

# Predicting impacts of climate change on biodiversity: a role for semi-mechanistic community-level modelling

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## ABSTRACT

**Aim** Robust and reliable predictions of the effects of climate change on biodiversity are required in formulating conservation and management strategies that best retain biodiversity into the future. Significant challenges in modelling climate change impacts arise from limitations in our current knowledge of biodiversity. Community-level modelling can complement species-level approaches in overcoming these limitations and predicting climate change impacts on biodiversity as a whole. However, the community-level approaches applied to date have been largely correlative, ignoring the key processes that influence change in biodiversity over space and time. Here, we suggest that the development of new ‘semi-mechanistic’ community-level models would substantially increase our capacity to predict climate change impacts on biodiversity.

**Location** Global.

**Methods** Drawing on an expansive review of biodiversity modelling approaches and recent advances in semi-mechanistic modelling at the species level, we outline the main elements of a new semi-mechanistic community-level modelling approach.

**Results** Our quantitative review revealed a sharp divide between mechanistic and non-mechanistic biodiversity modelling approaches, with very few semi-mechanistic models developed to date.

**Main conclusions** We suggest that the conceptual framework presented here for combining mechanistic and non-mechanistic community-level approaches offers a promising means of incorporating key processes into predictions of climate change impacts on biodiversity whilst working within the limits of our current knowledge.

## Keywords

Conservation, correlative, metacommunity, planning, process, species.

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## INTRODUCTION

Climate change represents a major threat to biodiversity, especially when coupled with other global change drivers, such as habitat destruction, fragmentation and exotic species invasion (Ehrlich & Pringle, 2008). Halting biodiversity loss in the long term requires careful formulation of conservation and management strategies that best retain biodiversity under climate change. Identifying the most robust and effective conservation strategies for the future therefore depends strongly on reliable and spatially explicit predictions of the likely effects of climate change on biodiversity.

To address this need, considerable scientific attention has been given to developing quantitative approaches to predict biodiversity outcomes under spatially explicit scenarios of global change (Botkin *et al.*, 2007). Such predictions can provide valuable information for planning configurations of retained habitat (e.g. through protection and restoration) that best allow biodiversity to persist in the face of climate change. In keeping with well-established principles of systematic conservation planning (Margules & Pressey, 2000), our focus here is on planning for persistence of biological diversity at a regional or global level. This necessitates modelling approaches capable of predicting not only changes in species, or assemblages of species,

occurring at individual locations in a region, but also the amount of diversity retained collectively across the entire region. We further assume that the fundamental objective of systematic conservation planning is to maximize retention (or minimize loss) of biodiversity as a whole (Margules & Pressey, 2000). To adequately inform systematic conservation planning, predictions are therefore required in terms of the expected retention of biological diversity across all species in many taxonomic groups, rather than just a small subset of focal species.

Although there is an urgent need for reliable, spatially explicit predictions for how climate change will affect biodiversity, generating such predictions is strongly constrained by three major limitations in our current knowledge of biodiversity (Fig. 1). The first limitation is that many species are yet to be discovered and described, the so-called Linnaean shortfall (Brown & Lomolino, 1998). We are still uncertain as to exactly how much diversity we need to model. The second limitation is that our knowledge of the current distribution of most species is poor and is generally based on sparse ecological surveys (the Wallacean shortfall: Lomolino, 2004). We do not have good knowledge of which species occur where. The third key limitation in our knowledge of biodiversity, which we here call the ‘Hutchinsonian shortfall’ (Fig. 1), is that for most species, we still have inadequate knowledge of the attributes that influence their fundamental and realized niches. We are therefore limited in our ability to mechanistically predict changes in the occurrences and abundances of species based on their physiological attributes and interactions with other species. These three shortfalls in our knowledge place a strong constraint on modelling approaches aiming to predict the effects of climate change on biodiversity.

