al., 2004; see below). Species that cover large geographic areas (e.g. Bruni et al., 2024) and that are primarily influenced by macroclimatic conditions might be best modelled using whole-range SDMs (e.g. tree species in central and south America; Scherrer et al., 2021). Also, species that are in equilibrium with climate (e.g. several plants or birds; Araujo & Pearson, 2005) might also be properly modelled with this approach (e.g. Thuiller et al., 2005). Fitting such whole-range SDMs at the global or continental scale most commonly relies on coarse-resolution bioclimatic variables (e.g. 30-arcsecond resolution climate data, CHELSA; Karger et al., 2023) and coarse species distribution data, such as IUCN range maps (Hurlbert & Jetz, 2007; Maréchaux et al., 2017; Thuiller et al., 2019) or occurrence databases (e.g. GBIF, Troudet et al., 2017; or BIEN, Maitner et al., 2017).

8.2 | Small-extent and fine-resolution SDMs

This option is suitable when the whole species range is included in a reasonably small and isolated extent (e.g. region) allowing to use fine-resolution ecologically meaningful environmental predictors (e.g. Engler et al., 2011 for plant species in distinct European mountains). These SDMs are particularly useful for mapping the distribution of (i) medium to small range taxa that are entirely contained within a region (i.e. endemic species) and thus can be modelled with regional data without the risk of niche truncation (Hopkins & Burr, 2009; Lomba et al., 2010), (ii) rare species with low sample sizes that are not well represented outside the region (Amirkhiz et al., 2021; Mateo, Gaston, et al., 2019) or (iii) species with a discontinuous range containing disjoint populations (e.g. different mountaintops) of regionally endemic subspecies or genotypes (e.g. Agudo et al., 2023; Collart et al., 2021; Engler et al., 2011; Pearman et al., 2010; Smith et al., 2019). In these cases, regional SDMs can be crucial for local or regional conservation planning. However, this approach is not appropriate when the study region does not encompass the entire environmental tolerances of the species because predictions would then be affected by niche truncation. For instance, projecting SDMs to geographic areas or time periods different from those used for model training (e.g. for predicting potential invasions or projecting future climate effects) is more likely to yield inaccurate or wrong predictions because these areas are more likely to involve non-analogous conditions. Methods like multivariate environmental similarity surfaces (MESS; Elith et al., 2010) or equivalent measures (Owens et al., 2013) can be used to constrain projections within the range of conditions used for model fitting (Fitzpatrick & Hargrove, 2009; Ludwig et al., 2023; Petitpierre et al., 2017). Relative to large-extent and coarse-resolution SDMs, this approach tends to use finer resolution distribution (such as those available for national or regional monitoring programmes) and climatic (e.g. ForestClim for microclimate temperature in European Forests; Haesen et al., 2023) data and to also include non-climatic variables (topography, hydrology, soil, land use, etc.).

9 | REMAINING CHALLENGES AND FUTURE PERSPECTIVES

Although significant developments have recently been made around N-SDMs, many challenges remain for improving N-SDMs. In particular, N-SDMs can be enhanced by improving the conceptual framework and methodological standards behind them, particularly when applied to climate change and spatiotemporal projections (Araujo et al., 2019; Zurell et al., 2020). This understanding should be closely aligned with the study goals (Austin, 2007), the species occurrences available (Maréchaux et al., 2017; McPherson et al., 2006), and the climate and environmental predictors (Austin & Van Niel, 2011; Mod et al., 2016; Regos et al., 2019) being used, as well as how these predictors are expected to drive species distribution patterns at the different spatial scales considered (McGill, 2010; Pearson & Dawson, 2003).

The N-SDM methodology could particularly be improved to better capture the drivers of species distributions and abundance at multiple resolutions (Brambilla et al., 2024; Dovers et al., 2024; Patiño et al., 2023) and extents (McGill, 2010; Pearson & Dawson, 2003). Yet, there are still very few examples of such N-SDM studies. At the global scale, macroclimate variables are often expected to have the strongest influence, while at more local scales, land cover and land use variables are expected to be more influential. For instance, for plants, topography or substrate variables (e.g. soils, geology) should become increasingly important toward finer scales (Mateo, Gaston, et al., 2019; Mod et al., 2016; Pearson & Dawson, 2003). However, some work demonstrated that the effect of land use on the distribution of species can persist over large spatial extents (e.g. ~50-km pixels; Riva et al., 2023; Sales et al., 2022), implying that the long-standing assumption that climate is generally sufficient to explain the global distribution of species ranges (e.g. Thuiller, Araujo, et al., 2004) might not always be robust. Microclimatic conditions are also recognized as increasingly important (Haesen et al., 2023; Lembrechts et al., 2022), acting as micro-refugia that can help species persist under stressful conditions (Lenoir et al., 2017). Future N-SDM studies might test whether finer predictors (e.g. land use) should also be included (with climate) in the whole-range model. The N-SDM approach aims to mitigate these issues by integrating influences across scales (McGill, 2010; Riva et al., 2023; Vicente et al., 2014), thereby offering more nuanced and actionable insights for preservation efforts (Amirkhiz et al., 2021; Carroll et al., 2010; Lomba et al., 2010; Mateo, Gaston, et al., 2019), and providing a more informed foundation for conservation planning and landscape management (Guisan et al., 2013; Mateo, Gaston, et al., 2019; Tulloch et al., 2016).

