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Invited Review

Applications of species distribution modeling to paleobiology

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ABSTRACT

Species distribution modeling (SDM: statistical and/or mechanistic approaches to the assessment of range determinants and prediction of species occurrence) offers new possibilities for estimating and studying past organism distributions. SDM complements fossil and genetic evidence by providing (i) quantitative and potentially high-resolution predictions of the past organism distributions, (ii) statistically formulated, testable ecological hypotheses regarding past distributions and communities, and (iii) statistical assessment of range determinants. In this article, we provide an overview of applications of SDM to paleobiology, outlining the methodology, reviewing SDM-based studies to paleobiology or at the interface of paleo- and neobiology, discussing assumptions and uncertainties as well as how to handle them, and providing a synthesis and outlook. Key methodological issues for SDM applications to paleobiology include predictor variables (types and properties; special emphasis is given to paleo-climate), model validation (particularly important given the emphasis on cross-temporal predictions in paleobiological applications), and the integration of SDM and genetics approaches. Over the last few years the number of studies using SDM to address paleobiology-related questions has increased considerably. While some of these studies only use SDM (23%), most combine them with genetically inferred patterns (49%), paleoecological records (22%), or both (6%). A large number of SDM-based studies have addressed the role of Pleistocene glacial refugia in biogeography and evolution, especially in Europe, but also in many other regions. SDM-based approaches are also beginning to contribute to a suite of other research questions, such as historical constraints on current distributions and diversity patterns, the end-Pleistocene megafaunal extinctions, past community assembly, human paleo-biogeography, Holocene paleoecology, and even deep-time biogeography (notably, providing insights into biogeographic dynamics >400 million years ago). We discuss important assumptions and uncertainties that affect the SDM approach to paleobiology – the equilibrium postulate, niche stability, changing atmospheric CO₂ concentrations – as well as ways to address these (ensemble, functional SDM, and non-SDM ecoinformatics approaches). We conclude that the SDM approach offers important opportunities for advances in paleobiology by providing a quantitative ecological perspective, and hereby also offers the potential for an enhanced contribution of paleobiology to ecology and conservation biology, e.g., for estimating climate change impacts and for informing ecological restoration.

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1. Introduction

The distribution and abundance of organisms in the past is a key issue for paleobiology as well as for its parent disciplines, geology and biology. For both paleo- and neobiology, the spatial distribution of organisms and the changes herein through time are fundamental for understanding the evolution of biodiversity, its geographic patterns (Lomolino et al., 2010), and how to best preserve it (Margules and Pressey, 2000; Willis et al., 2010). For geology, the past distribution of organisms is an important component of biostratigraphy and -chronology (Agustí et al., 2001; Fischer, 2002)

Abbreviations: SDM, species distribution modeling; DVM, dynamic vegetation model; GCM, general circulation model; AOGCM, atmosphere-ocean general circulation model; RCM, regional climate model.

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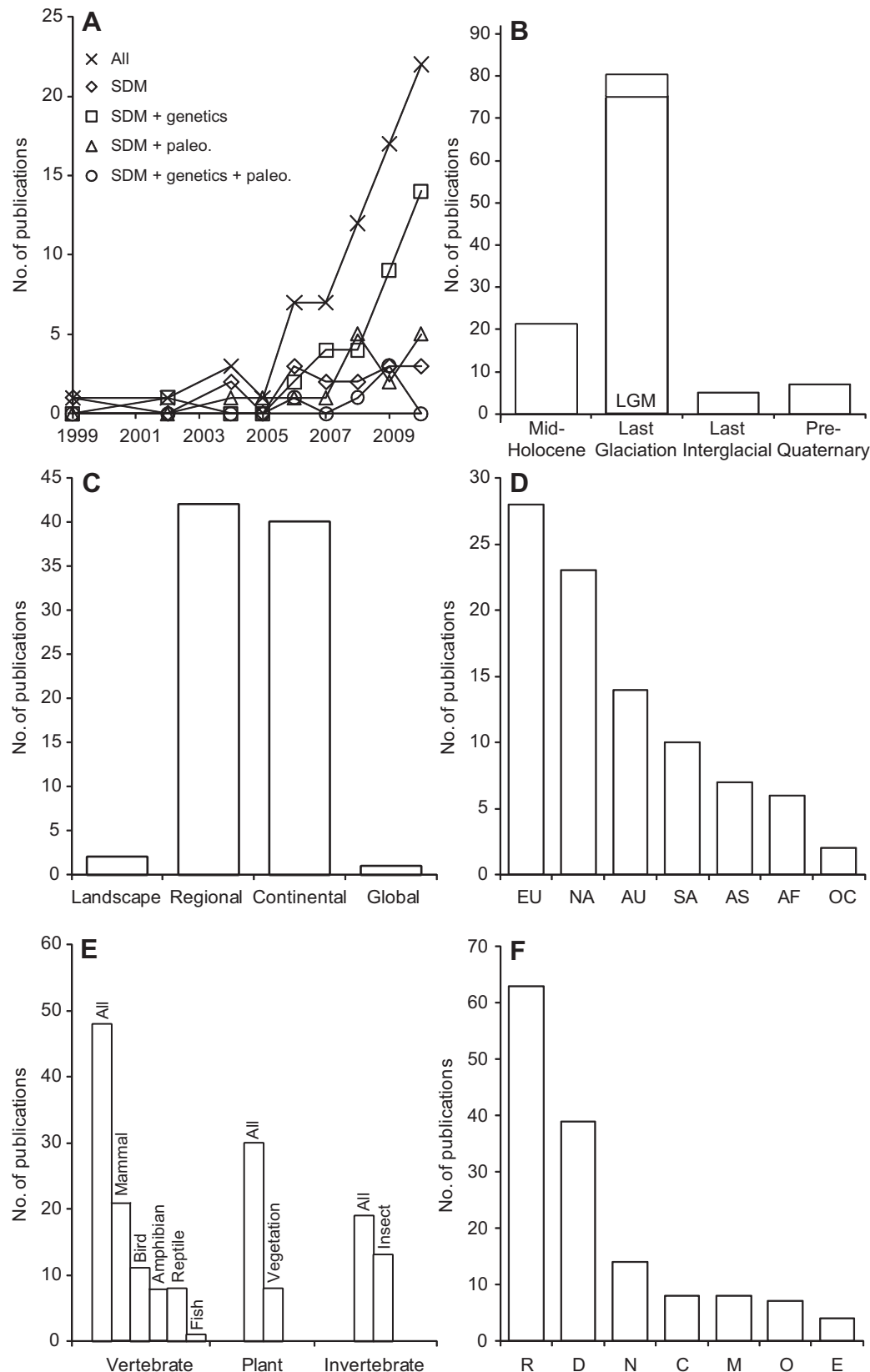


Fig. 1. Summary of paleobiological SDM applications, encompassing SDM-based studies which use paleoclimate simulations and/or paleoecological records, primarily compiled by an ISI Web of Science search (see Appendix for details): (A) Change in number of publications using SDM in paleobiology from 1998 to March 2011 (in total of 82 publications): all publications (diamond), and publications combining hindcasting and phylogeography (triangles), SDM and paleoecological records (circles), or hindcasting, phylogeography, and paleoecological records in combination (crosses). (B) Time periods assessed: mid-Holocene (c. 3.6–8 ka BP), Last Glaciation (mainly LGM at c. 21 ka BP, including a few studies for 30 ka BP and 42 ka BP [indicated separately at the top of the bar]), Last Interglacial (c. 120 ka–140 ka), or pre-Quaternary (>2.6 my). (C) Study scale (extent): landscape (10–200 km),

and paleoclimatology (Wolfe, 1995; Mosbrugger, 1997), and has been instrumental for the development of plate tectonics theory (Lomolino et al., 2010).

A key challenge for all areas related to the distribution of species is the “Wallacean shortfall”, or the incomplete information on species distributions (Lomolino et al., 2010). While this is true for current species distributions, it is obviously much more of a problem for past species distributions. Traditionally, the only source of information on species distributions in the prehistoric past has been fossil and subfossil remains of organisms. While this source of information remains the only direct evidence for the occurrence of an organism at a given place and time in the past, such remains are often scarce and generally provide an incomplete, coarse and biased reflection of past distributions. In the past 40 years, the direct paleontological evidence has increasingly been supplemented by cladistics, phylogenetics and phylogeography, allowing us to estimate past distributions from current distributions of clades, lineages, and genetic diversity within species or narrow lineages (Rosen, 1978; Ronquist, 1997; Walker and Avise, 1998; Sanmartín and Ronquist, 2004; Avise, 2009). While highly valuable sources of information, these methods also have their limitations; geographical reconstructions can be highly dependent on assumed speciation, extinction, and dispersal models, and in the case of phylogeography, often involve simplified, qualitative environmental scenarios (e.g., Taberlet et al., 1998; Walker and Avise, 1998).

Species distribution modeling (SDM; including habitat modeling and ecological niche modeling) refers to statistical and/or mechanistic approaches to the assessment of range determinants and prediction of species occurrence across space and/or time. This approach offers the possibility for investigating core theoretical issues in ecology (Svenning et al., 2008b, 2010; Oswald et al., 2010) and evolutionary biology (Graham et al., 2004; Nogués-Bravo et al., 2008; Paul et al., 2009) and has important applications to conservation and global change biology (Thomas et al., 2004; Thuiller et al., 2005; Broennimann et al., 2007; Araújo et al., 2011). As the SDM approach allows taking advantage of the rapidly increasing wealth of environmental data and has experienced rapid methodological development, utilization of SDM has grown substantially during the last decade. Furthermore, SDM applications are not restricted to distributions of species, but may also be applied to modeling distributions of other taxonomic entities or ecological or ecosystem types, such as tropical wet forest (Carnaval and Moritz, 2008) or tropical seasonally dry forest (Werneck et al., 2011). Methodological approaches and advances in SDM have been subjected to several reviews (Franklin, 1995, 2009; Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005; Elith and Leathwick, 2009). The SDM approach is now increasingly being applied to paleobiology and to studies that bridge neo- and paleobiology, notably phylogeography, biogeography, and macroecology (Fig. 1). More specifically, SDM complements fossil and genetic evidence by providing:

- (i) Quantitative and potentially high-resolution predictions of the past distribution of organisms (e.g., Eeley et al., 1999; Stigall Rode and Lieberman, 2005; Stigall and Lieberman, 2006), a contribution that is not only of theoretical importance, but also of practical utility for targeted location of new paleobiological field sites (Stigall Rode and Lieberman, 2005).