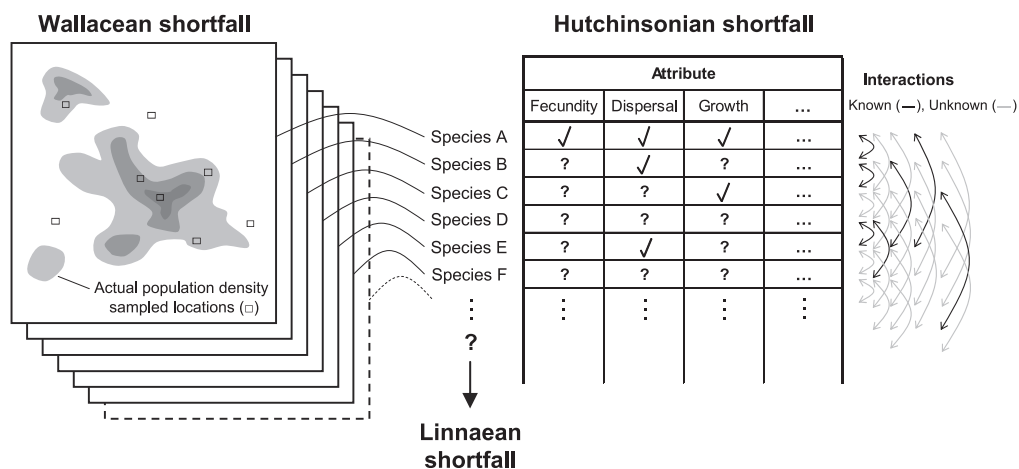
**EXISTING APPROACHES**

The most common approach to predicting impacts of climate change on biodiversity has been to model expected changes in

the distributions of individual species (Elith & Leathwick, 2009). Species distribution modelling (SDM) has most frequently been applied to predict the effects of climate change on the spatial distribution of one or a relatively small number of species at a time (Thuiller, 2003). These predictions can be useful in developing conservation strategies for species of particular conservation concern, but are less relevant to conservation planning for biodiversity as a whole. In contrast, the application of SDM to all the species in a taxonomic group provides a clearer representation of climate change impacts on biodiversity for a region and has been previously applied to taxa such as birds, amphibians and reptiles in Europe (Araújo *et al.*, 2006; Huntley *et al.*, 2008), as well as birds and mammals in Africa (Thuiller *et al.*, 2006; Hole *et al.*, 2009).

Species distribution modelling has been successful in dealing with limited information on the current distribution of species (the Wallacean shortfall). However, the utility of SDM in predicting patterns in diversity for all the species in a taxonomic group depends on the availability of suitable information for all component species, which varies with the group of interest and the location and size of the region being examined. For taxonomic groups that are well studied across a region (e.g. typically birds, mammals and reptiles), SDM is a powerful approach to predict spatially explicit effects of climate change on biodiversity. Species-level modelling is less appropriate for predicting diversity patterns for taxonomic groups that are poorly studied or highly species-rich across the region of interest (e.g. plants and invertebrates in tropical forests).

A complementary strategy to SDM in predicting the impacts of climate change on biodiversity, given the shortfalls in our knowledge, is to shift the focus of modelling from individual species to attributes of biodiversity at the community level (Ferrier & Guisan, 2006). Applications of community-level modelling in predicting climate change impacts have included spatially explicit models of change in species richness (e.g.



**Figure 1** The difficulty in predicting how biodiversity will respond to climate change stems from three key limitations: the Linnaean shortfall, in our discovery and description of species; the Wallacean shortfall in our knowledge of the explicit spatial distribution of species; and the Hutchinsonian shortfall in our knowledge of the attributes of species (and their interactions) which mechanistically influence how their distributions change over time.

Menendez *et al.*, 2006; Sommer *et al.*, 2010), continuous gradients of turnover in species composition (e.g. Duckworth *et al.*, 2000; Ferrier *et al.*, 2007) and discrete community 'types' (e.g. Brzeziecki *et al.*, 1995; Hilbert & Ostendorf, 2001). The primary advantage of community-level modelling is that it can be applied more readily to highly diverse, poorly studied taxonomic groups and hence offers a basis for predicting climate change impacts on biodiversity in situations where insufficient data are available for modelling each species individually (Mokany *et al.*, 2010). Community-level modelling is, however, less well suited to generating predictions for better-known species of particular conservation concern, and therefore complements, rather than competes with, species-level modelling of climate change impacts.

