ECOLOGICAL SOUNDING

Predicting the past distribution of species climatic niches

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ABSTRACT

Predicting past distributions of species climatic niches, hindcasting, by using climate envelope models (CEMs) is emerging as an exciting research area. CEMs are used to examine veiled evolutionary questions about extinctions, locations of past refugia and migration pathways, or to propose hypotheses concerning the past population structure of species in phylogeographical studies. CEMs are sensitive to theoretical assumptions, to model classes and to projections in non-analogous climates, among other issues. Studies hindcasting the climatic niches of species often make reference to these limitations. However, to obtain strong scientific inferences, we must not only be aware of these potential limitations but we must also overcome them. Here, I review the literature on hindcasting CEMs. I discuss the theoretical assumptions behind niche modelling, i.e. the stability of climatic niches through time and the equilibrium of species with climate. I also summarize a set of 'recommended practices' to improve hindcasting. The studies reviewed: (1) rarely test the theoretical assumptions behind niche modelling such as the stability of species climatic niches through time and the equilibrium of species with climate; (2) they only use one model class (72% of the studies) and one palaeoclimatic reconstruction (62.5%) to calibrate their models; (3) they do not check for the occurrence of non-analogous climates (97%); and (4) they do not use independent data to validate the models (72%). Ignoring the theoretical assumptions behind niche modelling and using inadequate methods for hindcasting CEMs may well entail a cascade of errors and naïve ecological and evolutionary inferences. We should also push integrative research lines linking macroecology, physiology, population biology, palaeontology, evolutionary biology and CEMs for a better understanding of niche dynamics across space and time.

Keywords
Climate change, climate envelope models, forecasting, fossil record, hindcasting, niche dynamics, physiological limits, population processes.

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INTRODUCTION

Biogeography, systematics, population biology and related research areas are currently converging upon a new cross-disciplinary framework (Diniz-Filho *et al.*, 2008) for understanding the patterns of distribution of life on Earth. They are beginning to share both theories and methods, and some of their potential routes of integration have recently been discussed (Richards *et al.*, 2007; Kozak *et al.*, 2008; Swenson, 2008). One of the concepts laying the foundation of this cross-disciplinary framework is the species niche (Hutchinson, 1957). The niche of a species (*sensu* the fundamental Grinnellian niche in Soberón, 2007) delimits the environmental conditions for which the intrinsic growth rate is positive. Climate envelope models

(CEMs) in particular are becoming widely used to clarify evolutionary questions by projecting a species' niche to different periods in the past.

Hindcasting CEMs are applied to a variety of research questions such as species extinctions (Martínez-Meyer *et al.*, 2004; Nogués-Bravo *et al.*, 2008a), speciation mechanisms (Peterson & Nyári, 2008, Solomon *et al.*, 2008), plant diversification (Yesson & Culham, 2006), ecological niche conservatism (Martínez-Meyer *et al.*, 2004; Martínez-Meyer & Peterson, 2006; Peterson & Nyári, 2008; Pearman *et al.*, 2008a), past distribution of different taxa such as trees, lizards, humans or marine species (Eeley *et al.*, 1999; McGuire *et al.*, 2007; Banks *et al.*, 2008; Benito-Garzón *et al.*, 2008; Bigg *et al.*, 2008; Rodríguez-Sánchez & Arroyo, 2008), location of Pleistocene refugia (Hugall *et al.*,

2002; Peterson *et al.*, 2004; Bonaccorso *et al.*, 2006; Benito-Garzón *et al.*, 2007; Carstens & Richards, 2007; Knowles *et al.*, 2007; Waltari *et al.*, 2007; Carnaval & Moritz, 2008; Dépraz *et al.*, 2008; Svenning *et al.*, 2008a; Fløjgaard *et al.*, 2009; Moussalli *et al.*, 2009; VanDerWal *et al.*, 2009), hotspots (Carnaval *et al.*, 2009) and historical migration pathways (Ruegg *et al.*, 2006; Benito-Garzón *et al.*, 2007; Carstens & Richards, 2007; Waltari & Guralnick, 2009). One of the most promising and exciting applications of CEMs in phylogeographical research is to propose alternative hypotheses concerning past population structure and potential migration pathways. The predictions of these hypotheses are then tested using coalescence methods and genetic data (Richards *et al.*, 2007). However, the reliability of the phylogeographical conclusions is based on the projections of the CEMs. Therefore, rigorous procedures to hindcast CEMs is of the utmost importance, because failure to do so may well entail a cascade of errors.