- (ii) Statistically formulated, testable ecological hypotheses regarding past distributions and communities and their dynamics (e.g., Stigall Rode and Lieberman, 2005; Knowles et al., 2007; Richards et al., 2007; Eckert, 2011).
- (iii) Statistical assessment of determinants of organism distributions (Rodríguez-Sánchez and Arroyo, 2008).

Most applications of SDM are based on statistical assessments of relationships between species presence and potential drivers (Guisan and Zimmermann, 2000). However, an important alternative approach in SDM is based on physiologically-informed mechanistic models (Kearney and Porter, 2009) and can be defined to include dynamic vegetation models (DVM) (e.g., Prentice et al., 2011). These mechanistic approaches may have high predictive ability if they are based on well-understood relationships. In paleobiology, these mechanistic models have especially been used for predicting the occurrence of major vegetation types or functional types (Allen et al., 2010; Pound et al., 2011; Prentice et al., 2011) and have been integrated into atmospheric general circulation models for paleoclimate (e.g., Ramstein et al., 2007). However, their general applicability to predict past distributions beyond the level of coarse organism types is limited by the requirements for a thorough understanding of the physiology and ecology of the organisms in question. Reflecting the high demands for their parameterization (Rodríguez-Sánchez et al., 2010) and their fundamentally different methodology, here we will focus on statistically-based SDM, although mechanistic models are discussed in Section 4.2.2.

In this article, we provide an overview of the applications of SDM to paleobiology. We first outline the methodology and then review how SDM has been applied to shed light on important questions in paleobiology or at the interface of paleo- and neo-biology, covering both established as well as novel, emerging applications. To provide a synthetic overview we performed a comprehensive literature review, covering 82 publications (Fig. 1, Appendix). Next, we discuss how to handle the assumptions and uncertainties affecting the SDM approach and its application to paleobiology. Finally, we provide a synthesis and outlook for the contribution of SDM to paleobiology.

2. Methodology

Species have responded to past environmental changes in individualistic and complex manners, from tolerance and evolutionary adaption *in situ*, to small- and large-scale migration, to local and global extinctions (Huntley and Webb, 1989; Jackson and Overpeck, 2000; McGill et al., 2005). Modeling past dynamics of species distributions using SDM is therefore not a simple endeavor, but requires careful integration of data and methods as well as considered handling of assumptions and limitations. The scientific literature on SDM from the last two decades contains an impressive amount of studies assessing and discussing theoretical assumptions and methodological approaches (e.g., Franklin, 1995; Peterson and Cohoon, 1999; Guisan and Zimmermann, 2000; Pearson and Dawson, 2003; Hampe, 2004; Guisan and Thuiller, 2005; Elith et al., 2006; Heikkinen et al., 2006; Pearson et al., 2006; Jiménez-Valverde et al., 2008; Thuiller et al., 2008; Elith and Leathwick, 2009; Nogués-Bravo, 2009; Lavergne et al., 2010). Here we focus

regional (200–2000 km), continental (2000–10000 km), or global (following Pearson and Dawson, 2003). (D) Study regions: Europe (EU), North America (NA), Australia and New Zealand (AU), Africa (AF), Asia (AS), or oceans (OC). (E) Organism groups. (F) Main study aims: R, location of refugia or past distribution patterns in general; D, effect of past distribution patterns on diversification within or among species; N, niche conservatism; C, determinants of current patterns of species diversity or ranges; M, migration pathways from past to present distributions; O, other aim, e.g., methodological; E, extinction.

on those aspects that we consider of particular importance when applying SDM to paleobiology.

2.1. General methodological considerations

Species distribution modeling, as described here, involves the following steps: (i) spatial or spatiotemporal linking of species distribution records to potential driving factors or their correlates; (ii) estimation (and often testing) of distribution-driver relationships, including ecological niche estimates, (iii) prediction of species' realized range (actual occurrences) or potential range (suitable habitat) in space within the same time period, or (iv) in another time period. Hind-casting refers to the latter, where a model calibrated on data for a given period (often the present) is used to predict the range in a preceding period. While focus is often on (iv), as will be described in detail below (Fig. 1), SDM applications to paleobiology may also stop at step (ii) or (iii). See Fig. 2 for an overview.

2.1.1. Species distribution records

The quality and quantity of species distribution data available is crucial for the SDM approach, and critical aspects such as sample size, sampling bias, and modeling remedies for the latter have been broadly discussed in the literature (Jiménez-Valverde and Lobo, 2006; Pearson et al., 2007; Phillips et al., 2009; Veloz, 2009; Mateo et al., 2010). SDM applications that rely on paleodistributional data also face these challenges, often to a greater extent due to the paucity of such data. Although SDM can be successfully implemented with limited distribution data, robust inference and prediction is likely to depend on a fair sample size – ideally with a minimum of 10–20 observations per predictor (Harrell, 2001).

2.1.2. Predictors

Several types of predictors can be included in SDM. Environmental predictors can be classified as resource, direct, or indirect gradient variables, representing consumed resources, environmental factors with physiological importance that are not consumed, and variables with no direct importance but which correlate with one or more resource or direct gradients,

respectively (Guisan and Zimmermann, 2000). The use of mechanistically relevant resource and direct gradient variables are likely to result in models of greater general applicability (Guisan and Zimmermann, 2000), notably in terms of cross-temporal transferability (see below). However, species distributions are not just constrained by the abiotic environment, but also by biotic interactions and dispersal (Soberón, 2007). Hence, it may also be relevant to include biotic predictors (Preston et al., 2008; Meier et al., 2010) and predictors that represent dispersal constraints (De Marco et al., 2008; Svenning et al., 2008b; Blach-Overgaard et al., 2010); these have rarely been implemented in paleobiological applications of SDM thus far. However, using large numbers of highly intercorrelated predictor variables may cause inference problems and reduce predictive ability, and so care should be taken to choose only those which best describe the ecological limitations of a species (cf. e.g., Graham, 2003).

Among environmental predictors, climatic data are the most widely used; in part because many studies focus on climate effects (see Section 3. Applications), but also due to the perceived dominant role of climate as a control on distributions at the coarse spatial scales typically studied (Pearson and Dawson, 2003) (Fig. 1). Further, for cross-temporal predictions, predictor types are restricted to those available for all time periods under consideration, with climate often the only information available for past environments. The main source of paleoclimatic data for SDM studies are past climatic reconstructions based on general circulation models (GCMs; or AOGCMs when the climatic model integrates an atmospheric-ocean coupled model). These simulation models provide spatially-explicit outputs of large-scale patterns of temperature and precipitation. Their spatial grain resolution tends to be 2°–5°, although higher resolution (to 25–50 km) may be achieved by embedding a regional climate model (RCM) for a specific region into a GCM. An important source of paleoclimatic reconstructions is the Paleoclimate Modelling Intercomparison Project (PMIP, <http://pmip3.lscce.ipsl.fr/>).

Higher spatial resolution of paleoclimatic reconstructions can be achieved using statistical downscaling procedures (e.g., Svenning et al., 2008a). WorldClim currently provides statistically

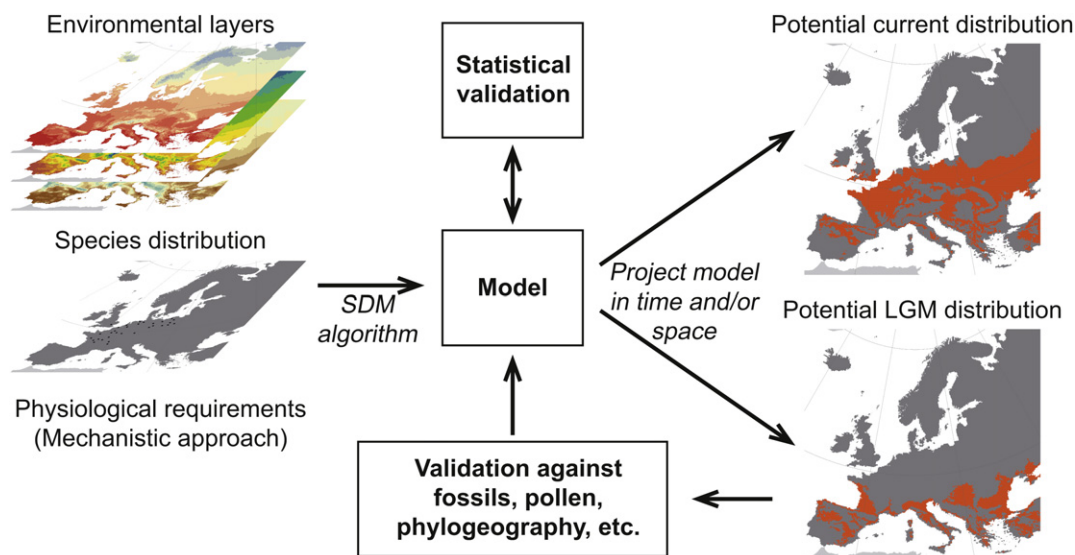


Fig. 2. An overview of the SDM approach: occurrences of a hypothetical species and environmental layers containing climatic variables (here from CRU: <http://www.cru.uea.ac.uk/cru/data/hrg.htm> New et al., 2002) are linked through a modeling algorithm. Mechanistic approaches include data such as species physiological requirements, e.g., as obtained from lab experiments. The ability of the model to predict the data can be evaluated statistically and settings in the modeling procedure can be fine-tuned to obtain the best model. The model can then be projected onto the input climatic variables to predict the current potential distribution (red area) or it can be projected onto climate reconstructions from different time periods or geographic extents to predict the species potential distribution in time and space. These projections can be further evaluated by comparison to fossil finds, phylogeographic reconstructions, etc.