Another key methodological improvement to optimally apply N-SDMs will be to evaluate the best N-SDM strategy for integrating models and/or predictions at different scales (Table 1), an area ripe for innovation (Chevalier et al., 2021; Goicolea et al., 2024). Currently, there is no one-size-fits-all method, and the variety of approaches developed (Table 1) underscores the complexity of combining multiscale predictions (Chevalier et al., 2021; Mateo, Aroca-Fernández, et al., 2019). Comprehensive theoretical and methodological comparisons, including mathematical formalism (outlined in Chevalier et al., 2021), are crucial for rigorously and systematically assessing the strengths and weaknesses of the different N-SDM approaches (as initiated in Table 1; see also Dovers et al., 2024; Foster et al., 2024 for non-N-SDM examples), for instance through the use of artificial data and virtual species approaches (Chevalier et al., 2021). This would guide the selection of the optimal approach given the purposes of a study and the type of organisms modelled. The evolving landscape of hierarchical modelling calls for novel approaches that can seamlessly meld insights from global to local scales, enhancing the precision and applicability of N-SDMs. Other important methodological developments will be the incorporation of species with limited data, for example through applying an ensemble of small models (ESMs; Breiner et al., 2015; Lomba et al., 2010; see, e.g. Adde et al., 2023) to include rare species (see, e.g. Amirkhiz et al., 2021) and to account for dependencies between species, for example through multispecies or joint N-SDMs (as, e.g. for SDMs; Brun et al., 2024; Poggiato et al., 2021). While these developments exist for regular SDMs, implementing these options within N-SDMs should enhance their robustness and applicability.

10 | CONCLUSIONS

At a time marked by a growing need for predicting the effect of climate change and other anthropogenic pressures (e.g. land-use change, fragmentation, pollution, biological invasions) on species distributions at fine scales, and amidst calls for enhancing standards of models and predictions that feed major biodiversity assessments (Araujo et al., 2019), the importance of spatially nested SDMs (N-SDMs) has remained neglected. Our review highlighted that situations of niche truncation are frequent in regional and national assessments and underscored the critical importance of N-SDMs as key tools to develop untruncated regional climate change forecasts of species distributions at fine resolution over restricted extents. As such, further development and testing of N-SDMs is crucial if we are to derive robust future projections of species distribution under climate and other environmental change scenarios, until SDMs can eventually be applied for most species at high resolution over large geographic extents.

AUTHOR CONTRIBUTIONS

Antoine Guisan proposed and designed the review, made a first review of the literature and wrote a full first draft of the manuscript, and of all initial figures, boxes and Table 1. All co-authors contributed to the partial restructuring and writing of all subsequent versions of the manuscript, table, boxes and captions that led to the final version. Olivier Broennimann redrew Figure 1 with help from Antoine Guisan, Teresa Goicolea and Olivier Broennimann redrew Figure 2, Mathieu Chevalier and Antoine Guisan redrew Figure 3, Antoine Guisan and Alejandra Zarzo-Arias redrew Figure 4. Mathieu Chevalier, Rubén G. Mateo, Bart Steen, Antoine Adde helped Antoine Guisan revise Table 1.

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CONFLICT OF INTEREST STATEMENT

None.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

No data are associated with the paper.

STATEMENT OF INCLUSION

The group of co-authors includes both women and men at different stages of research career, including several early career researchers. The manuscript results from a history of collaboration between the co-authors spread between Switzerland, Spain, the Netherlands, Belgium and France. All researchers who contributed ideas used in this manuscript were included as co-authors.

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REFERENCES

Adde, A., Külling, N., Rey, P.-L., Fopp, F., Brun, P., Broennimann, O., Lehmann, A., Petitpierre, B., Zimmermann, N. E., Pellissier, L., Altermatt, F., & Guisan, A. (2024). Projecting untruncated climate change effects on species' climate suitability: Insights from an alpine country. *Global Change Biology*, *30*, e17557.

Adde, A., Rey, P.-L., Brun, P., Külling, N., Fopp, F., Altermatt, F., Broennimann, O., Lehmann, A., Petitpierre, B., Zimmermann, N. E., Pellissier, L., & Guisan, A. (2023). N-SDM: A high-performance computing pipeline for nested species distribution modelling. *Ecography*, *2023*, e06540.

Agudo, A. B., Pico, X., Mateo, R. G., Arnald, M., Torices, R., & Álvarez, I. (2023). Unravelling plant diversification: Intraspecific genetic differentiation in hybridizing Anacyclus species in the western Mediterranean Basin. *American Journal of Botany*, *110*, e16121.

Amirkhiz, R. G., Dixon, M. D., Palmer, J. S., & Swanson, D. L. (2021). Investigating niches and distribution of a rare species in a hierarchical framework: Virginia's Warbler (*Leiothlypis virginiae*) at its northeastern range limit. *Landscape Ecology*, *36*, 1039–1054.

Anderson, R. P. (2013). A framework for using niche models to estimate impacts of climate change on species distributions. *Annals of the New York Academy of Sciences*, *1297*, 8–28.

Araujo, M. B., Anderson, R. P., Barbosa, A. M., Beale, C. M., Dormann, C. F., Early, R., Garcia, R. A., Guisan, A., Maiorano, L., Naimi, B., O'Hara, R. B., Zimmermann, N. E., & Rahbek, C. (2019). Standards for distribution models in biodiversity assessments. *Science Advances*, *5*(1), eaat4858. https://doi.org/10.1126/sciadv.aat4858

Araujo, M. B., & Guisan, A. (2006). Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, *33*, 1677–1688.

Araujo, M. B., & Pearson, R. G. (2005). Equilibrium of species' distributions with climate. *Ecography*, *28*, 693–695.

Araujo, M. B., Thuiller, W., Williams, P. H., & Reginster, I. (2005). Downscaling European species atlas distributions to a finer resolution: Implications for conservation planning. *Global Ecology and Biogeography*, *14*, 17–30.