CEMs are sensitive, among other issues, to theoretical assumptions (Araújo & Guisan, 2006; Pearman *et al.*, 2008b), to model classes (Hijmans & Graham, 2006; Pearson *et al.*, 2006) or to projections in non-analogous climates (Thuiller *et al.*, 2004). Since the pioneering paper by Guisan & Zimmermann (2000), different studies have summarized and discussed ways to improve the usefulness of CEMs for assessing the impacts of global change in biodiversity (i.e. Guisan & Thuiller, 2005; Araújo & Guisan, 2006; Araújo & New, 2007; Thuiller *et al.*, 2008). Here I first discuss the main theoretical assumptions, i.e. the stability of climatic niches and species–climate equilibrium, behind niche modelling. Second, I summarize the basic standard modelling procedures that scientists working in niche modelling have widely accepted. Third, I review the procedures followed by studies hindcasting CEMs to past geological periods (27 studies, Table 1) and I compare them with the points summarized in the second step. I also propose a brief outlook suggesting the integration of different disciplines to gain a better insight into niche dynamics through time. Finally I offer potential routes to deal with the specific challenges related to hindcast CEMs.

THEORETICAL ASSUMPTIONS

The stability of climatic niches through time

The climatic niches of species are potentially the result of inheriting the climatic niches of their ancestors, and the result of adaptation of species to past and current climatic conditions that allow them to persist. One of the main theoretical assumptions for transferring the projections of CEMs through time is the temporal stability of climatic niches, hereafter called niche stability. We should not confuse niche stability through time with the concept of niche conservatism. Niche conservatism (Harvey & Pagel, 1991) refers to closely related species within a phylogenetic tree that are more ecologically similar than would be expected based on their phylogenetic relationships (Losos, 2008a). On the contrary, niche stability only takes into account the similarity of the climatic conditions that allows a *single* species to persist through time. Thus, the main theoretical

assumption behind CEMs should not be phylogenetic niche conservatism (PNC) but niche stability of species through time, although PNC can provide support for niche stability. Finding PNC among phylogenetically closely related species indicates that their current niches are similar (Peterson *et al.*, 1999; Prinzing *et al.*, 2001), and it is assumed that their niches have also remained similar to one another in evolutionary time. However, many clades do not exhibit PNC for some ecological traits (Losos, 2008a; but see also Wiens, 2008; Losos, 2008b) and we need more research to assess the generality of PNC. Using large datasets on species distributions, climatic conditions and phylogenetic trees, we should assess not simply whether there is niche conservatism overall, but which climatic axes contribute to PNC and which ones do not.

CEMs assume non-significant evolutionary or/and ecological change in a species niche as a response to changing environmental conditions along time (Fig. 1). However, evidence suggests that niche shifts have occurred for many species (Pearman *et al.*, 2008b), implying a questionable ability of CEMs to project climatic niches to past periods. For example, niche shifts could be the result of genetic variation for traits related to climate performance (Skelly *et al.*, 2007; Ebeling *et al.*, 2008), a change in the fundamental niche, or because of competition with different species during different periods of time. Whether niche shifts are a general pattern or not may well be a scale-dependent phenomenon. For example, ecological mechanisms such as competitive displacement or environmental tolerance that trigger niche shifts at a local scale might be non-significant at a regional or a continental scale (Prinzing *et al.*, 2002). An unanswered question is whether the temporal scale (100 years, 10,000 years or 1,000,000 years) used in each study underlies the conflicting findings about PNC and niche stability, as recently suggested by A. T. Peterson (personal communication, 2009).

The challenges of modelling species climatic niches for past periods of time have been highlighted in recent review papers (Belyea, 2007; Richards *et al.*, 2007; Kozak *et al.*, 2008) and also in many of the case studies reviewed here. However, only 22% of the studies I examined quantitatively assess the assumption of niche stability. Their approaches for testing niche shifts along time are still in their infancy, but they are a promising starting point. For example, Martínez-Meyer *et al.* (2004) and Martínez-Meyer & Peterson (2006) assessed the ability of ecological niches, as modelled in one time period, to predict the distribution of the climatic niche of species in another period, and vice versa. Peterson and Nyári (2008) proposed a test using information on lineage membership of particular populations of *Schifornis turdina* in the Neotropics. They developed genetic algorithm for rule set production (GARP) models based on all seven possible sets of six phylogroups, and tested the ability of each replicate model to anticipate the geographical distribution of the climatic niches of a seventh phylogroup. Pearman *et al.* (2008a) used multivariate techniques to estimate changes in the niche position of tree species in Europe between the mid-Holocene and the present. Rodríguez-Sánchez & Arroyo (2008) qualitatively assessed the ecological niche conservatism of *Laurus*, comparing climatic response curves for past and present

Table 1 An overview of the 32 papers whose methods were reviewed.