downscaled high-resolution (30'' or 2.5') PMIP-based climatic surfaces for the Last Interglacial (~130 ka BP) and Last Glacial Maximum (LGM, c. 21 ka BP) (<http://www.worldclim.org/past>), and WorldClim data have been used in 38% of the studies addressing paleobiological questions with SDM (Appendix). Although statistical downscaling offers the chance to use detailed past climatic information while accounting for ecologically important small-scale climate variability (cf. Ackerly et al., 2010), this approach also has important limitations. Statistical downscaling usually combines macroclimatic anomalies between past and current conditions with current high-resolution climate data to estimate past high-resolution climate patterns. Hence, this approach assumes that the relationship between large- and small-scale climate variables is stationary over time, an assumption which is unlikely to always hold. A direct consequence of any such temporal nonstationarity is that downscaling might produce errors that could propagate across scales (Katz, 2002). GCM-based paleoclimatic reconstructions have largely been restricted to the Late Quaternary, notably LGM and the mid-Holocene, but simulations for pre-Quaternary periods such as the Late Miocene (e.g., Steppuhn et al., 2006; Pound et al., 2011), Mid-Pliocene (Haywood and Chandler, 2009), and the Early Cretaceous (Haywood, 2004) have recently been developed. As a result, GCMs have so far mainly contributed to Late Quaternary SDM applications, but see Rodríguez-Sánchez and Arroyo (2008) and Yesson and Culham (2006).

Pre-Quaternary studies have instead mostly relied upon sedimentologically-derived variables, generalized into spatially continuous surfaces from locality data using geostatistical modeling (e.g., Maguire and Stigall, 2009; Walls and Stigall, 2011). These variables include lithology, biofacies, limestone bedding, limestone thickness, inferred water depth, crocodilian presence (as a temperature indicator), vegetation cover interpreted from soil horizons, C₄-plant representation based on stable isotopes in paleosols and teeth, and paleobotanically-determined ecotope (Maguire and Stigall, 2009; Dudgeon and Stigall, 2010; Walls and Stigall, 2011).

2.1.3. Model algorithms

Many different SDM algorithms exist (Fig. 2). Some require evidence of both species presence and absence (e.g., generalized linear models (GLM) and generalized additive models (GAM)), while others are optimized for presence-only data – often the only distributional data available in paleobiology (e.g., rectilinear bioclimatic envelopes (Bioclim) and machine learning methods based on maximum entropy (Maxent; Phillips et al., 2006)). We refer to the literature for comprehensive treatments and comparisons of modeling algorithms (e.g., Guisan and Zimmermann, 2000; Elith et al., 2006; Hijmans and Graham, 2006; Franklin, 2009). Importantly, different algorithms may provide substantially deviating predictions (Pearson et al., 2006), and it is therefore good practice to test the robustness of one's findings by using several contrasting SDM algorithms (e.g., Svenning et al., 2008a; Fløjgaard et al., 2009; Nogués-Bravo, 2009; Vega et al., 2010). However, only 20% of the studies included in the Appendix used more than one algorithm.

2.1.4. Validation

Key applications of SDM to paleobiology involve predicting the distribution of species across space and time, often via hindcasting. It is thus important to validate model transferability (its predictive ability on data sets on which it has not been calibrated, such as from a different geographic region or time period), to the greatest extent possible (e.g., Randin et al., 2006). Several different validation strategies have been developed (Araújo et al., 2005). Resubstitution

evaluates predictive ability on the same data on which the model was calibrated; however, this approach does not guard against over-fitting and is likely to provide over-optimistic model assessments (Araújo et al., 2005). A better approach, and the most commonly used in SDM, randomly splits the data into calibration and validation data sets (Araújo et al., 2005). The models are calibrated and then projected onto the validation data set, with predictive success quantified using different statistical measures (Fielding and Bell, 1997); for discussions of their properties and pros and cons, see Allouche et al. (2006), Lobo et al. (2008) and Mouton et al. (2010). Data splitting can be repeatedly performed via bootstrapping, randomization, or *k*-fold partitioning/cross-validation (Fielding and Bell, 1997). A special case of the latter is leave-one-out or Jackknife sampling, where *n* samples of 1 case are tested sequentially, using the remaining *n* – 1 cases as the calibration data set (Fielding and Bell, 1997). Jackknife approaches are recommended for validating models based on small numbers of occurrences (Pearson et al., 2007), and are thus particularly useful for paleobiological SDM applications, where calibration utilizes scarce fossil records. However, as normally implemented, the data splitting approach is affected by spatial and temporal autocorrelation, which causes non-independence of the calibration and validation data sets (Araújo et al., 2005), introducing similar over-optimism as resubstitution. As a consequence, geographic partitioning approaches have been developed to maximize the spatial independence of calibration and validation data (Fløjgaard et al., 2009; Morueta-Holme et al., 2010).

Ideally, SDM applications for cross-temporal prediction should be evaluated with data from independent periods, directly testing temporal transferability (Araújo et al., 2005; Dobrowski et al., 2011). As data from the same region from different time periods may still be affected by spatial autocorrelation, calibration and validation data sets should ideally come from different regions. However, such data may be difficult or impossible to obtain in most cases, and data availability poses a major restriction on the extent to which validation can be optimized. Probably reflecting such limitations, a recent review of hindcasting studies found that only 30% had used independent data to validate their models (Nogués-Bravo, 2009). Lack of independent validation may lead to erroneous inferences; hence, in all cases, as a minimum, careful consideration should be given to the predictive ability of models across space and time. Some paleobiological SDM applications have, in fact, obtained temporally independent validation using present-day occurrence records in conjunction with dated fossil occurrences (e.g., Martínez-Meyer et al., 2004). External information has also been used to provide some independent validation, e.g., by comparing SDM-based estimates of suitable past conditions with paleoecological evidence for the study taxon or ecologically similar groups (Svenning et al., 2008a; Alsos et al., 2009; Fløjgaard et al., 2009), comparing pollen-based tree-line reconstructions to SDM-predictions of suitable areas for a non-forest species such as the woolly mammoth (*Mammuthus primigenius*) (Nogués-Bravo et al., 2008), or comparing SDM-based estimates of glacial refugia with refugium locations inferred from phylogeography (e.g., Waltari et al., 2007) (Fig. 2).

2.2. Integrating SDM and genetics approaches

The integration of paleobiological data with phylogeographic and phylogenetic information has strongly advanced our understanding of a range of biogeographic, paleoecological, and evolutionary questions over the last two decades (e.g., Hewitt, 2000; McLachlan et al., 2005; Bartish et al., 2006; Magri et al., 2006; Dalén et al., 2007; Barnett et al., 2009; Bunce et al., 2009; Davison et al., 2011), and effective synthesis of SDM with this

integrated paleo-phylogeographic approach offers the potential for further substantial advances in these research areas (e.g., Eckert, 2011), although few studies hitherto have taken advantage of all three disciplines (Cheddadi et al., 2006; Carnaval and Moritz, 2008; Alsos et al., 2009; Galbreath et al., 2009; Maguire and Stigall, 2009) (Fig. 1). Furthermore, for many species insufficient paleoecological records exist to infer patterns of past distributions, such as LGM refugia or migration routes. As a result, SDM is increasingly highlighted as an important tool for testing phylogeographic hypotheses (Knowles et al., 2007; Richards et al., 2007; Smith, 2007; Kozak et al., 2008) and applied in different ways in an increasing number of studies (Cheddadi et al., 2006; Carstens and Richards, 2007; Knowles et al., 2007; Waltari et al., 2007; Vega et al., 2010). Typically, estimates of species past distributions from SDM-based hindcasting and phylogeography are consistent (e.g., Ruegg et al., 2006). One important methodological study compared LGM refugia from both methods for 20 North American terrestrial vertebrate species, and found an average refugial area overlap of 52%, with spatially correlated refugia estimates for a clear majority of species (Waltari et al., 2007). However, a few studies have found clear discrepancies (e.g., Morris et al., 2010). One study, on a New Zealand forest beetle, highlights the difficulty of integrating even apparently similar results of both methods without being able to directly establish a temporal framework via molecular dating (Marske et al., 2011).

Methodological developments are rapidly advancing integration of phylogeography and SDM: the relationship between species' past distributions and their phylogeography can now be directly tested using a variety of coalescent methods which generate test statistics to explicitly compare biogeographic hypotheses, which can be (and often are) generated using SDM (e.g., Richards et al., 2007). In one approach, phylogenies are simulated under alternative scenarios, yielding a probability distribution for the test statistics generated under each historical hypothesis (e.g., Carstens and Richards, 2007). Alternatively, hierarchical approximate Bayesian computation bypasses the phylogeny and uses parameter values randomly drawn from the coalescent prior distributions to approximate the posteriors under multiple biogeographic scenarios (e.g., Carnaval et al., 2009). These methods allow comparison of past distributions as well as range dynamics among co-distributed species. The next step, direct simulation of a species' distributional shift across space and time, incorporates current and hindcasted distributions into time-forward models of the demographic process and provides one of the first spatially and temporally explicit models of a species' distributional shift and contingent effects on patterns of genetic variation (Knowles and Alvarado-Serrano, 2010; see also Currat et al., 2004).

3. Applications

Over the last few years the number of studies using SDM to address questions in paleobiology or at the interface of paleo- and neobiology has increased considerably (Fig. 1). While some of these studies only use SDM (23%), most combine hindcasting with genetically inferred patterns (49%), paleoecological records (22%), or both (6%). As will be evident from the following review of different SDM applications, clear temporal, scale, taxonomic and geographic biases exist in published studies (Fig. 1).