Austin, M. (2007). Species distribution models and ecological theory: A critical assessment and some possible new approaches. *Ecological Modelling*, *200*, 1–19.

Austin, M. P., & Meyers, J. A. (1996). Current approaches to modelling the environmental niche of eucalypts: Implication for management of forest biodiversity. *Forest Ecology and Management*, *85*, 95–106.

Austin, M. P., Nicholls, A. O., & Margules, C. R. (1990). Measurement of the realized qualitative niche—Environmental niches of 5 eucalyptus species. *Ecological Monographs*, *60*, 161–177.

Austin, M. P., & Smith, T. M. (1989). A new model for the continuum concept. *Vegetatio*, *83*, 35–47.

Austin, M. P., & Van Niel, K. P. (2011). Improving species distribution models for climate change studies: Variable selection and scale. *Journal of Biogeography*, *38*, 1–8.

Barbet-Massin, M., Thuiller, W., & Jiguet, F. (2010). How much do we overestimate future local extinction rates when restricting the range of occurrence data in climate suitability models? *Ecography*, *33*, 878–886.

Barbosa, A. M., Real, R., & Vargas, J. M. (2009). Transferability of environmental favourability models in geographic space: The case of the Iberian desman (*Galemys pyrenaicus*) in Portugal and Spain. *Ecological Modelling*, *220*, 747–754.

Barbosa, A. M., Real, R., & Vargas, J. M. (2010). Use of coarse-resolution models of species' distributions to guide local conservation inferences. *Conservation Biology*, *24*, 1378–1387.

Bazzichetto, M., Lenoir, J., Da Re, D., Tordoni, E., Rocchini, D., Malavasi, M., Barták, V., & Sperandii, M. G. (2023). Sampling strategy matters to accurately estimate response curves' parameters in species distribution models. *Global Ecology and Biogeography*, *32*(10), 1717–1729. https://doi.org/10.1111/geb.13725

Bellamy, C., Boughey, K., Hawkins, C., Reveley, S., Spake, R., Williams, C., & Altringham, J. (2020). A sequential multi-level framework to improve habitat suitability modelling. *Landscape Ecology*, *35*, 1001–1020.

Bombi, P., & D'Amen, M. (2012). Scaling down distribution maps from atlas data: A test of different approaches with virtual species. *Journal of Biogeography*, *39*, 640–651.

Brambilla, M., Bazzi, G., & Ilahiane, L. (2024). The effectiveness of species distribution models in predicting local abundance depends on model grain size. *Ecology*, *105*, e4224.

Breiner, F. T., Guisan, A., Bergamini, A., & Nobis, M. P. (2015). Overcoming limitations of modelling rare species by using ensembles of small models. *Methods in Ecology and Evolution*, *6*, 1210–1218.

Brun, P., Karger, D. N., Zurell, D., Descombes, P., de Witte, L. C., de Lutio, R., Wegner, J. D., & Zimmermann, N. E. (2024). Multispecies deep learning using citizen science data produces more informative plant community models. *Nature Communications*, *15*, 4421.

Bruni, E. P., Rusconi, O., Broennimann, O., Adde, A., Jauslin, R., Krashevska, V., Kosakyan, A., du Châtelet, E. A., Alcino, J. P. B., Beyens, L., Blandenier, Q., Bobrov, A., Burdman, L., Duckert, C., Fernández, L. D., Souza, M. B. G. E., Heger, T. J., Koenig, I., Lahr, D. J. G., … Mitchell, E. A. D. (2024). Global distribution modelling of a conspicuous Gondwanian soil protist reveals latitudinal dispersal limitation and range contraction in response to climate warming. *Diversity and Distributions*, *30*, e13779.

Bush, A., Catullo, R. A., Mokany, K., Thornhill, A. H., Miller, J. T., & Ferrier, S. (2018). Truncation of thermal tolerance niches among Australian plants. *Global Ecology and Biogeography*, *27*, 22–31.

Carlson, B. Z., Randin, C. F., Boulangeat, I., Lavergne, S., Thuiller, W., & Choler, P. (2013). Working toward integrated models of alpine plant distribution. *Alpine Botany*, *123*, 41–53.

Carrillo-García, C., Girola-Iglesias, L., Guijarro, M., Hernando, C., Madrigal, J., & Mateo, R. G. (2023). Ecological niche models applied to post-megafire vegetation restoration in the context of climate change. *Science of the Total Environment*, *855*, 158858.

Carroll, C., Johnson, D. S., Dunk, J. R., & Zielinski, W. J. (2010). Hierarchical Bayesian spatial models for multispecies conservation planning and monitoring. *Conservation Biology*, *24*, 1538–1548.

Charney, N. D., Record, S., Gerstner, B. E., Merow, C., Zarnetske, P. L., & Enquist, B. (2021). A test of species distribution model transferability across environmental and geographic space for 108 Western north American tree species. *Frontiers in Ecology and Evolution*, *9*, 689295.

Chevalier, M., Broennimann, O., Cornuault, J., & Guisan, A. (2021). Data integration methods to account for spatial niche truncation effects in regional projections of species distribution. *Ecological Applications*, *31*, e02427.

Chevalier, M., Broennimann, O., & Guisan, A. (2024). Climate change may reveal currently unavailable parts of species' ecological niches. *Nature Ecology & Evolution*, *8*, 1298–1310.

Chevalier, M., Zarzo-Arias, A., Guélat, J., Mateo, R. G., & Guisan, A. (2022). Accounting for niche truncation to improve spatial and temporal predictions of species distributions. *Frontiers in Ecology and Evolution*, *10*, 944116.