Reference (year)	Taxon	Region	Time periods	Number of AOGCMs or RCM	Number of model classes	Model classes	Number of climatic variables	Independent validation
Banks et al. (2008)	Humans	Europe	21 kyr BP	1	1	GARP	4	No
Benito-Garzón et al. (2007)	Trees	Iberian Peninsula	0 and 21 kyr BP	2	1	Random forest	6	No
Benito-Garzón et al. (2008)	Trees	Iberian Peninsula	0, 6 and 21 kyr BP	1	1	Random forest	6	No
Bigg et al. (2008)	Cod	North Atlantic Ocean	0 and 21 kyr BP	1	1	Maxent	1	No
Bonaccorso et al. (2006)	Birds and woody plants	Amazon Basin	0 and 21 kyr BP	2	1	GARP	2	No
Carnaval and Moritz (2008)	Forest types	Amazonian Basin	0, 6 and 21 kyr BP	1	2	BIOCLIM and Maxent	7	No
Carnaval et al. (2009)	Frogs	Brazilian Atlantic forest	0, 6 and 21 kyr BP	1	*	Maxent	*	*
Carstens and Richards (2007)	Trees and herptiles	North America	0 and 21 kyr BP	1	1	Maxent	19	No
Calleja et al. (2009)	Trees	Iberian Peninsula	0, 6 and 21 kyr BP	1	1	Random forest	6	No
Dépraz et al. (2008)	Snails	Alps	0 and 21 kyr BP	1	1	BIOCLIM	5	No
Eeley et al. (1999)	Forest types	South Africa	0, 6 and 21 kyr BP	*	1	BIOCLIM	PCA of 19	No
Flojgaard et al. (2009)	Small mammals	Europe	0 and 21 kyr BP	2	2	Maxent and BIOCLIM	2–5	Yes
Hijmans & Graham (2006)	Trees	South America	0 and 21 kyr BP	1	4	BIOCLIM, Domain, GAM and Maxent	6 and 19	No
Hugall et al. (2002)	Snails	Australia	0 and 21 kyr BP	†	1	BIOCLIM	3	No
Knowles et al. (2007)	Grasshoppers	North America	0 and 21 kyr BP	1	1	Maxent	19	No
Martínez-Meyer et al. (2004)	Mammals	North America	0 and 21 kyr BP	†	1	GARP	2	Yes
Martínez-Meyer & Peterson (2006)	Plants	North America	0 and 21 kyr BP	1	1	GARP	3	Yes
McGuire et al. (2007)	Lizards	North America	0 and 21 kyr BP	1	1	Maxent	19	No
Moussalli et al. (2009)	Lizards	Australia wet tropics	0, 5, 7.5 and 18 kyr BP	1	1	Logistic regression	2	No
Nogués-Bravo et al. (2008a)	Mammoth	Eurasia	0, 6, 21, 30, 42 and 126 kyr BP	1	3	Mahalanobis distance, BIOCLIM and Maxent	3	Yes
Pearman et al. (2008a)	Trees	Europe	0 and 6 kyr BP	1	1	GBR	5	Yes
Peterson et al. (2004)	Birds	North America	0, 6 and 21 kyr BP	2	1	GARP	*	No
Peterson and Nyári (2008)	Birds	Amazon Basin	0 and 21 kyr BP	2	2	GARP and Maxent	7	No
Rodríguez-Sánchez & Arroyo (2008)	Trees	Mediterranean Basin	0 kyr BP and late Pliocene	2	1	Maxent	3	Yes
Ruegg et al. (2006)	Birds	North America	0 and 21 kyr BP	1	1	BIOCLIM	10	No
Solomon et al. (2008)	Ants	Amazon Basin	0 and 21 kyr BP	1	1	Maxent	20	No
Svenning et al. (2008a)	Trees	Europe	0 and 21 kyr BP	2	2	BIOCLIM and Maxent	12 and 3	No
Yesson & Culham (2006)	Plants	World	0 kyr BP and mid-Miocene	1	1	BIOCLIM	10	No
Varela et al. (2009)	Spotted hyena	Africa and Eurasia	0 and 126 kyr BP	1	1	GLM	2	No
VanDerWal et al. (2009)	Forest types	Australia wet tropics	0, 5, 7.5 and 18 kyr BP	1	1	Maxent	7	No
Waltari et al. (2007)	Mammals, herptiles and birds	North America	0 and 21 kyr BP	2	2	Maxent and GARP	19	Yes
Waltari and Guralnick (2009)	Mammals	North America	0 and 21 kyr BP	2	2	Maxent and GARP	19	Yes

AOGCM, atmosphere–ocean coupled general circulation model; RCM, regional climate model; GAM, general additive model; GBR, generalized boosted regression; PCA, principal components analysis.

*No information is available in the text.

†The authors used other types of information.