3.1. Glacial refugia

Many studies have used SDM-based hindcasting – often in combination with phylogeographic analyses – to test evolutionary and biogeographic scenarios, especially in relation to how species have responded to the Quaternary climate changes (Fig. 3). The

most frequent application of SDM to paleobiological studies is to identify glacial refugia during the Last Ice Age, and particularly during the LGM (Figs. 1 and 3, Appendix). Key goals of these studies have either been (i) to test biogeographic and evolutionary scenarios, or (ii) as a basis for quantifying past climate change impacts on present-day species distribution and diversity patterns. Given dramatic climatic and environmental impacts of the Quaternary, glacial refugia have been assigned a core role in the evolutionary and distributional dynamics of species and populations through the Quaternary, as evidenced in the traditional paradigms for European phylogeography (Taberlet et al., 1998; Hewitt, 2000).

3.1.1. Testing biogeographic and evolutionary scenarios

The role of glacial refugia has been extensively debated in Europe, with a central discussion over whether species only survived the LGM in southern European refugia, or also survived glacial maxima in northerly locations, with possibilities for long-term *in situ* evolutionary development in the north as well as postglacial recolonization from within Central and Northern Europe. Traditional paleoecological reconstructions have suggested that temperate and boreal species were restricted to the Mediterranean peninsulas (Van der Hammen et al., 1971; Huntley and Birks, 1983; Lang, 1994), and classical phylogeographic paradigms for Europe have accordingly emphasized postglacial expansions from these southern refugia (Taberlet et al., 1998; Hewitt, 2000). In the last decade, this paradigm has been challenged by both new paleoecological studies (e.g., Willis et al., 2000; Stewart and Lister, 2001; Willis and Van Andel, 2004; Binney et al., 2009; Heikkilä et al., 2009; Kelly et al., 2010; Välranta et al., 2011), new phylogeographic studies (e.g., Petit et al., 2003; Magri et al., 2006; Schmitt, 2007), as well as syntheses (e.g., Bhagwat and Willis, 2008).

Currently there is increasing evidence for northern refugia, but their organism scope, quantitative importance, and exact locations remain relatively open questions. A number of SDM studies have contributed to the discussion concerning the extent to which temperate and boreal species – including trees – occurred north of the Alps in Europe during the LGM (Cheddadi et al., 2006; Leroy and Arpe, 2007; Svenning et al., 2008a). An SDM study of 7 boreal and 15 temperate European tree species showed that climatic conditions suitable for boreal trees existed broadly across Central and Eastern Europe into the East European Plain during the LGM, while conditions suitable for temperate trees were largely restricted to Southern Europe and the Black Sea region (Fig. 3; Svenning et al., 2008a; also cf. Leroy and Arpe (2007) and Allen et al. (2010)). The study did not take the low atmospheric CO₂ concentrations and high wind speeds during the LGM into account – these additional limiting factors probably reduced tree distributions and densities well below those expected purely from the climatic conditions (Svenning et al., 2008a). SDM-based studies of small mammals and for a pond snail have confirmed these findings (Cordellier and Pfenninger, 2009; Fløjgaard et al., 2009; Vega et al., 2010). Furthermore, SDM-based studies of current arctic and subarctic plant and animal species (Fig. 3; Banks et al., 2008a; Alsos et al., 2009; Fløjgaard et al., 2009; Habel et al., 2010) have also confirmed the strong paleoecological and phylogeographic evidence for the widespread suitability of European LGM environments north of the Alps for such species (Birks and Willis, 2008).

SDM has also been applied to elucidate other biogeographic questions in the region, e.g., refugia locations within Southern Europe (e.g., Rodríguez-Sánchez and Arroyo, 2008; Alba-Sánchez et al., 2010). While the SDM part of most of these studies only involved hindcasting, Banks et al. (2008a) also predicted the LGM range from LGM fossil records. The predicted potential LGM range

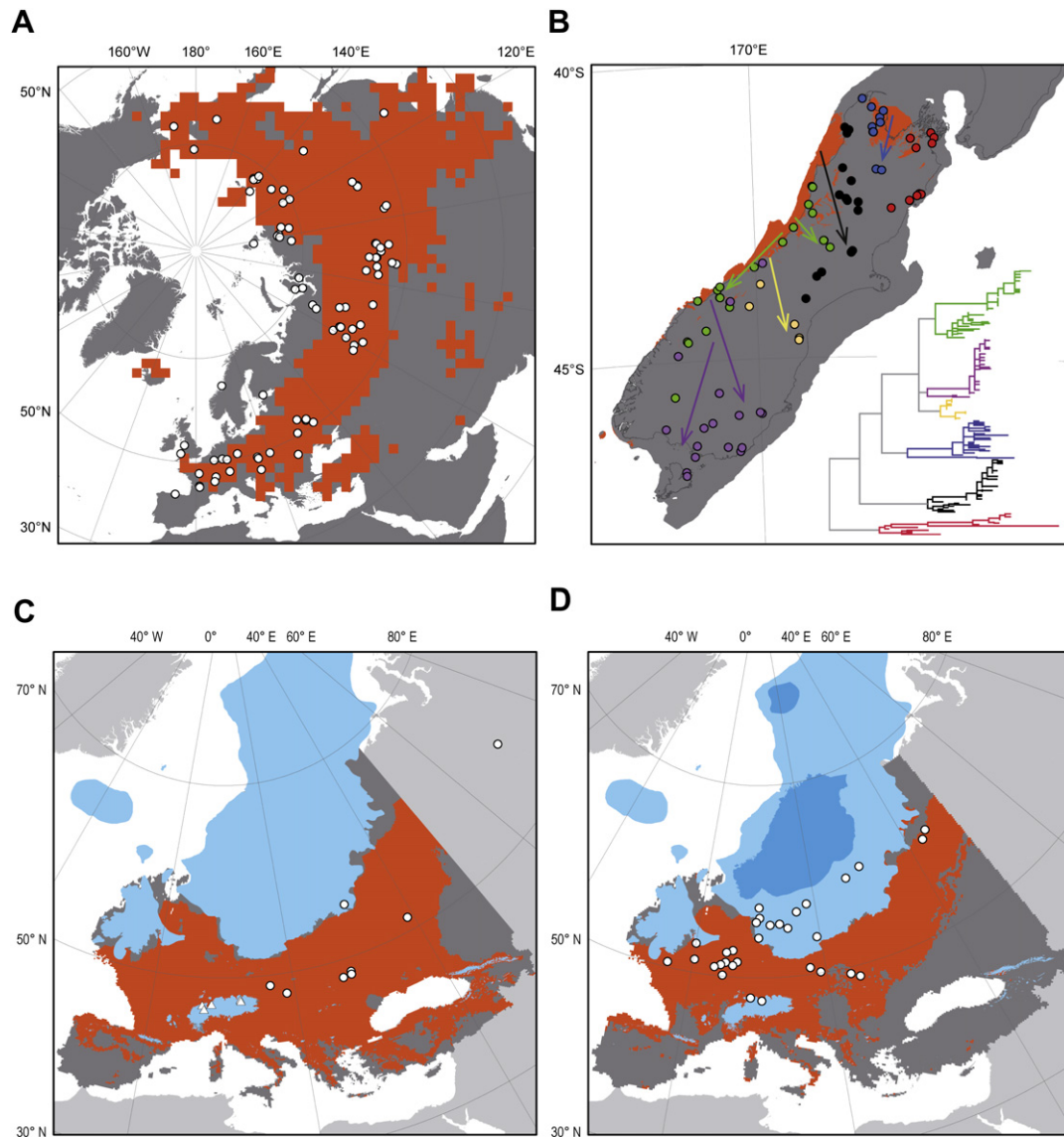


Fig. 3. Applications of SDM to elucidate Late Pleistocene distributions: (A). SDM-estimated potential LGM distribution in Eurasia (red area) of woolly mammoth (*M. primigenius*) using fossils (dots) dated to the LGM (c. 21,000 ka BP) (Nogués-Bravo et al., 2008). (B) Mitochondrial DNA phylogeny and hindcast-estimated LGM refugia for the beetle *Agryrtodes labralis* (Leiodidae) from the South Island of New Zealand (Marske et al., 2009). Modern collection localities are shown with colors corresponding to clades in the phylogeny. Arrows indicate hypothesized dispersal routes out from the refugia. (C) Hindcast-estimated LGM distribution of spruce (*Picea*, red area) and fossil LGM (25–17 ka) records: triangles, pollen records (European Pollen Database (<http://europeanpollendatabase.net/data/>); circles, macrofossils (from Willis and Van Andel, 2004; Binney et al., 2009; Heikkilä et al., 2009 and Väiranta et al., 2011). For details on the SDM, see Svenning et al. (2008a). LGM ice sheet extent (light blue area) follows Ehlers and Gibbard (2004). (D). Hindcast-estimated LGM distribution of dwarf willow (*Salix herbacea*) and LGM and late-glacial macrofossils (dots) (Alsos et al., 2009). The ice extent in the late-glacial (Younger Dryas) is now also shown (dark blue area; Ehlers and Gibbard, 2004). Legend otherwise as in (C).

for red deer (*Cervus elaphus*) covered the Balkans (despite few fossil finds here), and was largely disjunct between Southwestern Europe and Italy on one hand, and the Balkans on the other (Banks et al., 2008a). These results provide an independent explanation for key aspects of this species' phylogeographic pattern in Europe, namely a strong differentiation into a western- and Balkan-centered clade, evidence for long-term population stability in the Balkan clade, and no latitudinal haplotype diversity decline within the Balkans (Skog et al., 2009).