Despite the attractiveness of community-level modelling in predicting impacts of climate change on biodiversity as a whole, the approaches applied to date have been based largely on correlative (non-mechanistic) relationships between community-level diversity attributes and environmental variables. While these correlative models are well suited to dealing with limitations in our current knowledge of biodiversity (Fig. 1), they ignore the important processes that influence the response of biodiversity to environmental change (e.g. dispersal, interspecific interactions, adaptation). There is a real and pressing need to develop new community-level approaches that are flexible in dealing with limited information yet robust in incorporating key mechanisms.

At the species level, recent work has addressed the deficiencies of purely correlative approaches by fusing elements of these approaches with mechanistic (or process-based) elements to create semi-mechanistic models. For example, correlative species distribution models have been combined with mechanistic models of dispersal (Engler & Guisan, 2009), spatially explicit metapopulation models (Keith *et al.*, 2008) and metabolic theory (Cheung *et al.*, 2008), to generate predictions of change in the distribution and abundance of individual species under global change scenarios. These approaches use correlative habitat modelling to predict the potential distribution of a species using limited data on its current distribution, within which realized abundance is further constrained and shaped by mechanistic processes. Semi-mechanistic models emerging at the species level point to the possible advances that can be made by synthesizing mechanistic and non-mechanistic model elements.

## A WAY FORWARD: SEMI-MECHANISTIC COMMUNITY-LEVEL MODELLING

We suggest that one of the most profitable future avenues in modelling climate change impacts on biodiversity will be the development of semi-mechanistic models at the community level. A semi-mechanistic community-level approach would retain the features of existing correlative community-level models to deal with shortfalls in our knowledge of biodiversity (Fig. 1), but would incorporate key mechanistic processes in predicting how diversity will change over time as environ-

mental conditions vary. By adopting both mechanistic and non-mechanistic elements, a semi-mechanistic community-level approach has the potential to be: (1) simple to apply using available information, (2) theoretically robust by being based on the key processes structuring communities and (3) applicable to any taxonomic group and thereby relevant to biodiversity as a whole.

The non-mechanistic elements in a semi-mechanistic community-level approach may include correlations between community diversity indices and environmental variables (Sommer *et al.*, 2010), strong correlative patterns in community structure (e.g. species area theory, species abundance distributions; Connor & McCoy, 1979), or statistically generated 'synthetic' data for the attributes of component species (Austin *et al.*, 2006). In contrast, the important mechanistic elements may include movement/dispersal of organisms in space, interactions between organisms (e.g. predation, competition, mutualism) and the capacity of organisms to adapt as environmental conditions change (e.g. behavioural, phenotypic and genotypic adaptation; Williams *et al.*, 2008).

A deep pool of mechanistic community-level theory can be drawn upon to incorporate key processes influencing community change into semi-mechanistic community-level modelling. Existing mechanistic approaches include metacommunity theory (Mouquet *et al.*, 2006), food web theory (Cohen *et al.*, 2003), neutral theory (Hubbell, 2001), metabolic theory of ecology (Brown *et al.*, 2004) and trait-based community assembly theory (Keddy, 1992; see Appendix S1 in the Supporting Information). Despite the broad range of mechanistic community models available, their application to predict climate change impacts for large regions has generally been restricted by limitations in the information required to parameterize them. Fusion of mechanistic modelling with correlative approaches has the potential to help address these limitations.

In broad terms, semi-mechanistic models can be seen as an effective way of balancing the three desirable properties of ecological models: generality, precision and reality (Levins, 1966). A purely correlative approach sacrifices generality, as correlative relationships may not hold as the context changes. Likewise, a purely mechanistic approach sacrifices precision, as such models are widely applicable but often not as precise as a correlative approach for a specific context, because of lack of knowledge in terms of the mechanism involved or model parameters (Guisan & Zimmermann, 2000). A semi-mechanistic approach necessitates some loss of either precision or generality, compared to purely correlative or mechanistic modelling. The key challenge in formulating a hybrid modelling approach therefore lies in finding the most robust and efficient way to balance the precision and generality of correlative and mechanistic model elements, such that more accurate predictions of climate change impacts on biodiversity are achieved.