Non-robust practices are in dark grey (less than two palaeoclimatic reconstructions, less than two model classes and more than 10 variables used to model the climatic niche of species). Good practices are in light grey. The selection of the thresholds to consider a procedure as non-robust is subjective but broadly agrees with standard modelling practices that people working in niche modelling have widely accepted.
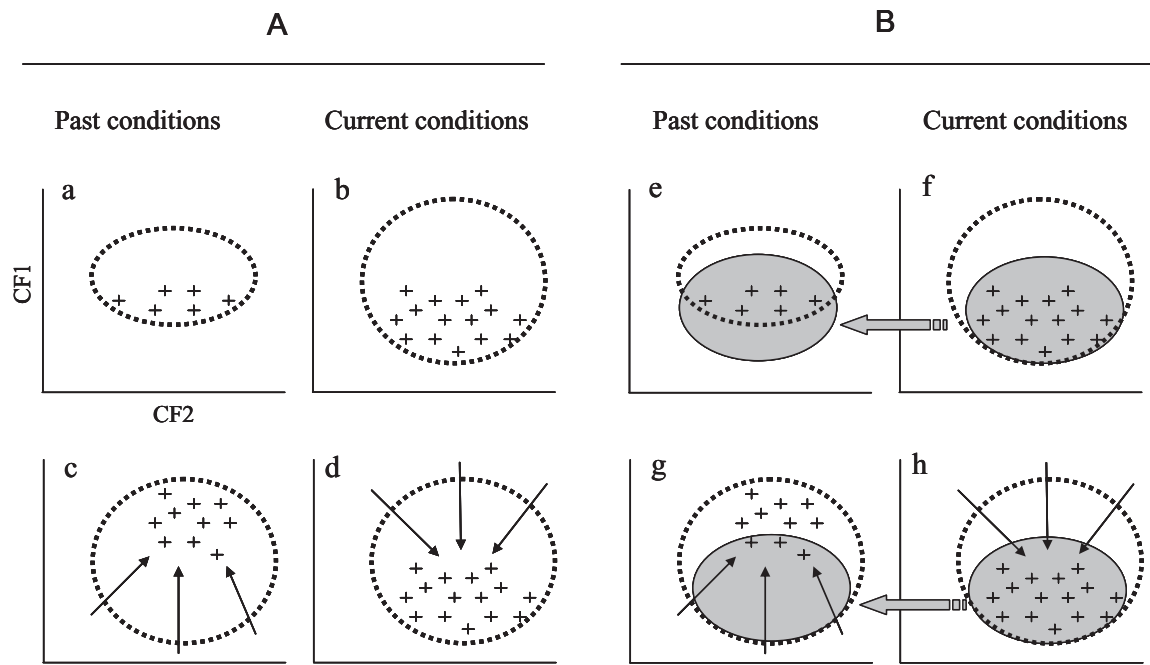
Figure 1 Alternative niche shift scenarios and their implications for projecting climatic niches through time. Both panels A and B represent niches in environmental space (CF1, climatic factor 1; CF2, climatic factor 2). Panel A shows the fundamental niche of a hypothetical species X (dotted circle) and the location of the same species (realized niche; plus signs). Parts (a) and (b) show a change in the fundamental and in the realized niche because of an evolutionary change. Parts (c) and (d) show no change in the fundamental niche but a change in the realized niche because of a different set of species competing for the resources (black arrows represent the competition). Panel B duplicates panel A but including a modelled climatic envelope (grey circles). Climatic envelopes are calibrated at current conditions and projected to past conditions. Niche shifts would imply a scarce degree of temporal transferability and therefore a challenge to be resolved in studies predicting the past distribution of species climatic niches.

conditions. Nogués-Bravo *et al.* (2008a) tested for differences between the climatic conditions occupied by the woolly mammoth using fossil records at three time periods during the late Pleistocene; this test was performed in environmental space, which aids our understanding of changes in the climatic niche of species through time.

A new method for evaluating niche stability is to use metrics that have previously been used to quantify PNC. In a recent paper (Warren *et al.*, 2008), different metrics were proposed to quantify niche overlap between sister species. Taking the metrics in Warren *et al.* (2008) and changing species X and Y for time periods t_1 and t_2 would allow one to test the niche stability of a single species X. This approach would require information about the distribution of the analysed species and climate conditions for more than one time period (i.e. the current distribution of a species, and the distribution of dated fossil records of the same species for past periods). Fossil records may be a biased representation of the past distribution of any species, but the approach of Warren and colleagues may overcome this challenge with a randomization procedure that reduces bias in the sampling of each species with respect to environmental tolerances.

Species–climate equilibrium

CEMs assume equilibrium between species distribution and the climate. Species are said to be at equilibrium with climate if they occur in all climatically suitable areas whilst being absent from all unsuitable ones (*sensu* Araújo & Pearson, 2005). Failure to colonize suitable areas is related to the dispersal ability of species and to biotic interactions. We currently know, for example, that many European tree species are not in equilibrium with climate (Svenning & Skov, 2004) as a consequence of post-glacial dispersal limitations (Svenning *et al.*, 2008b), and that this dispersal limitation also affects the patterns of species richness of different taxa (Svenning & Skov, 2007; Araújo *et al.*, 2008). Among the possible set of biotic interactions, human impacts play a key role in shaping the distribution of species (Channel & Lomolino, 2000) and in species richness (Nogués-Bravo *et al.*, 2008b); therefore human impacts on biodiversity are one of the key factors affecting equilibrium between species distribution and the climate. We need more research to increase our understanding of the role of humans in competitive displacement. Specifically, it is of the utmost importance to assess human-induced contractions or expansions of species ranges for as many species as possible. A potential framework to deal with this assessment (Channel & Lomolino, 2000) is to reconstruct the historical ranges of species and to relate them to human impacts. Thus, we urgently need to develop detailed spatial data for both humans and other species concerning their past distributions, population densities for different historical moments and the intensity of different waves of colonization.