As in Europe, the occurrence of northern and perhaps cryptic glacial refugia and their biogeographic-evolutionary implications have been discussed in North America (Watts, 1980; Williams et al., 2000; Rowe et al., 2004; McLachlan et al., 2005). For example, a combined phylogeography and SDM study of American beech (*Fagus grandifolia*) identified southern coastal parts of eastern

North America as likely glacial refugia (Morris et al., 2010). The restriction of some forest species to lower latitudes also had consequences for organisms in other biomes; desert biomes in western North America were replaced by woodlands during the LGM (Swetnam et al., 1999), with warm desert organisms possibly persisting in isolated refugia at lower latitudes. However, hindcasting and phylogeographic results for the desert pocket mouse (*Chaetodipus penicillatus*) both indicate that some populations were isolated in northern refugia during LGM (Jezkova et al., 2009). North American studies have also concentrated on mountainous species currently restricted to "Sky Islands" and the degree to which their ranges were extended during the LGM, using a combination of SDM and phylogenetics (Carstens and Richards, 2007; Knowles et al., 2007; Galbreath et al., 2009; Waltari and Guralnick, 2009; also cf. Gugger et al., 2010). In a rare marine

example, Bigg et al. (2008) used SDM, ecophysiological parameters and genetic data to estimate Pleistocene range dynamics in Atlantic cod (*Gadus morhua*).

Only a few SDM-based studies have assessed impacts of Pleistocene climate changes on East-Asian biota (Sakaguchi et al., 2010; Flanders et al., 2011). Sakaguchi et al. (2010) studied whether coastal lands temporarily exposed during the LGM might have contributed to postglacial northward colonization of a deciduous tree on the Japanese Archipelago. By taking the lower sea level into account, the authors estimated that the species might have persisted up to several hundred kilometers farther north than previously thought. In contrast, SDM and phylogeographic analyses of the bat *Rhinolophus ferrumequinum* in China and Japan suggest it did not undergo dramatic glacial range contractions (Flanders et al., 2011).

SDM-based approaches have also been employed to identify glacial refugia at middle to high latitudes in the Southern Hemisphere. For New Zealand, generalized additive models have previously been used to examine the distribution of southern beech (*Nothofagus* spp.), whose disjunct range across the western South Island has been attributed to Pleistocene glaciation (Leathwick, 1998). More recently, SDM and phylogeography have identified LGM refugia for two forest beetles (Marske et al., 2009, 2011; Fig. 3) and the stick insect *Argosarchus horridus* (Buckley et al., 2009) outside of those previously estimated from paleoclimatic data (Alloway et al., 2007), indicating that forest persistence on the glaciated South Island was more widespread than previously thought. In contrast, another stick insect *Clitarchus hookeri* apparently retreated to low latitudes of the North Island (Buckley et al., 2010), an analog to the European southern refugia paradigm. In South America, SDM-based studies indicate areas of stable geographic distribution in two of the three *Hordeum* species in Patagonia (Jakob et al., 2009) and that the cold-hardy tree *Nothofagus pumilio* may have survived in refugia at the very tip of South America rather than colonizing from further north (Premoli et al., 2010).

The role of climatically stable areas for survival, evolution, diversification, and the associated development of current species diversity and endemism patterns is also being discussed for the Tropics, particularly the longstanding debate on the role of Pleistocene refugia in Amazonia (Haffer, 1997; Colinvaux and Deoliveira, 2001; Stropp et al., 2009). Bonaccorso et al. (2006) modeled the LGM distribution of forest and savanna plants and birds to investigate the degree to which forest fragmented and savanna spread across Amazonia during the LGM, finding some support for forest fragmentation. Likewise, SDM and phylogenetic breaks in the neotropical bird *Schiffornis* spp. supported Pleistocene climate fluctuation as a driver of speciation in this group (Peterson and Nyári, 2008), and multiple glacial refugia for Amazonian leaf-cutter ants (*Atta* spp.) have similarly been identified as important drivers of phylogenetic diversity in the region (Solomon et al., 2008). Nevertheless, Werneck et al. (2011) found evidence against the “Pleistocene Arc Hypothesis”, which proposes that seasonally dry forests formed a larger, more coherent biome across northern South America during the LGM than at present. Outside the Amazon Basin, the Brazilian Atlantic Forest has become a key case study for how to statistically integrate SDM and phylogeographic data (Carnaval and Moritz, 2008; Carnaval et al., 2009), and the Australian Wet Tropics (Hugall et al., 2002; Moussalli et al., 2009; VanDerWal et al., 2009; Bell et al., 2010; Graham et al., 2010) constitute another well-known tropical system. In contrast, SDM approaches have rarely been applied to the effect of Quaternary climate change in tropical Africa (Lawson, 2010; Schidelko et al., 2011), Madagascar (Chan et al., 2011) or Asia (Lim et al., 2011). An exception, Lim et al. (2011) combined phylogeographic and SDM

analyses to assess whether east and west Sundaland rainforest bird populations intermixed during glacial sea-level minima, finding support for persistent habitat barriers throughout the glacial, in agreement with previous suggestions of a glacial Sundaland savanna corridor (Bird et al., 2005).

In many cases glacial refugia may be located in specific smaller areas within broader refugial regions, as discussed for the Mediterranean region (Médail and Diadema, 2009), with implications for phylogeographic, species richness, and endemism patterns. SDM-based hindcasting has helped pinpoint such small refugia within larger refugial regions, notably in the Australian Wet Tropics (Hugall et al., 2002; Moussalli et al., 2009), the Brazilian Atlantic Forest (Carnaval and Moritz, 2008; Carnaval et al., 2009), the Alps (Dépraz et al., 2008), and the Iberian Peninsula (Benito Garzón et al., 2007; Benito Garzón et al., 2008; Rodríguez-Sánchez and Arroyo, 2008; Calleja et al., 2009; Alba-Sánchez et al., 2010); for a synthetic discussion, see Rodríguez-Sánchez et al. (2010). In these studies, the SDM-based approach provided predictions of intra-regional glacial refugia which may explain complex patterns in phylogeography and endemism in these regions.

3.1.2. Quantifying past climate change impacts on present-day species distributions and diversity

Over the last decade there has been increasing interest in if and how history (e.g., past climate stability and time-lagged migration) shape current species distributions and diversity patterns. Several studies have examined the importance of climate stability through time, calculated from paleoclimatic simulations, as determinants of current patterns of species diversity (Graham et al., 2006, 2010; Svenning and Skov, 2007; Araújo et al., 2008; Carnaval and Moritz, 2008). Climate stability has been assessed either as the difference between past and current climate (e.g., Svenning and Skov, 2007) or by static or dynamic continuity in the occurrence of suitable habitats (Graham et al., 2006, 2010; Carnaval and Moritz, 2008). The effect of time-lagged migration has been assessed by using accessibility to postglacial recolonization from glacial refugia as a predictor of current patterns (Svenning et al., 2008b; Fløjgaard et al., 2011; Normand et al., 2011) (Fig. 4). An emerging consensus from these studies is that small-ranged species are concentrated in or close to long-term climatically stable areas (Svenning and Skov, 2007; Fløjgaard et al., 2011; Fig. 4), while the distributions of some widespread species may also be constrained by accessibility to postglacial recolonization from glacial refugia (Svenning et al., 2008b; Normand et al., 2011).

3.2. End-Pleistocene megafaunal extinctions

The Late Pleistocene and early Holocene witnessed the extinction of a large proportion of Earth's large terrestrial animals (megafauna), with extinctions of varying intensity in all regions (Barnosky et al., 2004). Reasons for this massive and selective extinction have been subjected to a longstanding and still unsettled debate, with climate change and overkill by modern humans proposed as the two main mechanisms (Barnosky et al., 2004; Surovell et al., 2005; Gillespie, 2008; Pushkina and Raia, 2008; Prideaux and Gully, 2010). Several SDM-based studies have attempted to test these hypotheses. Martínez-Meyer et al. (2004) used SDM in combination with LGM occurrence records for eight extinct North American megafaunal mammal taxa (*Canis dirus*, *Mammuth americanum*, *Mammuthus columbi*, *Equus conversidens*, *Platygonus compressus*, *Camelops hesternus*, *Bison bison antiquus*, and *Oreamnos harringtoni*) to test for changes in the available area of climatically suitable conditions for these species between the LGM and the present, finding that the suitable area generally increased, contrary to expectation if these extinctions were

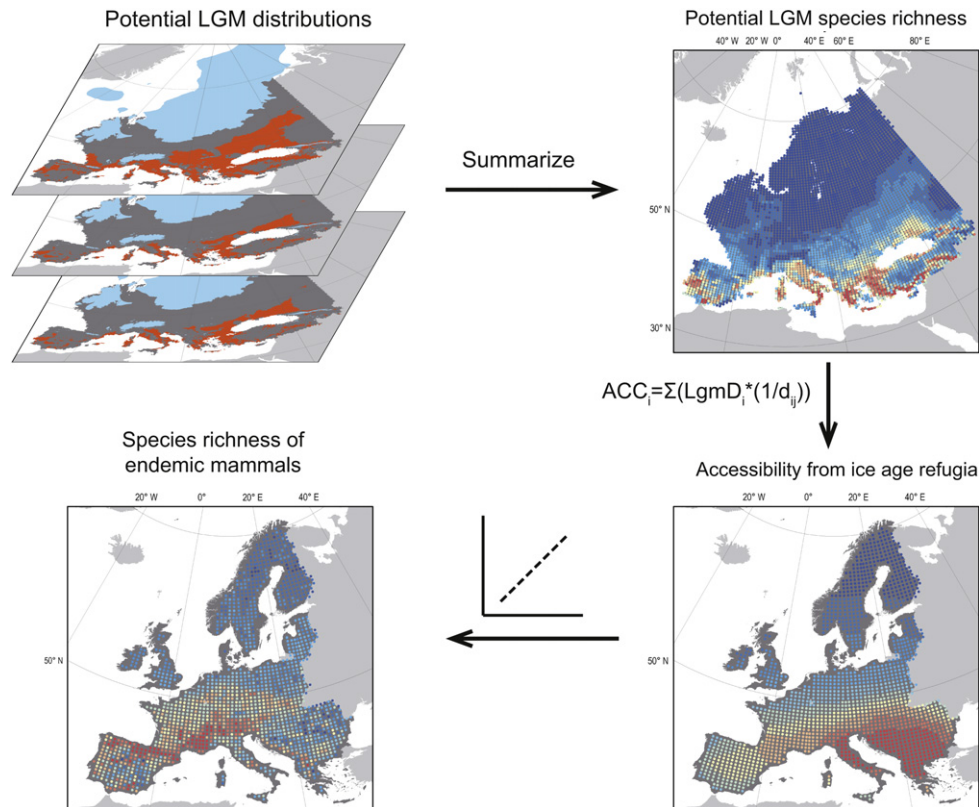


Fig. 4. Quantifying past climate change impacts on present-day species distributions and diversity patterns: accessibility to postglacial recolonization from ice age refugia as a driver of current richness of Western Palearctic endemic mammals in Europe: the potential LGM distribution is estimated using SDM for each species (red areas; blue: ice sheet Ehlers and Gibbard, 2004), then summed across species to estimate potential LGM species richness (species richness increases from blue to red). Accessibility to recolonization is then calculated as the sum of all inverse distances to the estimated refugia, weighted by their LGM richness ($LgmD_i$; LGM species richness in grid cell i ; d_{ij} : distance between grid cell i and j ; i : grid cell for which the accessibility is being calculated; accessibility increases from blue to red). Accessibility explains 25% of variation in endemic species richness (Fløjgaard et al., 2011).