Clark, J. S., & Gelfand, A. E. (2006). *Hierarchical modelling for the environmental sciences: Statistical methods and applications* (p. 205). Oxford University Press.

Collart, F., Hedenas, L., Broennimann, O., Guisan, A., & Vanderpoorten, A. (2021). Intraspecific differentiation: Implications for niche and distribution modelling. *Journal of Biogeography*, *48*, 415–426.

Collart, F., Kiebacher, T., Quetsch, M., Broennimann, O., Guisan, A., & Vanderpoorten, A. (2024). To what extent can we predict variation of bryophyte and tracheophyte community composition at fine spatial scale along an elevation gradient? *Science of the Total Environment*, *926*, 171741.

del Barrio, G., Harrison, P. A., Berry, P. M., Butt, N., Sanjuan, M. E., Pearson, R. G., & Dawson, T. (2006). Integrating multiple modelling approaches to predict the potential impacts of climate change on species' distributions in contrasting regions: Comparison and implications for policy. *Environmental Science & Policy*, *9*, 129–147.

Diez, J. M., & Pulliam, H. R. (2007). Hierarchical analysis of species distributions and abundance across environmental gradients. *Ecology*, *88*, 3144–3152.

Dovers, E., Popovic, G. C., & Warton, D. I. (2024). A fast method for fitting integrated species distribution models. *Methods in Ecology and Evolution*, *15*, 191–203.

El-Gabbas, A., & Dormann, C. F. (2018). Wrong, but useful: Regional species distribution models may not be improved by range-wide data under biased sampling. *Ecology and Evolution*, *8*, 2196–2206.

Elith, J., Kearney, M., & Phillips, S. (2010). The art of modelling range-shifting species. *Methods in Ecology and Evolution*, *1*, 330–342.

Elith, J., & Leathwick, J. R. (2009). Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, *40*, 677–697.

Engler, R., Randin, C. F., Thuiller, W., Dullinger, S., Zimmermann, N. E., Araujo, M. B., Pearman, P. B., Le Lay, G., Piedallu, C., Albert, C. H., Choler, P., Coldea, G., De Lamo, X., Dirnbock, T., Gegout, J. C., Gomez-Garcia, D., Grytnes, J. A., Heegaard, E., Hoistad, F., … Guisan, A. (2011). 21st century climate change threatens mountain flora unequally across Europe. *Global Change Biology*, *17*, 2330–2341.

Ferrier, S., Ninan, K. N., Leadley, P., Alkemade, R., Acosta, L. A., Akçakaya, H. R., Brotons, L., Cheung, W. W. L., Christensen, V., Harhash, K. A., Kabubo-Mariara, J., Lundquist, C., Obersteiner, M., Pereira, H. M., Peterson, G., Pichs-Madruga, R., Ravindranath, N., Rondinini, C., & Wintle, B. A. (2016). *IPBES: The methodological assessment report on scenarios and models of biodiversity and ecosystem services*. Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES).

Fitzpatrick, M. C., & Hargrove, W. W. (2009). The projection of species distribution models and the problem of non-analog climate. *Biodiversity and Conservation*, *18*, 2255–2261.

Fletcher, R. J., McCleery, R. A., Greene, D. U., & Tye, C. A. (2016). Integrated models that unite local and regional data reveal larger-scale environmental relationships and improve predictions of species distributions. *Landscape Ecology*, *31*, 1369–1382.

Foster, S. D., Peel, D., Hosack, G. R., Hoskins, A., Mitchell, D. J., Proft, K., Yang, W. H., Uribe-Rivera, D. E., & Froese, J. G. (2024). 'RISDM': Species distribution modelling from multiple data sources in R. *Ecography*, *2024*, e06964.

Fournier, A., Barbet-Massin, M., Rome, Q., & Courchamp, F. (2017). Predicting species distribution combining multi-scale drivers. *Global Ecology and Conservation*, *12*, 215–226.

Franklin, J. (2010). *Mapping species distributions: Spatial inference and prediction*. Cambridge University Press.

Franklin, J., Davis, F. W., Ikegami, M., Syphard, A. D., Flint, L. E., Flint, A. L., & Hannah, L. (2013). Modeling plant species distributions under future climates: How fine scale do climate projections need to be? *Global Change Biology*, *19*, 473–483.

Gallien, L., Douzet, R., Pratte, S., Zimmermann, N. E., & Thuiller, W. (2012). Invasive species distribution models - how violating the equilibrium assumption can create new insights. *Global Ecology and Biogeography*, *21*, 1126–1136.

Gastón, A., Ciudad, C., Mateo-Sánchez, M. C., García-Viñas, J. I., López-Leiva, C., Fernández-Landa, A., Marchamalo, M., Cuevas, J., de la Fuente, B., Fortin, M. J., & Saura, S. (2017). Species' habitat use inferred from environmental variables at multiple scales: How much we gain from high-resolution vegetation data? *International Journal of Applied Earth Observation and Geoinformation*, *55*, 1–8.

Gastón, A., & García-Viñas, J. I. (2010). Updating coarse-scale species distribution models using small fine-scale samples. *Ecological Modelling*, *221*, 2576–2581.

Gelman, A., Carlin, J. B., Stern, H. S., Dunson, D. B., Vehtari, A., & Rubin, D. B. (2013). *Bayesian data analysis*. Chapman and Hall/CRC Press.

Girvetz, E. H., & Greco, S. E. (2009). Multi-scale predictive habitat suitability modeling based on hierarchically delineated patches: An example for yellow-billed cuckoos nesting in riparian forests, California, USA. *Landscape Ecology*, *24*, 1315–1329.