In summary, climate predictions through time may well be seriously misleading because of the possible lack of equilibrium between species distributions and climate in many different taxa. Therefore we should establish approaches to assess the degree of this equilibrium. However, new evidence indicates that even when model results suggest a climatic equilibrium for a species' distribution, the time transferability of niche models does not necessarily provide realistic results (Varela *et al.*, 2009). I suggest two potential ways to deal with the challenge of equilibrium between species distributions and climate for hindcasting or forecasting CEMs. The first one is to hindcast only those species that are in equilibrium or near to equilibrium with climate. A proxy metric to measure equilibrium between species distributions and climate is range filling (Svenning & Skov, 2004), the realized/potential range size ratio (*R/F*). Because different model classes may well produce completely different potential range sizes (Pearson *et al.*, 2006), a consensus approach (Araújo *et al.*, 2005) may be a robust option for measuring *R/F*. The second way is to implement key population processes, such as dispersal and/or local extinction (see De Marco *et al.*, 2008), which affect the degree of equilibrium between species distributions and climate. Implementing these processes for hindcasting species climatic niches will allow us, on the one hand, to simulate colonization and local extinctions, and therefore to increase the reliability of the projections through time. On the other hand, hindcasting species climatic niches including colonization and local extinctions for species with a good record of fossil remains will allow us to validate the accuracy of these novel methods to improve projections through time. In this sense, hindcasting species climatic niches for those species with a good fossil record would be an apt arena for validating and improving CEMs. Some meritorious advances in niche modelling have incorporated dispersal. Iverson *et al.* (2004) combined a habitat model with a model of habitat colonization for predicting the future distribution of tree species in North America using cellular automata (but see Thuiller *et al.*, 2008, for a list of some limitations of this kind of approach). Also using cellular automata, range expansion and contractions (De Marco *et al.*, 2008) may be simulated based on local colonization and extinction constrained by local climatic suitability.

Model calibration

The multi-temporal calibration approach

CEMs statistically relate the known geographical range of a species with the climatic conditions within that range at a given period of time. So far, CEM approaches for hindcasting have developed models using locations from either the current range or the past range. Unfortunately, these approaches do not satisfactorily resolve the challenge of niche shifts for accurately projecting niches through time. A new kind of multi-temporal calibration approach (Fig. 2) has recently been used for the woolly mammoth; this more suitably captures the different set of climatic conditions that a species uses through time (Nogués-Bravo *et al.*, 2008a). The climatic niche of the woolly mammoth was calibrated using the geographical location of dated fossil remains belonging to three different periods (42 kyr BP, 30 kyr BP and 21 kyr BP). The projection of this multi-calibrated niche for these periods and for 126 kyr BP and 6 kyr BP accurately modelled the distribution of the climatic niche of woolly mammoths. The same approach, but pooling the native and invasive ranges of spotted knapweed in Europe and North America, was recently used for predicting current and future biological invasions (Broennimann & Guisan, 2008). Their results show that the multi-temporal calibration approach can improve predictions of the extent of invasion of spotted knapweed in North America. We need more research to test whether including the climatic conditions that allowed species to survive through different periods of time, temporal multi-calibration, performs better than calibrating the niche with only one time slice.

The effects of different model classes, climate change scenarios and the number of variables

There is a current consensus amongst researchers working on niche modelling that it is important to use more than one climatic reconstruction for each time period (i.e. projections based on different general circulation models or regional climate models) and more than one model class (i.e. Maxent, GARP, Mahalanobis distance, random forest). The patterns and mag-
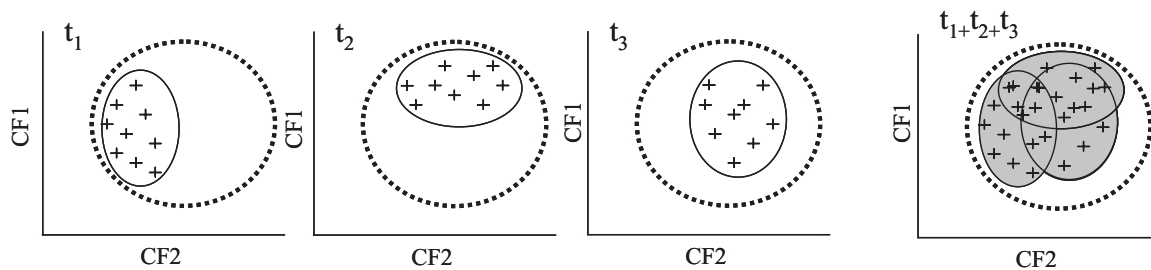