climatically driven. Varela et al. (2010) obtained a similar result for the regionally extinct spotted hyena (*Crocota crocuta*) in Europe. In contrast, a similar study of the range dynamics of the woolly mammoth (*M. primigenius*) in Eurasia over the last 126,000 years (Fig. 3) showed a strong reduction in suitable area during interglacials (Last Interglacial and the Holocene), favoring a climate-driven extinction process, but also demonstrating how a significant human impact may have provided the final blow to the species (Nogués-Bravo et al., 2008). An explanation for these apparently inconsistent results may lie in the former species having temperate distributions, while the woolly mammoth predominantly occupied colder areas during the last glacial (Fig. 3).

3.3. Holocene paleoecology

Species distribution modeling has also shed light on ecological and biogeographic questions within the Holocene. Although a wealth of high-quality paleoecological data are available for the recent past, and assumptions such as niche stasis (cf. Section 4.1.2. Niche stability, niche evolution and ecological niche shifts) are less dubious over shorter periods, Holocene SDM applications are surprisingly few (Fig. 1). As the Holocene has also witnessed substantial climatic variation, with periods of warmer and colder conditions than at present (Ruddiman, 2001), SDM-based studies of the ecological and biogeographic dynamics during this period may offer important insights for climate change biology. Several studies have used SDM to illuminate the potential effects of mid-Holocene climate on tree species distributions in the Iberian

Peninsula (with simultaneous assessment of the potential impacts of the LGM). Benito Garzón et al. (2007) demonstrated that conditions during the mid-Holocene would have allowed wide re-expansions from the glacial refugia already by 6000 years ago. A subsequent study addressed similar issues for the tertiary relict evergreen tree *Prunus lusitanica* (Portuguese laurel), finding that its mid-Holocene potential range was similar to its present range, but much greater than at LGM (Calleja et al., 2009). A third study provided evidence for the stable but disjunct distribution of the firs *Abies alba* and *Abies pinsapo* in the region from the LGM over the mid-Holocene to the present (Alba-Sánchez et al., 2010). These studies were based on hindcasting models calibrated on present-day distribution, with no independent validation across time. In contrast, Pearman et al. (2008a) directly addressed this issue by studying shifts of the realized niche in seven widespread European tree species over the last 6000 years, validating hindcasting predictions against mid-Holocene pollen records, and, conversely, applying SDM to these pollen records and validating their forecasting predictions for the present against current tree species distributions. Despite a high degree of model transferability between the two periods, there were also noteworthy discrepancies: the late-successional dominants *Fagus sylvatica* and *Picea abies* are known to have been largely absent from northwestern Europe during the mid-Holocene, but the hindcasting models showed that their absence cannot be explained by Holocene climate given their current climate niches, leaving dispersal limitation as the most likely cause of their absence (cf. Svenning and Skov, 2004; Giesecke et al., 2006). Furthermore, the seven

species differed in the extent to which their realized niche shifted between the two periods, with an apparent tendency for greater niche stability in late-successional species. Mid-Holocene hindcasting has also been used to assess suture zone dynamics between glacial refugia in the Australian Wet Tropics (Moritz et al., 2009). By mapping 18 contact zones for 16 animal taxa, SDM results indicated a strong clustering of contact zones in a narrow rainforest corridor between two major glacial refugia, suggesting that this corridor was unsuitable for the species during the mid-Holocene and that the current suture zone has been established during the last few thousand years (Moritz et al., 2009). These applications illustrate the capacity of SDM-based approaches to shed light on complex ecological and biogeographic hypotheses also in the near-time.

3.4. Deep-time biogeography

SDM has also provided insights into range and diversity dynamics preceding the Quaternary (Fig. 1). As an early example, the role of climate in the Plio-Pleistocene extinctions of numerous tree genera in Europe was assessed by comparing simple bioclimatic tolerance estimates for regionally extinct, relictual, or widespread genera estimated from their current distributions outside Europe (Svenning, 2003). The study documented that genera widespread in Europe are more cold-tolerant than those which went extinct in Europe or survived as relicts, and that relicts are more drought-tolerant than regionally extinct genera (Svenning, 2003). The assumption of niche stability (cf. Section 4.1.2. Niche stability, niche evolution and ecological niche shifts) poses a key challenge for deep-time hindcasting studies. Nevertheless, paleoclimatic reconstructions based on climate tolerances estimated from current ranges appear successful into the Paleogene part of the Tertiary, suggesting that niche stability does apply to some groups over that length of time (Mosbrugger, 1997; Moe and Smith, 2005; Mosbrugger et al., 2005). In any case, as a background for such studies it is recommendable to test for niche stability by assessing model transferability across time (e.g., Martínez-Meyer et al., 2004; Rodríguez-Sánchez and Arroyo, 2008) or space, between regions isolated on a similar time-scale (Peterson, 1999; also cf. Svenning, 2003). At least one study involving hind- and forecasting across millions of years satisfied these considerations: Rodríguez-Sánchez and Arroyo (2008) investigated range contraction of the subtropical laurophyllous tree genus *Laurus* in Europe over the last 3 million years, and found virtually identical climate response curves for the Pliocene and present, with strong model transferability between the two periods. Ecologically, the model documented a contraction in the suitable area for *Laurus* over this time period, with a particularly strong reduction during the LGM (Rodríguez-Sánchez and Arroyo, 2008).

In contrast to the hindcasting approach, several studies have used SDM to elucidate the driving factors of range dynamics by modeling past species occurrences as a function of past environmental conditions (e.g., Stigall Rode and Lieberman, 2005; Stigall and Lieberman, 2006). Notably, the regional distribution of brachiopod species approximately 446 million years ago in the Late Ordovician was modeled as a function of different paleoenvironmental factors (Dudei and Stigall, 2010; Walls and Stigall, 2011). The authors were able to link changes in range size to changes in environmental heterogeneity (Dudei and Stigall, 2010; Walls and Stigall, 2011). Niche dynamics (stability vs. evolution) were quantified by comparing models calibrated on different time periods, and while certain periods were characterized by niche stability, in others niche evolution predominated, with implications for rapid abiotic changes and biological invasions (Dudei and Stigall, 2010; also cf. Walls and Stigall, 2011). Using a similar approach, Maguire

and Stigall (2009) found evidence for niche stability in the horse *Cormohipparion occidentale* during the Late Tertiary.

Other deep-time applications of SDM include estimating range sizes to test for links between range size and extinction risk and between range continuity and speciation. The former has been addressed for North American brachiopods and bivalves during the Devonian biodiversity crisis (Stigall Rode and Lieberman, 2005) and North American horses during the Late Tertiary (14.2 million years ago) (Maguire and Stigall, 2009). Interestingly, both studies found evidence for a temporally variable importance of range size, with large range size conferring a survival advantage in some time intervals, but not in others. Maguire and Stigall (2009) also found that speciation rates in horses were higher when species ranges were more fragmented, consistent with increased possibilities for niche partitioning and vicariant speciation.

3.5. Other applications

Species distribution modeling (under the name eco-cultural niche modeling) has been applied to archaeological data to quantify habitable areas in Europe for Upper Paleolithic human populations during the LGM, assess climatic niche differences between two (Solutrean and Epigravettian) techno-complexes and evaluate which factors constrained their distributions (Banks et al., 2008b). An SDM-based approach has also been used to investigate the role of climate in controlling mammal community assembly in Pleistocene Britain, with special attention to combinations of extant species without modern analog (Polly and Eronen, 2011). They also estimated paleoclimatic conditions from SDM-based climatic envelopes of the coexisting mammal species in a given fauna (Polly and Eronen, 2011). Similar approaches have also been used to reconstruct paleoclimate as far back as the early and middle Tertiary using insects and plants (Mosbrugger, 1997; Moe and Smith, 2005; Mosbrugger et al., 2005).

4. Assumptions, uncertainties and solutions

4.1. Assumptions and uncertainties

Numerous assumptions and uncertainties affect the application of the SDM approach to paleobiology. Most fundamentally, the SDM approach is based on the assumption that species' ranges reflect their ecology, including intrinsic and extrinsic range-limiting factors. This approach is linked to niche theory (e.g., Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005; Soberón, 2007; Hirzel and Le Lay, 2008; Soberón and Nakamura, 2009), although it may also reflect non-niche processes such as time-limited dispersal constraints (Svenning et al., 2008b; Paul et al., 2009). We refer to the literature for extensive discussion of the link between niche theory, niche terminology, and SDM (Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005; Soberón, 2007; Hirzel and Le Lay, 2008; Soberón and Nakamura, 2009). However, we note that niches as modeled by SDM typically correspond to the Grinnellian niche (habitat niche), i.e., the non-consumable, non-interactive environmental conditions such as climate required or tolerated by a species (Soberón, 2007; Soberón and Nakamura, 2009). However, SDM may also include resources or other dynamically-linked factors (Soberón and Nakamura, 2009), e.g., interacting species (Preston et al., 2008; Meier et al., 2010), in which case the niches modeled more corresponds to the realized Hutchinsonian niche (Hutchinson, 1957). In either case, a niche can be thought of as the external conditions that allow populations of a species to maintain positive growth rates (Soberón and Nakamura, 2009).