## LEARNING FROM EXISTING APPROACHES

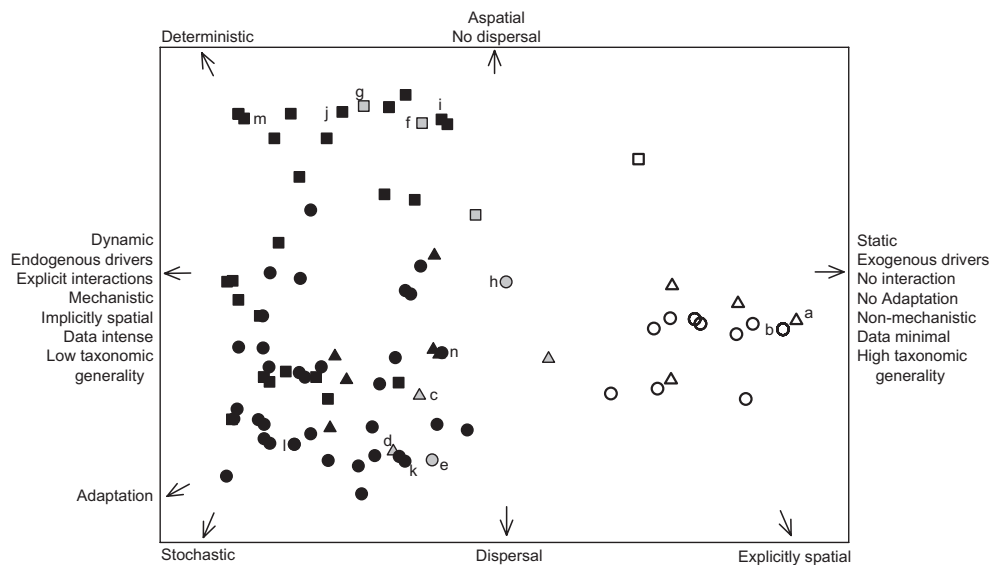
Before framing a new semi-mechanistic community-level modelling approach in more detail, it is valuable to first

thoroughly assess the types of biodiversity modelling approaches already available. Given a broad perspective on the many ways both mechanistic and non-mechanistic biodiversity models have approached the challenge of predicting biodiversity change, fruitful avenues for the development of new semi-mechanistic models may quickly become apparent.

To inform the development of new semi-mechanistic community-level biodiversity models, we conducted an expansive review of existing biodiversity modelling approaches spanning levels of organization from populations to meta-communities. We focussed particularly on recent novel and promising approaches to understanding community change over space and time. To provide a meaningful comparison between modelling approaches, we extracted information from each approach on eleven important model attributes: biotic scale (population, community, metacommunity); treatment of space (aspatial, implicitly spatial, explicitly spatial); treatment of time (static, dynamic); model drivers (endogenous, exogenous, both); interspecific interactions considered (explicitly, not explicitly); dispersal considered (yes, no); adaptation considered (yes, no); predictive approach (non-mechanistic, semi-mechanistic, mechanistic); model dynamics (deterministic, stochastic); data requirements (low, high) and taxonomic generality (general, specific). We used this information to ordinate the approaches using multiple correspondence analysis (Nenadic & Greenacre, 2007). We provide a full account of our review of modelling approaches in Appendix S1.

Ordinating biodiversity modelling approaches by their key attributes (Fig. 2) provides a powerful way of visually assessing their commonalities and differences, revealing a complex milieu of approaches sharing various types and numbers of attributes. The schism between mechanistic and non-mechanistic biodiversity modelling is clearly evident from this ordination (Fig. 2). Despite the generality achieved by mechanistic models and the precision achieved by correlative models (Levins, 1966), very few modelling approaches combine both mechanistic and non-mechanistic elements.