Figure 2 Multi-temporal calibration approach. A hypothetical species X shifting its niche along different past periods (t_1, t_2 and t_3) in the climatic space (CF1, climatic factor 1; CF2, climatic factor 2). The figure shows the fundamental niche of a hypothetical species (dotted circle; assuming no change in the fundamental niche); the location of the same species (realized niche; plus signs) and the multi-temporal calibrated climatic envelope (grey circle). The multi-temporal calibrated niche could be projected in the geographical space for t_1, t_2 and t_3 and for other periods not used in the multi-temporal calibration procedure.

nitude of climate change scenarios for past and future periods differ among different circulation models and therefore it is a source of uncertainty that might affect the results of the CEMs (Beaumont *et al.*, 2008). Also, different model classes may well produce completely different projections (Pearson *et al.*, 2006) and the ability to model the distribution of the climatic niche of species along time differs widely (Hijmans & Graham, 2006). Unfortunately, 62.5% of the papers reviewed here use only one climatic reconstruction, and even more problematically, 72% use only one model class (Table 1). Furthermore, the use of many climatic variables to model the climatic niche of species may lead to overfitting of the model, and thus misrepresentations of the distribution of the climatic niche of species (Beaumont *et al.*, 2005). Using a large number of variables leads to less robust results than using a small number, although results vary among model classes (Hijmans & Graham, 2006). Also, the size of the predicted distributions of species climatic niches is negatively correlated with the number of climatic variables used in the model. Progressive addition of climatic variables causes a gradual narrowing of the distributions of the climatic niches (Beaumont *et al.*, 2005). On the contrary, the use of few variables might tend to overestimate the niche of species. Therefore we need to reach a balance between the number of species occurrences and the number of climatic variables to calibrate the niches. To reduce the number of variables, we can use external procedures such as principal component analyses or internal variable selection methods such as the one included in GARP and the stepwise ones included in regression-based approaches.

The numbers of climatic variables used in the papers I review here vary widely. Whereas some studies use a small number of climatic variables, others use large sets of climatic variables (Table 1). Thirty per cent of the case studies use more than 10 climatic variables. Despite this large number, all the different sets of climatic variables reviewed for this study try to summarize only four main aspects of the climatic niche: mean annual values of temperature and rainfall, their seasonality and extreme climatic parameters, such us the minimum temperature of the coldest month.

A related problem is the lack of comparability among studies. Whilst mature disciplines usually follow the same analytical protocols to make the results comparable across studies, the studies reviewed herein use different numbers and types of palaeoclimatic reconstruction, model classes and climatic variables. For example, four of the studies assess the controversial refugia hypothesis in the Amazon Basin during the Pleistocene (Table 1). They use different climatic reconstructions, model classes and number of variables, and therefore their conclusions are difficult to compare. Moreover, some studies (see Table 1) do not publish their methodological procedures. We should include sufficient information in our studies about the modelling protocols to make the results more comparable and useful in meta-analyses. As a minimum, I recommend publishing: the number of cases for the species distribution dataset, the names and spatial resolutions of the current and past palaeoclimate datasets, the modelling techniques and the type of calibration and validation procedures.

Model projection

There is solid evidence of the occurrence of non-analogous fossil assemblages in Quaternary palaeoecological records (Jackson & Williams, 2004; Williams & Jackson, 2007). These non-analogous communities might be related to the occurrence of non-analogous climate conditions in the past, and to the idiosyncratic responses of each species to climate change because of their unique genetic heritage, their own physiological traits and the different pool of competing species (Graham & Grimm, 1990); but see (Lyons, 2003). Calibrating the climatic niche of species under current conditions and projecting them to non-analogous conditions in the past would lead to spurious response curves and therefore to naïve projections (Thuiller *et al.*, 2004). However, only one of the studies reviewed herein assessed the occurrence of non-analogous climate conditions for the time periods used to project the climatic niches (Fløjgaard *et al.*, 2009). One way to deal with this problem is to calibrate the niche of species using fossil records and palaeoclimatic reconstruction across different time periods, a multi-temporal calibration approach, and then to project this multi-temporal climatic niche to the same periods used to calibrate the model (Nogués-Bravo *et al.*, 2008a). Another way is to assess the geographical distribution of non-analogous climates, as has been done to assess the potential occurrence of non-analogous climates in the future (Ohlemüller *et al.*, 2004; Williams *et al.*, 2007). Delimiting the geographical distribution of non-analogous climate conditions may well clarify the credibility of the projections across the study region.

Finally, projecting the climatic niche of species to past or future periods is not projecting the distribution of species. The realized niche of species and the geographical area occupied by this realized niche are the result of the interaction of mechanisms operating at large scales (Grinnellian niche) and small scales such as, for example, biotic interactions (Eltonian niche). The studies I have reviewed tend to confound the climatic niche with the distribution of the species and this confusion has profound implications for interpreting their results.