4.1.1. Equilibrium postulate

An often stated key assumption of the SDM approach is the equilibrium postulate, i.e., that a species occurs everywhere the environment is suitable and only in these places (Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005). These requirements are, however, likely to be violated, as species ranges may be in disequilibrium with the current environment due to dispersal limitation, source-sink dynamics, or biotic interactions (Fig. 5; Leathwick, 1998; Pulliam, 2000; Guisan and Thuiller, 2005; Svenning et al., 2008b; Paul et al., 2009). However, in fact, frequently methodologies and applications of SDM will not be so restrictive, as some degree of environmental disequilibrium does not preclude achieving reliable niche estimates in geographical space (Fig. 5). The quality of niche estimates and how strongly they are influenced by disequilibrium in geographic space will depend on how environmental conditions are distributed geographically relative to the species' distribution. Geographic disequilibrium may furthermore affect the predicted range dynamics. For example, in SDM-based predictive modeling of future range shifts, it is often assumed that all species will either fail to disperse completely or that all species will be able to fully occupy suitable geographic areas, resulting in strong differences in predictions (Thomas et al., 2004; Thuiller et al., 2005). Accurately incorporating dispersal into predictive models, especially across large spatiotemporal scales, is not easy, and rare, stochastic dispersal events can be highly important, as highlighted by molecular evidence for rare trans-oceanic dispersal events which sometimes have had large impacts on community assembly (Pennington and Dick, 2004; Renner, 2004; Dick et al., 2007).

4.1.2. Niche stability, niche evolution and ecological niche shifts

A critical assumption for SDM-based hind- or forecasting is niche stability over the study period, as niche evolution and other non-evolutionary niche shifts will reduce model transferability across time. Over relatively short periods, such as the LGM to present (~21,000 years), evolutionary niche changes are less likely

than for longer time spans, although they could still have occurred (Davis and Shaw, 2001; Bradshaw et al., 2006; Peterson, 2011). In addition, shifts in the realized niche may occur for other reasons, like changes in biotic interactions (including human impacts), extinction of ecologically distinct lineages within a taxon (exemplified by the late-glacial extinction of a *Picea* species in eastern North America which was clearly more temperate than any of the remaining species (Jackson and Weng, 1999), or fluctuating effects of broad-scale changes in the physical environment (like changes in atmospheric CO₂ concentrations, see below).

As previously discussed, Pearman et al. (2008a) quantified shifts in the realized niche between the mid-Holocene and the present for seven European tree species, finding moderate to large shifts in some early-successional species. The observed shifts were attributed to biotic interactions, including a positive effect of anthropogenic disturbance on early-successional species (Pearman et al., 2008a). Another instructive case, the spotted hyena (*C. crocuta*), is now endemic to Africa, but was widely distributed and common across Eurasia during the Middle and Late Pleistocene (Varela et al., 2009, 2010). Intriguingly, while SDM modeling of the current distribution suggests that the species is presently distributed in broad-scale equilibrium with climate in Africa, hindcasting to the Last Interglacial (126,000 years ago) of Europe and Africa predicts Europe as largely unsuitable despite abundant fossil evidence for its widespread presence in Europe at this time (Varela et al., 2009). The authors highlight habitat barriers as a potential cause of the current absence of the species from Europe; other possibilities include the extinction of cold-adapted genotypes or, more likely, that the severe end-Pleistocene megafaunal extinction in Europe may have deprived Europe of the prey base to sustain this large carnivore (Varela et al., 2010; Polly and Eronen, 2011). From a methodological perspective, the *C. crocuta* case illustrates that current equilibrium with climate does not guarantee model transferability in time (Varela et al., 2009).

To these examples of shifts in the realized niche across paleoecological time-scales is added SDM-based evidence for similar

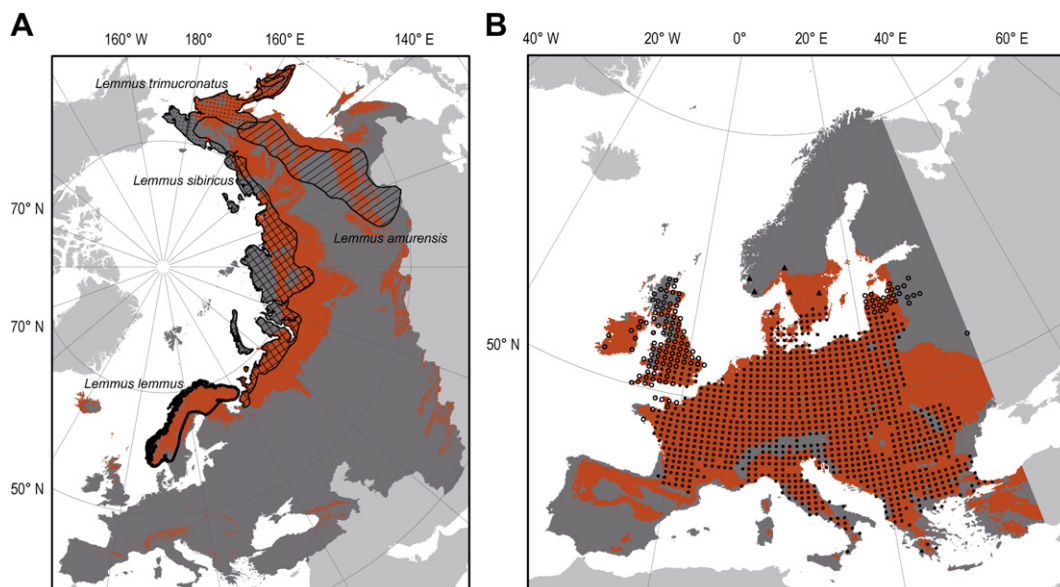


Fig. 5. Geographic range disequilibrium with climate and SDM-based niche estimates: (A) Current actual distribution (outlined; Scandinavia) and SDM-predicted climatically suitable area (red) for the lemming (*Lemmus lemmus*). Unoccupied climatically suitable parts of the predicted distribution roughly overlap the distributions of closely related species *Lemmus sibiricus* (cross-hatched), *Lemmus amurensis* (hatched), and *Lemmus trimucronatus* (dotted), suggesting biotic effects (Fløjgaard et al., 2009; range outlines from IUCN (2010)). (B) Current native distribution of hornbeam (*Carpinus betulus*) in Europe (black dots) and its SDM-estimated climatically suitable area (red; Svenning and Skov, 2004). Dispersal limitation is the probable cause of climatically suitable regions remaining unoccupied, as *C. betulus* has widely naturalized from introductions there (open circles, Jalas and Suominen, 1972–1994, and triangles, digitized from Jonsell (1999)). In both cases, range disequilibrium with climate has not precluded obtaining reasonable niche estimates.

shifts between the native and invasive range of exotic species (Broennimann et al., 2007), as well as anthropogenic exclusion of species from large, climatically-biased parts of their native range (Laliberté and Ripple, 2004). However, evidence for niche shifts must be balanced against abundant direct and indirect evidence for niche stability across broad organismal groups even at long-term geological and evolutionary time-scales (Mosbrugger, 1997; Peterson, 1999; Prinzing et al., 2001; Moe and Smith, 2005; Mosbrugger et al., 2005; Pearman et al., 2008b; Wiens et al., 2010). Nevertheless, where observed occurrence data exist for both time periods, it is clearly recommendable to test for niche stability rather than assume it. We note that the balance between niche stability and niche shifts is itself an interesting scientific topic which can be studied using SDM (Fig. 1; Peterson, 1999; Pearman et al., 2008b; Dudgeon and Stigall, 2010; Walls and Stigall, 2011).

Furthermore, SDM approaches generally also assume niche stability in space, i.e., that all populations of a species have the same niche. There is, of course, ample evidence that this is not always true (Davis and Shaw, 2001; Rehfeldt et al., 2008). Some methods allow such spatially non-stationary responses, notably Geographically Weighted Regression (Austin, 2007), although these have rarely been applied to SDM (see Wimberly et al., 2008 for an exception) and have not yet featured in paleobiological applications.

4.1.3. Changing CO₂ concentrations

Changes in atmospheric CO₂ concentrations are not particular to the industrial era, but have also occurred in the past, with CO₂ levels much higher (600–1000 ppm) than current levels (390 ppm) during most of the early Tertiary, and with 30% reductions during Pleistocene glacials (180–220 ppm) relative to interglacials (~280 ppm) (Breecker et al., 2010). Low CO₂ levels limited plant growth due to direct limiting effects (carbon starvation) on photosynthesis (Ward et al., 2005), reduced water-use efficiency of plants, increased the sensitivity of plants to carbon-depleting environmental stresses, as well as reduced the competitive ability of C₃ plants (including most woody species) relative to C₄ plants (mainly grasses) (e.g., Cowling, 1999; Crucifix et al., 2005). These CO₂ effects probably caused glacial vegetation to be less tree-dominated and more open than under a similar climate today, offering an explanation for the scarcity of trees in northwestern and central Europe during the LGM (Ramstein et al., 2007) despite suitable climate for hardy tree species (Svenning et al., 2008a). These effects on plants may not only change plant–climate relationships directly, but also indirectly via changes in competitive relationships and vegetation structure effects, with the latter also likely to influence animal–climate relationships. Hence, such CO₂ effects constitute a major challenge for accurate SDM-based cross-predictions between periods with differing CO₂ levels.