Goicolea, T., Adde, A., Broennimann, O., García-Viñas, J., Gaston, A., Aroca-Fernández, M. J., Guisan, A., & Mateo, R. G. (2024). Spatially-nested hierarchical species distribution models to overcome niche truncation in national-scale studies. *Ecography*, *2025*, e07328.

Guisan, A., & Rahbek, C. (2011). SESAM—A new framework integrating macroecological and species distribution models for predicting spatio-temporal patterns of species assemblages. *Journal of Biogeography*, *38*, 1433–1444.

Guisan, A., & Thuiller, W. (2005). Predicting species distribution: Offering more than simple habitat models. *Ecology Letters*, *8*, 993–1009.

Guisan, A., Thuiller, W., & Zimmermann, N. E. (2017). *Habitat suitability and distribution models, with applications in R*. Cambridge University Press.

Guisan, A., Tingley, R., Baumgartner, J. B., Naujokaitis-Lewis, I., Sutcliffe, P. R., Tulloch, A. I. T., Regan, T. J., Brotons, L., McDonald-Madden, E., Mantyka-Pringle, C., Martin, T. G., Rhodes, J. R., Maggini, R., Setterfield, S. A., Elith, J., Schwartz, M. W., Wintle, B. A., Broennimann, O., Austin, M., … Buckley, Y. M. (2013). Predicting species distributions for conservation decisions. *Ecology Letters*, *16*, 1424–1435.

Guisan, A., & Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling*, *135*, 147–186.

Haesen, S., Lenoir, J., Gril, E., De Frenne, P., Lembrechts, J. J., Kopecky, M., Macek, M., Man, M., Wild, J., & Van Meerbeek, K. (2023). Microclimate reveals the true thermal niche of forest plant species. *Ecology Letters*, *26*, 2043–2055.

Hannemann, H., Willis, K. J., & Macias-Fauria, M. (2016). The devil is in the detail: Unstable response functions in species distribution models challenge bulk ensemble modelling. *Global Ecology and Biogeography*, *25*, 26–35.

Hefley, T. J., & Hooten, M. B. (2016). Hierarchical species distribution models. *Current Landscape Ecology Reports*, *1*, 87–97.

Honeck, E. C., Moilanen, A., Guinaudeau, B., Wyler, N., Schlaepfer, M., Martin, P., Sanguet, A., Urbina, L., von Arx, B., Massy, J., Fischer, C., & Lehmann, A. (2020). Implementing green infrastructure for the spatial planning of peri-urban areas in Geneva, Switzerland. *Sustainability*, *12*, 1387.

Hopkins, R. L., & Burr, B. M. (2009). Modeling freshwater fish distributions using multiscale landscape data: A case study of six narrow range endemics. *Ecological Modelling*, *220*, 2024–2034.

Hortal, J., de Bello, F., Diniz-Filho, J. A. F., Lewinsohn, T. M., Lobo, J. M., & Ladle, R. J. (2015). Seven shortfalls that beset large-scale knowledge of biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *46*, 523–549.

Hortal, J., de Marco, P., Santos, A. M. C., & Diniz, J. A. F. (2012). Integrating biogeographical processes and local community assembly. *Journal of Biogeography*, *39*, 627–628.

Hurlbert, A. H., & Jetz, W. (2007). Species richness, hotspots, and the scale dependence of range maps in ecology and conservation.

Proceedings of the National Academy of Sciences of the United States of America, *104*, 13384–13389.

Hutchinson, G. E. (1957). Population studies—Animal ecology and demography—Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, *22*, 415–427.

Illán, J. G., Gutiérrez, D., & Wilson, R. J. (2010). The contributions of topoclimate and land cover to species distributions and abundance: Fine-resolution tests for a mountain butterfly fauna. *Global Ecology and Biogeography*, *19*, 159–173.

Isaac, N. J. B., Jarzyna, M. A., Keil, P., Dambly, L. I., Boersch-Supan, P. H., Browning, E., Freeman, S. N., Golding, N., Guillera-Arroita, G., Henrys, P. A., Jarvis, S., Lahoz-Monfort, J. J., Pagel, J., Pescott, O. L., Schmucki, R., Simmonds, E. G., & O'Hara, R. B. (2020). Data integration for large-scale models of species distributions. *Trends in Ecology & Evolution*, *35*, 56–67.

Jones, C. C., Acker, S. A., & Halpern, C. B. (2010). Combining local- and large-scale models to predict the distributions of invasive plant species. *Ecological Applications*, *20*, 311–326.

Karger, D. N., Chauvier, Y., & Zimmermann, N. E. (2023). chelsa-cmip6 1.0: A python package to create high resolution bioclimatic variables based on CHELSA ver. 2.1 and CMIP6 data. *Ecography*, *2023*, e06535.

Keil, P., Belmaker, J., Wilson, A. M., Unitt, P., & Jetz, W. (2013). Downscaling of species distribution models: A hierarchical approach. *Methods in Ecology and Evolution*, *4*, 82–94.

Kery, M., & Royle, J. A. (2015). *Applied hierarchical modeling in ecology: Analysis of distribution, abundance and species richness in R and BUGS*.

Koshkina, V., Wang, Y., Gordon, A., Dorazio, R. M., White, M., & Stone, L. (2017). Integrated species distribution models: Combining presence-background data and site-occupany data with imperfect detection. *Methods in Ecology and Evolution*, *8*, 420–430.

Lembrechts, J. J. (2023). Microclimate alters the picture. *Nature Climate Change*, *13*, 423–424.