Model validation

One of the most striking challenges of CEMs is to validate the projections of the climatic niches using independent data (Araújo *et al.*, 2005). The standard approach to validate a model in the research field of CEMs is to split the current distribution of the species into two sets: one for calibrating the model and one for validating it. Unfortunately, this approach is also the favourite of the reviewed studies. Only 30% of the studies use independent data to quantitatively validate the projections (Table 1). One potential way to independently validate a model is to use the location of refugia that have been identified based on phylogeographical analyses, and using CEM tools to make parallel predictions (Waltari *et al.*, 2007). A second method is to quantitatively assess the proportion of fossil occurrences of modelled species within the projected climatic niche of modelled species (Martínez-Meyer *et al.*, 2004; Waltari & Guralnick,
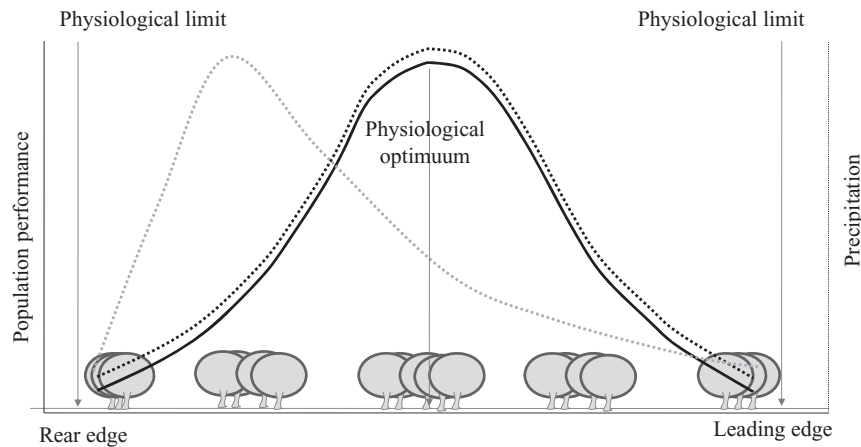
Figure 3 Population performance of a theoretical species X in relation to climate across its geographical range. The left *y*-axis and the continuous black line show the change in a theoretical population performance from the edges to the centre of the geographical range of species X. The right *y*-axis shows the change, across the geographical range of species X, of a climatic factor, precipitation. The black dotted line (theoretical pattern of precipitation p_1), follows the same patterns as population performance, suggesting that climate is controlling the performance of populations, and therefore a mechanistic link between the performance of populations and climate would be assumed. The grey dotted line (theoretical pattern of precipitation p_2), suggests a mismatch between climate and population performance and therefore a mechanistic link between the performance of populations and climate would not be assumed. Dotted lines could be also be understood as the climatic suitability predicted by a climate envelope model (CEM). When this is the case, the black dotted line indicates that the suitability projected by a CEM reflects the performance of populations and therefore it ensures the reliability of the predictions of the CEM.

2009). A third method, for animal species with well-studied habitat conditions, would be to use dated pollen records as an independent source of information. For example, the use of the treeline in Eurasia, based on pollen records (MacDonald *et al.*, 2000), was recently used to validate the climatic niche of the woolly mammoth (Nogués-Bravo *et al.*, 2008a).

PROJECTING CEMS THROUGH TIME: INTEGRATING DISCIPLINES

I have summarized the main basic challenges that CEMs face, and offered ways to develop better predictions of the past distribution of species climatic niches. Many of these basic challenges are not only pertinent to hindcasting but also to forecasting the distribution of species climatic niches. In any case, and beyond these basic challenges, we should develop integrative research lines across the frontiers of macroecology, physiology, population biology, palaeontology, evolutionary biology and CEMs for a better understanding of niche dynamics across space and time.

The response of species ranges to climate change may switch from range persistence to range shift. Range persistence is favoured for species or populations with a large amount of environmental tolerance or with high potential for microevolutionary change (see Parmesan, 2006, for a review on ecological and evolutionary responses to recent climate change). At the opposite extreme, range shift is expected if local populations go extinct and/or populations in the leading edge have a great capacity for dispersal and establishment in new regions without competing species. Therefore, we should first assess the effect of species physiological limits, the rates for microevolutionary

change and population processes such as dispersal or local extinctions on species distribution and secondly we should include them in the niche modelling procedures. A trait-based approach, where traits of species such as frost tolerance or water-logging tolerance are included in niche modelling, is currently a promising way to improve predictions of species distributions through time (Morin & Lechowicz, 2008). Specifically, it is important to know the physiological limits of species to gain a more robust insight into the fundamental niche of species and therefore to ensure the transferability of the projections of CEMs through time. For example, assessing the climatic limits that allow species to survive in laboratory or translocation physiological experiments, and integrating this information with climatic projections, will increase the robustness of CEM projections along time. Therefore, we need more research to quantify the variation in physiological constraints or species traits with climate (Chown & Gaston, 2008; Kearney *et al.*, 2008) and their influence on species distributions (Morin *et al.*, 2007).