4.1.4. Other assumptions and uncertainties

The SDM approach also involves additional assumptions depending on the exact methodology implemented, particularly concerning species' environmental response curves (Austin, 2007). Paleobiological SDM applications are also faced by paleobiology-specific problems like dating, taxonomic, taphonomic biases and uncertainties in the species records, e.g., from sediment reworking and redeposition, or long-distance transport of pollen. In addition, paleoenvironmental reconstructions are also affected by uncertainties. Notably, paleoclimatic simulations often produce results that differ from independent paleoclimatic information, both from direct geological or paleobiological estimates, or from other paleoclimatic simulations based on other climate models, and may also be more uncertain in some regions than others (e.g., Kageyama et al., 2001; Jost et al., 2005; Ramstein et al., 2007; Allen et al.,

2008). Different paleoclimatic simulations for the same time period (such as the LGM) are often divergent enough that hindcasting provide spatial predictions that differ substantially (e.g., Morris et al., 2010; Vega et al., 2010).

4.2. Solutions

4.2.1. Ensemble approaches

SDM-based predictions can be highly variable: predicted distribution changes for South African plant species under future climate change, for example, varied from 92% potential range size loss to 322% potential range size gain, as well as in the geographical location of those potential ranges (Pearson et al., 2006). Variability in model projections is intimately related to the empirical nature of the SDM approach and comes from numerous sources, such as the data set used to represent the distribution of species (initial conditions), the different algorithms used to calibrate and project the distribution of species (model classes), the parameters of such algorithms, and the different climate reconstructions (boundary conditions) (Araújo and New, 2007). Using several initial conditions, model classes, model parameters, and climate reconstructions and combining their SDM projections in an ensemble forecast framework has been proposed as a strategy to reduce model uncertainty (Araújo and New, 2007). Ensemble forecasting is deeply rooted in Laplacian probability and was formally described in the pioneering work by Bates and Granger (1969); see Araújo and New (2007) for a detailed description of ensemble forecasting and its conceptual roots. Given that an unknown condition cannot be exactly predicted (e.g., the past distributions of species), probabilistic forecasting postulates that an ensemble of different projections will provide a smaller mean prediction error than any single projection. New quantitative approaches have been developed to analyze uncertainties in large forecast ensembles, assess individual sources of model variability, and map the spatial distribution of this variability (Diniz-Filho et al., 2009). Given the highly uncertain or unknown past distributions of most species, hindcasting may well be improved using ensemble approaches (Nogués-Bravo, 2009). For predictive applications of SDM it is highly recommendable to at least explore several SDM algorithms, sets of predictor variables, and alternative paleoenvironmental reconstructions (if such exist) to assess these sources of uncertainty. Among the reviewed studies, 26% used >1 GCM and 16% used >1 SDM algorithm (Appendix). BIOMOD is an SDM platform specifically designed for ensemble forecasting (Thuiller et al., 2009). Still, multi-model approaches will not be immune to consistent biases in a given set of models, so this risk should be carefully considered (cf. Svenning et al., 2010).

4.2.2. Functional SDM approaches

More functional SDM approaches, including hybrid correlative and mechanistic approaches, offer ways to address some of the above challenges to SDM, such as capturing effects of dispersal limitation or changing atmospheric CO₂ concentrations. Process-based dynamic vegetation models, or simulation models of vegetation structure and dynamics, offer one solution, since they are based on mechanisms which include physiological effects of CO₂ and are directly linked to climate as well as atmospheric CO₂ concentrations (Woodward and Lomas, 2004). A major limitation of these models is their high data requirements, and so they have mainly been developed for broad functional plant types rather than individual species. Hybrid approaches offer an alternative way forward where more limited, specific mechanistic simulations are incorporated into the statistical SDM approach, e.g., for representing dispersal processes or the CO₂ effect. Notably, most approaches which integrate a mechanistic dispersal component into SDM accomplish this by delimiting which part of a suitable region can be

occupied at time $t + 1$ given a certain rate of expansion from the areas occupied at time t , sometimes with rates differing according to species-specific dispersal agents, e.g., wind- vs. ant-/rodent-dispersed seeds (Midgley et al., 2006; also cf. Skov and Svenning, 2004). Dispersal has also been represented using mechanistic dispersal simulations (Schurr et al., 2007) or complex integrated demographic and dispersal simulations (Nathan et al., 2011). Integrating mechanistic dispersal modeling into SDM has the potential to provide more dynamic and realistic representations of species range shifts, but at the expense of model simplicity. As a first application to take CO₂ effects into account, Rickebusch et al. (2008) estimated the CO₂-driven effect on soil water availability using a DVM and then used this as a predictor in SDM of future habitats for 108 European trees, finding significant differences in predicted habitat change between models with and without this CO₂ effects for many plant chorotypes (depending on the exact modeling implementation). While these methods have been implemented to predict future range shifts due to anthropogenic climate change, they have yet to be implemented to model past range shifts.

Simpler solutions to address the uncertainties facing SDM include developing mechanistic predictors for usage in a purely statistical SDM framework. For example, it may be possible to incorporate CO₂ effects into SDM by rescaling climate variables to better represent how they are functionally perceived by plants, as modulated by the CO₂ concentration. Optimally, this would be accomplished by species-specific effects linked to species functional traits. Likewise dispersal constraints may be captured by incorporating spatial filters as predictors in SDM (De Marco et al., 2008), as was done to elucidate the drivers of palm species ranges across Africa by Blach-Overgaaard et al. (2010). For more specific dispersal scenarios such as postglacial expansions from glacial refugia, dispersal constraints may be represented by distance-based measures of accessibility to postglacial recolonization from glacial refugia (Fig. 4; Fløjgaard et al., 2011; Svenning et al., 2008b).

4.2.3. Non-SDM ecoinformatic approaches

The SDM approach requires a minimum number of localities for reconstructing distributions. However, many species currently occur in limited areas and for many others our knowledge on their distribution is poor; this data limitation is even stronger concerning past distributions. This dearth of information might constrain the usefulness of SDM for paleobiology in some cases. For some applications it is possible to circumvent it by simply modeling spatiotemporal patterns in climate: Nogués-Bravo et al. (2010) used geographic shifts in the area and location of climate types (climate envelopes) over the Late Quaternary to elucidate end-Pleistocene extinction patterns across the globe. Ohlemüller et al. (2011) also used non-biological climate envelopes to identify potential source and sink locations for climate-driven species range shifts in Europe since the LGM, providing a novel perspective on the role of glacial refugia in European biogeography, including the existence and importance of cryptic northern glacial refugia (Stewart and Lister, 2001).

5. Synthesis and outlook

In conclusion, it is clear that the SDM approach offers important new opportunities for advances in paleobiology by providing quantitative and potentially high-resolution predictions of past distributions of organisms, statistical assessment of the drivers of these distributions, as well as insights into species and community dynamics; i.e., a quantitative ecological perspective on paleobiology. The SDM approach to paleobiology reflects the general rise in integrative ecoinformatics approaches, which – driven by methodological

developments in statistics and rapid increases in computing power and data availability – provide greatly enhanced opportunities for addressing complex and often large-scale questions (Hastings et al., 2005; Jones et al., 2006). The power of this integrative approach is especially apparent from the increasing number of studies that integrate SDM with genetics and paleobiology to provide major new insights into Quaternary biogeography, particularly the effects of Late Quaternary climate changes on past biogeographic dynamics and the role of glacial refugia, evolutionary changes, and present-day diversity and distribution patterns. The SDM approach is also beginning to yield novel insights into other aspects of paleobiology, such as the end-Pleistocene megafauna extinctions, biogeography of prehistoric humans, and even deep-time biogeography. A number of factors suggest a rapidly increasing scope for SDM-based applications to paleobiology: (i) continued development in computing and statistics in general; (ii) advances in SDM methodology (e.g., integration of SDM with population models (Nogués-Bravo et al., 2008; Brook et al., 2009); (iii) deployment in conjunction with phylogeographic and other genetic approaches; (iv) increasing availability of paleobiological data, notably from digitization efforts, but also from increasingly successful ancient DNA methods (e.g., Dalén et al., 2007; Leonard et al., 2007; Barnett et al., 2009; Bunce et al., 2009; Davison et al., 2011); and (v) strong progress in paleoenvironmental modeling, notably in paleoclimatology (e.g., Haywood, 2004; Salzmann et al., 2008; Haywood and Chandler, 2009; Pound et al., 2011).

The SDM approach also offers the potential for an enhanced contribution of paleobiology not just to modern ecology (e.g., in terms of assessing long-term constraints on current diversity and distribution patterns), but also to conservation biology. This stems not just from the novel general insights into biotic responses to climate change and invasions provided by SDM applications to paleobiology (e.g., Dudei and Stigall, 2010), but also from specifically conservation-oriented studies: e.g., combining SDM with genetic analyses and paleobiological data may inform conservation management by estimating future climate change impacts with respect to the occurrence of past long-term refugia and contingent genetic diversity (Alsos et al., 2009; Cordellier and Pfenninger, 2009; Galbreath et al., 2009; Gugger et al., 2010; Habel et al., 2011). Paleobiology-linked SDM applications may also inform ecological restoration, e.g., in the context of Pleistocene rewilding (Donlan, 2005); for example, a recent study used SDM to assess climatic suitability in western North America for three African and Asian megafaunal species that have been proposed for introduction as potential analogs for extinct North American megafauna (Richmond et al., 2010). While SDM has much to offer to paleobiology, paleobiology likewise offers SDM important possibilities. Notably, paleobiology provides an important background for testing predictive ability across time and under major climate change, forming a crucial basis for evaluating the ability of SDM to predict the biodiversity consequences of future climate change (Martínez-Meyer et al., 2004; Martínez-Meyer and Peterson, 2006; Pearman et al., 2008a).

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Appendix. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.quascirev.2011.06.012.

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