Lembrechts, J. J., van den Hoogen, J., Aalto, J., Ashcroft, M. B., De Frenne, P., Kemppinen, J., Kopecky, M., Luoto, M., Maclean, I. M. D., Crowther, T. W., Bailey, J. J., Haesen, S., Klinges, D. H., Niittynen, P., Scheffers, B. R., Van Meerbeek, K., Aartsma, P., Abdalaze, O., Abedi, M., … Lenoir, J. (2022). Global maps of soil temperature. *Global Change Biology*, *28*, 3110–3144.

Lenoir, J., Hattab, T., & Pierre, G. (2017). Climatic microrefugia under anthropogenic climate change: Implications for species redistribution. *Ecography*, *40*, 253–266.

Lomba, A., Pellissier, L., Randin, C., Vicente, J., Moreira, F., Honrado, J., & Guisan, A. (2010). Overcoming the rare species modelling paradox: A novel hierarchical framework applied to an Iberian endemic plant. *Biological Conservation*, *143*, 2647–2657.

Ludwig, M., Moreno-Martinez, A., Hölzel, N., Pebesma, E., & Meyer, H. (2023). Assessing and improving the transferability of current global spatial prediction models. *Global Ecology and Biogeography*, *32*, 356–368.

Maiorano, L., Cheddadi, R., Zimmermann, N. E., Pellissier, L., Petitpierre, B., Pottier, J., Laborde, H., Hurdu, B. I., Pearman, P. B., Psomas, A., Singarayer, J. S., Broennimann, O., Vittoz, P., Dubuis, A., Edwards, M. E., Binney, H. A., & Guisan, A. (2013). Building the niche through time: Using 13,000 years of data to predict the effects of climate change on three tree species in Europe. *Global Ecology and Biogeography*, *22*, 302–317.

Maitner, B. S., Boyle, B., Casler, N., Condit, R., Donoghue, J., II, Durán, S. M., Guaderrama, D., Hinchliff, C. E., Jørgensen, P. M., Kraft, N. J. B., McGill, B., Merow, C., Morueta-Holme, N., Peet, R. K., Sandel, B., Schildhauer, M., Smith, S. A., Svenning, J.-C., Thiers, B., … Enquist, B. J. (2017). The bien r package: A tool to access the botanical information and ecology network (BIEN) database. *Methods in Ecology and Evolution*, *9*, 373–379.

Maréchaux, I., Rodrigues, A. S. L., & Charpentier, A. (2017). The value of coarse species range maps to inform local biodiversity conservation in a global context. *Ecography*, *40*, 1166–1176.

Mateo, R. G., Aroca-Fernández, M. J., Gastón, A., Gómez-Rubio, V., Saura, S., & García-Viñas, J. I. (2019). Looking for an optimal hierarchical approach for ecologically meaningful niche modelling. *Ecological Modelling*, *409*, 108735. https://doi.org/10.1016/j.ecolmodel.2019.108735

Mateo, R. G., Gaston, A., Aroca-Fernandez, M. J., Broennimann, O., Guisan, A., Saura, S., & Garcia-Vinas, J. I. (2019). Hierarchical species distribution models in support of vegetation conservation at the landscape scale. *Journal of Vegetation Science*, *30*, 386–396.

Mateo, R. G., Mokany, K., & Guisan, A. (2017). Biodiversity models: What if unsaturation is the rule? *Trends in Ecology & Evolution*, *32*, 556–566.

Mateo, R. G., Morales-Barbero, J., Zarzo-Arias, A., Lima, H., Gómez-Rubio, V., & Goicolea, T. (2024). sabinaNSDM: An R package for spatially nested hierarchical species distribution modelling. *Methods in Ecology and Evolution*, *15*, 1796–1803.

McGill, B. J. (2010). Matters of scale. *Science*, *328*, 575–576.

McPherson, J. M., Jetz, W., & Rogers, D. J. (2006). Using coarse-grained occurrence data to predict species distributions at finer spatial resolutions: Possibilities and limitations. *Ecological Modelling*, *192*, 499–522.

Merow, C., Smith, M. J., Edwards, T. C., Guisan, A., McMahon, S. M., Normand, S., Thuiller, W., Wuest, R. O., Zimmermann, N. E., & Elith, J. (2014). What do we gain from simplicity versus complexity in species distribution models? *Ecography*, *37*, 1267–1281.

Miller, D. A. W., Pacifici, K., Sanderlin, J. S., & Reich, B. J. (2019). The recent past and promising future for data integration methods to estimate species' distributions. *Methods in Ecology and Evolution*, *10*, 22–37.

Mod, H. K., Scherrer, D., Luoto, M., & Guisan, A. (2016). What we use is not what we know: Environmental predictors in plant distribution models. *Journal of Vegetation Science*, *27*, 1308–1322.

Moudry, V., Keil, P., Cord, A. F., Gabor, L., Lecours, V., Zarzo-Arias, A., Bartak, V., Malavasi, M., Rocchini, D., Torresani, M., Gdulova, K., Grattarola, F., Leroy, F., Marchetto, E., Thouverai, E., Prosek, J., Wild, J., & Simova, P. (2023). Scale mismatches between predictor and response variables in species distribution modelling: A review of practices for appropriate grain selection. *Progress in Physical Geography: Earth and Environment*, *47*, 467–482.

Nogues-Bravo, D. (2009). Predicting the past distribution of species climatic niches. *Global Ecology and Biogeography*, *18*, 521–531.

Owens, H. L., Campbell, L. P., Dornak, L. L., Saupe, E. E., Barve, N., Soberon, J., Ingenloff, K., Lira-Noriega, A., Hensz, C. M., Myers, C. E., & Peterson, A. T. (2013). Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. *Ecological Modelling*, *263*, 10–18.

Pang, S. E. H., Zeng, Y., De Alban, J. D. T., & Webb, E. L. (2022). Occurrence–habitat mismatching and niche truncation when modelling distributions affected by anthropogenic range contractions. *Diversity and Distributions*, *28*, 1327–1343.