CEMs are statistical approaches that relate the known distribution of a species with the climatic conditions within that distribution. Thus, they do not include the key population parameters determining the geographical distribution of species such as colonization or local extinctions (Mustin *et al.*, 2009). Therefore, we should assess: (1) the relationships between climatic factors and key parameters for the persistence of populations across the geographical range of species (population performance); and (2) whether the climatic suitability predicted by CEMs is related to the performance of populations with climate (Fig. 3). This is necessary to increase the reliability of the predictions of CEMs through time. For example, Sanz *et al.*

(2009) recently analysed the spatial consistency across scales of the effects of climatic constraints on the regeneration success of the English yew (*Taxus baccata*) using performance information from yew populations throughout the whole European range. Another promising approach is to compare the spatial variation in the suitability predicted by CEMs with the spatial variation in population fitness (Thuiller & Albert, 2008) to assess the ability of CEMs to represent key population processes. Applying these approaches, i.e. integrating population biology and CEMs, to different taxa will allow us to understand whether climate is controlling population performances and therefore to find mechanistic links between the projections of CEMs and key population parameters behind species distributions. These approaches will benefit large-scale assessments of the impacts of climate change on species range dynamics along time based on the CEM outputs.

CONCLUSIONS

The convergence upon a cross-disciplinary framework of niche theory, palaeoclimatology, biogeography, phylogeography, eco-physiology, population biology and CEMs will allow us to deal with a wide range of biodiversity-related climate change questions such as the causes of extinctions, speciation, location of refugia and migration pathways, both in the past and the future. The papers reviewed herein on hindcasting constitute an excellent starting point, and the authors of many of the papers realize that there are potential limitations that need to be resolved when applying CEMs to past periods. Unfortunately, just being aware of the potential limitations without dealing with them is not sufficient to obtain strong inferences in science. The lack of a robust hindcasting procedure and infrequent comparability of the results need to be remediated to ensure the emergence of a reliable cross-disciplinary framework.

Below I summarize a set of 'recommended practices' to follow for hindcasting CEMs, although to achieve the whole set of recommended practices within each single study would be challenging. The practices are ranked by the potential negative impact upon the results of failing to implement each practice:

1. Before modelling the climatic niche of any species, we should test the assumption of niche stability through time, or at least carefully review the scientific literature to choose species with a certain degree of conservative evolutionary history and lower speciation rates. The further we travel back in time, the larger the potential impact of this assumption on our results would be. There are recent studies with large phylogenetic time trees for mammals (Bininda-Emonds *et al.*, 2007), birds (Hackett *et al.*, 2008), amphibians (Roelants *et al.*, 2007; Vieites *et al.*, 2007), ants (Moreau *et al.*, 2006) and beetles (Hunt *et al.*, 2007) that may well help us to choose what species or lineages have more conservative evolutionary histories.

2. Explore the species–climate equilibrium assumption before projecting climatic niches. The lack of equilibrium between species distribution and climate for many taxa is related to the dispersal ability of species, and therefore implementing key

population processes such as dispersal could improve the CEM projections mainly under non-equilibrium scenarios.

3. Multi-temporal calibration approaches to species niches might provide a better representation of the different climatic conditions that have allowed species to persist than classical approaches, and therefore they may improve the transferability of CEM projections along time.

4. Implement independent validation procedures. Fossil records mean that we can validate projections independently. In the cases where there are no fossil records, we should not validate the model using only the standard validation procedure (i.e. 70% of the cases to calibrate the model and 30% to validate). I encourage authors to use *k*-fold procedures. In a *k*-fold cross-validation, the data are divided into *k* different subsets (e.g. 10), the model is run *k* times and in each run a different set of cases is used as test cases and the other subsets are used as training cases.

5. Map regions with non-analogous climate conditions in the past. We should use these maps as indicators of the credibility of our projections.

6. Test the sensitivity of the projections to different palaeoclimatic reconstructions and model classes using at least two climatic reconstructions when available, and two model classes. We can achieve better hindcasting by using ensemble procedures (Araújo & New, 2007).

7. Include eco-physiological information and key population parameters affecting the distribution of species in niche modelling; this will increase the reliability of projections to past and future periods of time (Kearney *et al.*, 2008).

There are a wide variety of challenges that CEMs must overcome in order to improve the reliability of their predictions through time. As soon as possible, we should attempt to reach a robust modelling protocol to make our results more accurate. It is imperative that we move away from basic approaches and towards more fine-tuned ones. In this sense, hindcasting species climatic niches for species with a good fossil record, and therefore with well-known patterns of range contraction and expansion, would provide an apt arena in which to validate the robustness and usefulness of novel methods for improving CEMs.

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BIOSKETCH

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Editor: José Alexandre F. Diniz-Filho