



Community dynamics under environmental change: How can next generation mechanistic models improve projections of species distributions?



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ABSTRACT

Environmental change is expected to shift the geographic range of species and communities. To estimate the consequences of these shifts for the functioning and stability of ecosystems, reliable predictions of alterations in species distributions are needed. Projections with correlative species distribution models, which correlate species' distributions to the abiotic environment, have become a standard approach. Criticism of this approach centres around the omission of relevant biotic feedbacks and triggered the search for alternatives. A new generation of mechanistic process-based species distribution models aims at implementing formulations of relevant biotic processes to cover species' life histories, physiology, dispersal abilities, evolution, and both intra- and interspecific interactions. Although this step towards more structural realism is considered important, it remains unclear whether the resulting projections are more reliable. Structural realism has the advantage that geographic range shifting emerges from the interplay of relevant abiotic and biotic processes. Having implemented the relevant response mechanisms, structural realistic models should better tackle the challenge of generating projections of species responses to (non-analogous) environmental change. However, reliable projections of future species ranges demand ecological information that is currently only available for few species. In this opinion paper, we discuss how the discrepancy between demand for structural realism on the one hand and the related knowledge gaps on the other hand affects the reliability of mechanistic species distribution models. We argue that omission of relevant processes potentially impairs projection accuracy (proximity of the mean outcome to the true value), particularly if species range shifts emerge from species and community dynamics. Yet, insufficient knowledge that limits model specification and parameterization, as well as process complexity,

Abbreviations: C-SDM, correlative species distribution model; H-SDM, hybrid species distribution model; M-SDM, mechanistic species distribution model.

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increases projection uncertainty (variance in the outcome of simulated model projections). The accuracy–uncertainty–relation reflects current limits to delivering reliable projections of range shifts. We propose a protocol to improve and communicate projection reliability. The protocol combines modelling and empirical research to efficiently fill critical knowledge gaps that currently limit the reliability of species and community projections.

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1. Introduction

Climate change, in conjunction with other anthropogenic drivers, affects species and ecological communities. Projections (see Table 1) of the resulting consequences for species distributions and community dynamics are challenging and represent a knowledge frontier (Doak et al., 2008). At the same time, to sustain biodiversity and ecosystem services Loreau (2010), the demand for projections of ecosystem dynamics in changing environments will continue to increase. We need predictive models that provide reliable projections into the future, to inform and support decision-making and policy under rapidly changing conditions (Leadley et al., 2014; Mouquet et al., 2015; Thuiller et al., 2013).

To be reliable, model projections must be accurate and must minimize uncertainty (Table 1): “Accuracy” describes how closely model projections approximate a true value in the real system (Table 1). If accurate projections are repeated they will cluster around the true value. Accuracy might be estimated from model validation against true values in past and current situations. Unfortunately, the true value is unknown for future projections. Therefore, quantifying accuracy of future projections is impossible.

“Uncertainty” describes the level of variability among repeated model projections (Table 1). The more widespread the results of repeated projections are, the more uncertain we regard them. Uncertainty depends on the consideration, implementation, and parameterization of processes in a model. As processes can vary among model implementations, projection uncertainty can vary among models. Therefore, projection uncertainty is a model property that can be quantified within the remits of the model.

The above concepts do not allow quantifying reliability, as we cannot quantify accuracy of future projections, and can approximate full uncertainty only to the degree of the projection uncertainty of alternative model implementations and parametrizations. But the concepts allow us to identify potentially unreliable projections, i.e. projections that are potentially inaccurate or uncertain. Projections are uncertain, if the model outcome shows broad variance. Projections should be expected to be inaccurate, if they result from models that lack detail, even though the detail’s relevance (Table 1) for model projections is known or should be expected according to prior knowledge or theory.

In this opinion paper we discuss, whether reliable projections of species and community responses to climate change can be achieved given current knowledge; and how projection reliability can be improved within a frame of modelling and empirical research that aims at enhancing information. We particularly address species range shifts, where species need to track the geographic shift of their suitable climatic conditions (Chen et al., 2011; Hickling et al., 2006; Parmesan et al., 1999). We focus on species range shift projections, because of the growing interest in informing conservation policy of the potential risks of climate change to biodiversity (e.g. Root et al., 2003; Walther et al., 2005) and the repeated call for reliable predictions and decision-support. However, our arguments are also applicable to other areas of predictive modelling (Martin et al., 2015; Matthiopoulos et al., 2015), especially in the context of rapid, mixed environmental changes.

Several approaches exist to project the impact of climate change on the shifting of species distributions, with correlative species

distribution models (C-SDMs; also known as niche or climate envelope models) and highly mechanistic species distribution models (M-SDMs; also known as process-based models) being at the opposite ends of a gradient (Dormann et al., 2012).

The correlative approach relates observed geographical species distributions to local environmental conditions (Guisan and Zimmermann, 2000), following the assumption that the climatic and environmental niche is the major factor determining species range (Woodward and Williams, 1987). Subsequently, C-SDMs project future species distributions according to projected climate change, assuming that species either might disperse infinitely and immediately follow change in climatic conditions, or that they cannot disperse and therefore are restricted to future suitable areas within their current range (e.g. summarized by Engler and Guisan, 2009).

In the recent hybrid modelling approach (H-SDM), C-SDMs are enriched by consideration of additional ecological knowledge. H-SDMs usually start with niche estimates from C-SDMs and in the next step add single or few selected biotic factors or processes (Dormann et al., 2012), usually in a form that phenomenologically aggregates effects of underlying mechanisms. Examples are the inclusion of demography (Dullinger et al., 2012; Swab et al., 2015), the inclusion of the spatial distribution of interacting species to account for interspecific interactions (Kissling et al., 2010; Meier et al., 2010; Schweiger et al., 2008) or the consideration of species’ dispersal abilities (Boulangéat et al., 2012; Buse and Griebeler, 2011; De Cáceres and Brotons, 2012; Engler and Guisan, 2009; Meier et al., 2012).

M-SDMs go a step further by including detailed abiotic and biotic processes that mechanistically describe individual, species or community responses to climate change (e.g. Bocedi et al., 2014; Chuine and Beaubien, 2001; Kearney et al., 2008; Lischke et al., 2006; Scheller and Mladenoff, 2008). In forward simulations of M-SDMs, spatiotemporal dynamics of species range shifts emerge from the interplay of the biotic processes. The concept of M-SDMs follows the assumption that details about biotic interactions cannot be ignored when modelling responses to climate change. Lurgi et al. (2015) review types of M-SDM frameworks and their properties.

For reasons of clarity, in this paper, we do not treat H-SDMs as an own category, but concentrate on the two extremes C-SDMs and M-SDMs. H-SDMs can be considered either as enhancements of C-SDMs, if they consider biotic factors in a correlative approach, or as low-level M-SDMs, if they include single simplistic biotic processes. Generally, there is a continuum of structural realism, with some models including more, some less processes (Dormann et al., 2012).

Due to their methodological and structural differences, C-SDMs and M-SDMs are suitable for different aspects of species distribution modelling. C-SDMs are designed to exploit widely available data (e.g. species occurrence databases, spatial climatic variation). By contrast, M-SDMs are particularly well equipped to include detailed biotic processes (e.g. on species interactions, demography, dispersal, or physiology), but their parameterization is hard because of the lack of detailed ecological data (e.g. demographic rates). We argue that these technical differences, with respect to the inclusion of biotic processes and model parameterization, affect projection reliability.

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