Patiño, J., Collart, F., Vanderpoorten, A., Martin-Esquivel, J. L., Naranjo-Cigala, A., Mirolo, S., & Karger, D. N. (2023). Spatial resolution impacts projected plant responses to climate change on topographically complex islands. *Diversity and Distributions*, *29*, 1245–1262.

Pearman, P. B., D'Amen, M., Graham, C. H., Thuiller, W., & Zimmermann, N. E. (2010). Within-taxon niche structure: Niche conservatism, divergence and predicted effects of climate change. *Ecography*, *33*, 990–1003.

Pearman, P. B., Guisan, A., Broennimann, O., & Randin, C. F. (2008). Niche dynamics in space and time. *Trends in Ecology & Evolution*, *23*, 149–158.

Pearson, D., Dawson, T. P., & Liu, C. (2004). Modelling species distribution in Britain: A hierarchical integration of climate and land-cover data. *Ecography*, *27*, 285–298.

Pearson, R. G., & Dawson, T. E. (2003). Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Global Ecology and Biogeography*, *12*, 361–372.

Peterson, A. T., Cobos, M. E., & Jimenez-Garcia, D. (2018). Major challenges for correlational ecological niche model projections to future climate conditions. *Annals of the New York Academy of Sciences*, *1429*, 66–77.

Peterson, A. T., Soberón, J., Pearson, R. G., Anderson, R., Martínez-Meyer, E., Nakamura, M., & Araújo, M. P. (2011). *Ecological niches and geographic distributions*. Princeton University Press.

Petitpierre, B., Broennimann, O., Kueffer, C., Daehler, C., & Guisan, A. (2017). Selecting predictors to maximize the transferability of species distribution models: Lessons from cross-continental plant invasions. *Global Ecology and Biogeography*, *26*, 275–287.

Petitpierre, B., McDougall, K., Seipel, T., Broennimann, O., Guisan, A., & Kueffer, C. (2016). Will climate change increase the risk of plant invasions into mountains? *Ecological Applications*, *26*, 530–544.

Poggiato, G., Munkemuller, T., Bystrova, D., Arbel, J., Clark, J. S., & Thuiller, W. (2021). On the interpretations of joint modeling in community ecology. *Trends in Ecology & Evolution*, *36*, 391–401.

Pollock, L. J., Morris, W. K., & Vesk, P. A. (2012). The role of functional traits in species distributions revealed through a hierarchical model. *Ecography*, *35*, 716–725.

Qiao, H., Feng, X., Escobar, L. E., Peterson, A. T., Soberón, J., Zhu, G., & Papeş, M. (2019). An evaluation of transferability of ecological niche models. *Ecography*, *42*, 521–534.

Randin, C. F., Dirnbock, T., Dullinger, S., Zimmermann, N. E., Zappa, M., & Guisan, A. (2006). Are niche-based species distribution models transferable in space? *Journal of Biogeography*, *33*, 1689–1703.

Randin, C. F., Engler, R., Normand, S., Zappa, M., Zimmermann, N. E., Pearman, P. B., Vittoz, P., Thuiller, W., & Guisan, A. (2009). Climate change and plant distribution: Local models predict high-elevation persistence. *Global Change Biology*, *15*, 1557–1569.

Regos, A., Gagne, L., Alcaraz-Segura, D., Honrado, J. P., & Dominguez, J. (2019). Effects of species traits and environmental predictors on performance and transferability of ecological niche models. *Scientific Reports*, *9*, 4221.

Riva, F., Barbero, F., Balletto, E., & Bonelli, S. (2023). Combining environmental niche models, multi-grain analyses, and species traits identifies pervasive effects of land use on butterfly biodiversity across Italy. *Global Change Biology*, *29*, 1715–1728.

Riva, F., Martin, C. J., Galán Acedo, C., Bellon, E. N., Keil, P., Morán-Ordóñez, A., Fahrig, L., & Guisan, A. (2024). Incorporating effects of habitat patches into species distribution models. *Journal of Ecology*, *112*, 2162–2182.

Rocchini, D., Tordoni, E., Marchetto, E., Marcantonio, M., Barbosa, A. M., Bazzichetto, M., Beierkuhnlein, C., Castelnuovo, E., Gatti, R. C., Chiarucci, A., Chieffallo, L., Da Re, D., Di Musciano, M., Foody, G. M., Gabor, L., Garzon-Lopez, C. X., Guisan, A., Hattab, T., Hortal, J., … Malavasi, M. (2023). A quixotic view of spatial bias in modelling the distribution of species and their diversity. *npj Biodiversity*, *2*, 1–11.

Sales, L. P., Galetti, M., Carnaval, A., Monsarrat, S., Svenning, J.-C., & Pires, M. M. (2022). The effect of past defaunation on ranges, niches, and future biodiversity forecasts. *Global Change Biology*, *28*, 3683–3693.

Sanchez-Fernandez, D., Lobo, J. M., & Hernandez-Manrique, O. L. (2011). Species distribution models that do not incorporate global data misrepresent potential distributions: A case study using Iberian diving beetles. *Diversity and Distributions*, *17*, 163–171.

Sanguet, A., Wyler, N., Guinaudeau, B., Waller, N., Urbina, L., Huber, L., Fischer, C., & Lehmann, A. (2023). Mapping ecological infrastructure in a cross-border regional context. *Lands*, *12*, 2010.

Scherrer, D., Christe, P., & Guisan, A. (2019). Modelling bat distributions and diversity in a mountain landscape using focal predictors in ensemble of small models. *Diversity and Distributions*, *25*, 770–782.