Of the small number of semi-mechanistic community-level models that have been developed, several innovative approaches have applied mechanistic theory of community assembly and structure within a statistical mechanics framework (Shipley *et al.*, 2006; Dewar & Porte, 2008; Harte *et al.*, 2008). Under these approaches, community attributes are predicted statistically by maximizing entropy, given a number of underlying mechanistic constraints. A very different example of semi-mechanistic community-level modelling was presented by Bolliger (2005) who combined correlative community-level patterns with a spatiotemporal cellular automaton model to predict the distribution of community types. Although the few available examples of semi-mechanistic community-level models point to the potential utility in combining mechanistic and non-mechanistic model elements, these particular models are not suitable for predicting impacts of climate change on biodiversity over extensive regions, as



**Figure 2** An ordination of the main approaches used to understand and model biodiversity change over space and time. Symbols represent the biotic scale modelled (triangles = population, squares = community, circles = metacommunity) and the predictive approach applied [black = mechanistic ( $n = 70$ ), grey = semi-mechanistic ( $n = 8$ ), white = non-mechanistic ( $n = 22$ )]. Model attributes associated with different parts of the ordination space are given in surrounding text, with arrows indicating the direction of positive correlation. Selected modelling approaches annotated are species distribution modelling (SDM) for individual species (Thuiller, 2003 (a)); SDM for all species in a taxon (Hole *et al.*, 2009 (b)); semi-mechanistic SDM (Keith *et al.*, 2008 (c), Engler & Guisan, 2009 (d)); community-level correlative modelling (Menendez *et al.*, 2006 (b)); semi-mechanistic community-level models (Bolliger, 2005 (e), Shipley *et al.*, 2006 (f), Dewar & Porte, 2008 (g), Harte *et al.*, 2008 (h)); metabolic theory (Brown *et al.*, 2004 (i)); food web theory (Cohen *et al.*, 2003 (j)); neutral theory (Hubbell, 2001 (k), Zillio & Condit, 2007 (l)); Lotka-Volterra population theory (Lotka, 1925; Volterra, 1931 (m)), and; island biogeography (MacArthur & Wilson, 1967 (n)); Full ordination methods and results provided in Appendix S1.

they are either aspatial or do not incorporate environmental drivers.

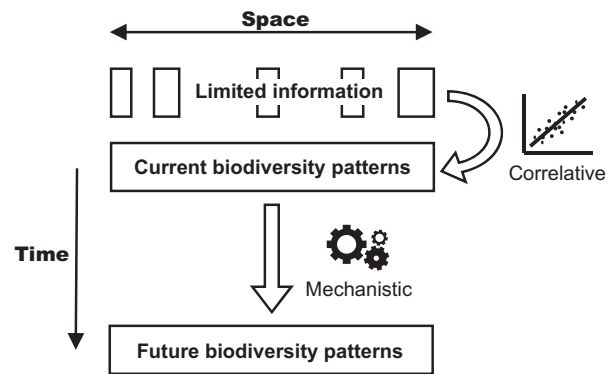
Of the purely mechanistic community-modelling approaches reviewed, several combine strong process-based modelling with minimal data requirements and so have significant potential to be adopted in a semi-mechanistic approach (Kerr *et al.*, 2007). For example, the metabolic theory of ecology (Brown *et al.*, 2004) is a community-level approach applying simple parameters (e.g. body size) to drive mechanistic models of biodiversity under varying conditions (temperature, resources). Metabolic theory has already been applied successfully in one semi-mechanistic community model (Harte *et al.*, 2008) and has made significant contributions to many other modelling approaches (e.g. food web theory: Cohen *et al.*, 2003).

The neutral metacommunity model of Hubbell (2001) also uses a small number of community-level parameters in its representation of community change through stochastic dispersal processes (ecological drift). Extensions of neutral theory to incorporate the role of spatial environmental variation in structuring communities (e.g. Zillio & Condit, 2007) highlight the adaptability of neutral theory and its potential in contributing to new semi-mechanistic biodiversity models. These examples point to the rich array of mechanistic community-level modelling approaches that could make a contribution to developing new semi-mechanistic approaches to predicting climate change impacts on biodiversity. A key challenge, however, is identifying and selecting mechanistic model elements that are simple enough, in terms of parameterization and computation, to be applicable across extensive real-world planning domains (e.g. whole eco-regions, countries or continents; Kerr *et al.*, 2007).