Scherrer, D., Esperon-Rodriguez, M., Beaumont, L. J., Barradas, V. L., & Guisan, A. (2021). National assessments of species vulnerability to climate change strongly depend on selected data sources. *Diversity and Distributions*, *27*, 1367–1382.

Sirami, C., Caplat, P., Popy, S., Clamens, A., Arlettaz, R., Jiguet, F., Brotons, L., & Martin, J.-L. (2017). Impacts of global change on species distributions: Obstacles and solutions to integrate climate and land use. *Global Ecology and Biogeography*, *26*, 385–394.

Smith, A. B., Godsoe, W., Rodriguez-Sanchez, F., Wang, H. H., & Warren, D. (2019). Niche estimation above and below the species level. *Trends in Ecology & Evolution*, *34*, 260–273.

Soberon, J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, *10*, 1115–1123.

Talluto, M. V., Boulangeat, I., Ameztegui, A., Aubin, I., Berteaux, D., Butler, A., Doyon, F., Drever, C. R., Fortin, M. J., Franceschini, T., Liénard, J., McKenney, D., Solarik, K. A., Strigul, N., Thuiller, W., & Gravel, D. (2016). Cross-scale integration of knowledge for predicting species ranges: A metamodelling framework. *Global Ecology and Biogeography*, *25*, 238–249.

Thuiller, W., Araujo, M. B., & Lavorel, S. (2004). Do we need land-cover data to model species distributions in Europe? *Journal of Biogeography*, *31*, 353–361.

Thuiller, W., Brotons, L., Araujo, M. B., & Lavorel, S. (2004). Effects of restricting environmental range of data to project current and future species distributions. *Ecography*, *27*, 165–172.

Thuiller, W., Guéguen, M., Renaud, J., Karger, D. N., & Zimmermann, N. E. (2019). Uncertainty in ensembles of global biodiversity scenarios. *Nature Communications*, *10*, 1446.

Thuiller, W., Lavorel, S., Araujo, M. B., Sykes, M. T., & Prentice, I. C. (2005). Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 8245–8250.

Troudet, J., Grandcolas, P., Blin, A., Vignes-Lebbe, R., & Legendre, F. (2017). Taxonomic bias in biodiversity data and societal preferences. *Scientific Reports*, *7*, 9132.

Tulloch, A. I. T., Sutcliffe, P., Naujokaitis-Lewis, I., Tingley, R., Brotons, L., Ferraz, K., Possingham, H., Guisan, A., & Rhodes, J. R. (2016). Conservation planners tend to ignore improved accuracy of modelled species distributions to focus on multiple threats and ecological processes. *Biological Conservation*, *199*, 157–171.

Velazco, S. J. E., Rose, M. B., De Marco, P. J. r., Regan, H. M., & Franklin, J. (2024). How far can I extrapolate my species distribution model? Exploring shape, a novel method. *Ecography*, *2024*, e06992.

Vetaas, O. R. (2002). Realized and potential climate niches: A comparison of four Rhododendron tree species. *Journal of Biogeography*, *29*(4), 545–554. https://doi.org/10.1046/j.1365-2699.2002.00694.x

Vicente, J. R., Gonçalves, J., Honrado, J. P., Randin, C. F., Pottier, J., Broennimann, O., Lomba, A., & Guisan, A. (2014). A framework for assessing the scale of influence of environmental factors on ecological patterns. *Ecological Complexity*, *20*, 151–156.

Vicente, J. R., Kueffer, C., Richardson, D. M., Vaz, A. S., Cabral, J. A., Hui, C., Araujo, M. B., Kuhn, I., Kull, C. A., Verburg, P. H., Marchante, E., & Honrado, J. P. (2019). Different environmental drivers of alien tree invasion affect different life-stages and operate at different spatial scales. *Forest Ecology and Management*, *433*, 263–275.

Vincent, C., Fernandes, R. F., Cardoso, A. R., Broennimann, O., Di Cola, V., D'Amen, M., Ursenbacher, S., Schmidt, B. R., Pradervand, J. N., Pellissier, L., & Guisan, A. (2019). Climate and land-use changes reshuffle politically-weighted priority areas of mountain biodiversity. *Global Ecology and Conservation*, *17*, e00589.

Webber, B. L., Yates, C. J., Le Maitre, D. C., Scott, J. K., Kriticos, D. J., Ota, N., McNeill, A., Le Roux, J. J., & Midgley, G. F. (2011). Modelling horses for novel climate courses: Insights from projecting potential distributions of native and alien Australian acacias with correlative and mechanistic models. *Diversity and Distributions*, *17*, 978–1000.

Yates, K. L., Bouchet, P. J., Caley, M. J., Mengersen, K., Randin, C. F., Parnell, S., Fielding, A. H., Bamford, A. J., Ban, S., Barbosa, A. M., Dormann, C. F., Elith, J., Embling, C. B., Ervin, G. N., Fisher, R., Gould, S., Graf, R. F., Gregr, E. J., Halpin, P. N., … Sequeira, A. M. M. (2018). Outstanding challenges in the transferability of ecological models. *Trends in Ecology & Evolution*, *33*, 790–802.

Zurell, D., Franklin, J., König, C., Bouchet, P. J., Dormann, C. F., Elith, J., Fandos, G., Feng, X., Guillera-Arroita, G., Guisan, A., Lahoz-Monfort, J. J., Leitão, P. J., Park, D. S., Peterson, A. T., Rapacciuolo, G., Schmatz, D. R., Schröder, B., Serra-Diaz, J. M., Thuiller, W., … Merow, C. (2020). A standard protocol for reporting species distribution models. *Ecography*, *43*, 1261–1277.

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