### FRAMING A NEW SEMI-MECHANISTIC COMMUNITY-LEVEL APPROACH

Here, we have argued that a semi-mechanistic community-level approach could represent one of the most promising avenues for the development of new models aiming to predict the impacts of climate change on biodiversity. The non-mechanistic component of such an approach could address limitations in data on the current spatial distribution of biodiversity (the Wallacean shortfall: Fig. 1) and the attributes of each species (the Hutchinsonian shortfall: Fig. 1). The mechanistic component in a semi-mechanistic approach could incorporate the key processes influencing biodiversity change over time (Fig. 3).

More specifically, the non-mechanistic component of a semi-mechanistic community-level approach could be used to generate predictions of current patterns in diversity over large regions (Fig. 3). Correlative community-level modelling approaches make use of data for all species in a taxon simultaneously, alleviating a limitation of species-level approaches that require substantial information for each species and thereby provide effective estimation of current diversity patterns. The biodiversity patterns predicted from



**Figure 3** A general conceptual framework for a semi-mechanistic community-level approach to predicting climate change impacts on biodiversity. Correlative model elements would be used to predict current patterns in biodiversity over space, and then mechanistic model elements would predict changes in biodiversity over time under climate change.

correlative community-level models could then form the initial conditions for a mechanistic model generating change in biodiversity over space and time as a result of changing environmental conditions and internal processes (dispersal, interspecific interactions, adaptation; Fig. 3).

Non-mechanistic approaches could be further applied to populate the required parameters of a mechanistic model with simulated values for species or community attributes, generated from known statistical distributions (Austin *et al.*, 2006; Gotelli *et al.*, 2009). For example, where data for a key physiological parameter are available for only a limited number of species, the mean and variance of this sample could be used to generate synthetic data for all remaining species, incorporating observed covariation with other attributes. Simulated data have been successfully applied in a broad range of community-modelling settings (e.g. Chave & Norden, 2007; Arita & Vazquez-Dominguez, 2008; Kleidon *et al.*, 2009) and may act as a key ingredient in overcoming the Hutchinsonian shortfall (Fig. 1) by allowing mechanistic models to be applied to real communities even where information on key attributes is grossly incomplete.

The output from such a semi-mechanistic model would be a spatially explicit prediction of the combined effects of environmental change and habitat configuration on the retention of all species within a given region (i.e.  $\gamma$ -diversity). Ideally, this would be a taxonomically generic approach, allowing for assessment of changes in biodiversity across a wide variety of taxonomic groups and environments (Mokany *et al.*, 2010). Predictions of biodiversity retention for alternative configurations of habitat could then be used to help identify priority areas for habitat protection and/or restoration. Semi-mechanistic community-level models are also likely to have a range of other applications, such as contributing to our understanding of the processes responsible for current spatial patterns in biodiversity.

In conclusion, we call for greater application of community-level approaches to complement species-level approaches in

predicting climate change impacts on biodiversity. These community-level approaches need to more effectively combine the complementary strengths of both mechanistic and non-mechanistic modelling components. Building on the success of semi-mechanistic models at the species level, we suggest that the development of new semi-mechanistic community-level models could significantly increase our capacity to predict the effects of climate change on biodiversity. Such predictions would be of great value to conservation planners and managers developing strategies to minimize the loss of biodiversity under climate change.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Detailed methods and results of the biodiversity modelling review.

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## BIOSKETCHES

**Karel Mokany** is a Postdoctoral Fellow with CSIRO Ecosystem Sciences, developing new approaches to predicting climate change impacts on biodiversity, through community-level modelling.

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Author contributions: K.M. and S.F. conceived the ideas; K.M. collated and analysed the data; K.M. led the writing.

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