Seeing the woods for the trees – when is microclimate important in species distribution models?

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 Potter *et al.,* (2013) highlight the challenges and provide recommendations for progress in representing microclimate in Species Distribution Models (SDMs), widely used to predict distributions by establishing relationships between climatic variables and species presence.   They show that the grid lengths of published SDMs are typically four orders of magnitude larger than the length of animals under study, and three orders of magnitude larger than plants. They conclude that the mismatch between the length scales of climate data and the species themselves is a major barrier for progress, and that the ideal spatial resolution for climate data in SDMs, notwithstanding practical constraints, is between 1 and 10 times the length of the organism.

At face value this statement is worrying for ecologists concerned with the practical challenges of modelling current or future climatic constraints on animal and plant distributions. The need for such predictions is pressing, but a spatially explicit and accurate representation of global or regional climate at a scale of a few centimetres is impractical, even with rapid advances in computer processing power and high resolution remote sensing data. While agreeing with many of the recommendations for progress proposed by Potter *et al*. (2013), we question whether aiming for such ultra-fine spatial resolution in all circumstances is a useful goal.

The apparent mismatch between the scale of climate data and the size of organisms is bridged implicitly in most SDMs with a "mean field approximation", by assuming that grid-cell average climatic variables are statistically meaningful predictors of the probability of species persistence. This assumption does not necessarily require that the gridded climate data accurately represent the microclimate experienced by any individual within that grid cell, or as Potter *et al.* (2013) suggest, that all species within a grid cell experience the same climate. The mean field approach simply requires that macroclimate is a good predictor of the aggregated population-level effect of many individual responses to the spatial and temporal variation in microclimate that influence individual performance. Often this is a reasonable assumption; while it is true that "current climate data are coarse because it is difficult and expensive to sample simultaneously at fine scales and geographical extents" (Potter et al., 2013), gridded climate data only exist at all because they are useful. Statistical correlations between large-scale climate and a range of physical and biological phenomena (not limited to species distributions) are well established, and frequently robust without downscaling to the scale of the mechanistic processes involved.

When studying thermal physiology, clearly it is desirable to take temperature measurements as close as possible to the organism (or organ) of interest. However, the aim of a SDM is not to predict physiological rates of an individual, but the presence or absence of populations, where the response variable is usually mapped at a similar resolution to the climate data itself. Linking SDMs to physiological mechanisms is clearly appealing in terms of understanding the mechanisms underlying species responses (Kearney and Porter 2004, Crozier and Dwyer 2006, Buckley *et al,* 2010), but downscaling coarse resolution climate data to an appropriate spatial and temporal scale (Kearney *et al.,* 2012) is only half of the challenge. Physiological rates must also be scaled, either explicitly or implicitly, up to higher levels of ecological organisation - to individual fitness, survival and reproductive rates, population dynamics (Buckley *et al.,* 2008) and possibly metapopulation

dynamics (Bennie *et al.,* 2013) before they finally translate into distribution maps at the desired ecological scale (Figure 1). Such ecological models may themselves be sensitive to mean field approximations (Morozov and Poggiale 2006) – for example scaling from individuals to populations or local populations to metapopulations. In practice, greater accuracy in describing the operative temperature of organisms (Bakken 1992) will only improve SDM predictions if coupled with accurate ecological models to scale from physiology to distribution.

To decide when to downscale climate data, we must first establish why we are doing it – the fact that coarse-scale climate data does not accurately represent the climate as experienced by an organism may not in itself be a sufficient reason. Representing microclimate in SDMs is likely to be desirable in at least three types of circumstance - when predictions of distribution are needed at a high resolution; when mechanistic insights into the physiology driving species responses to climate are required; and when the mean field approximation of classic SDMs is unsatisfactory and non-linear responses to microclimate availability become critical in determining the distribution of species at a large scale. We advocate a focus on identifying the conditions under which mean field approximations break down, and the spatial scales at which this breakdown occurs, in different systems, tested where possible against field observations. In this way we may strengthen general recommendations for the appropriate scales at which best to model the responses of species distributions to climate change.

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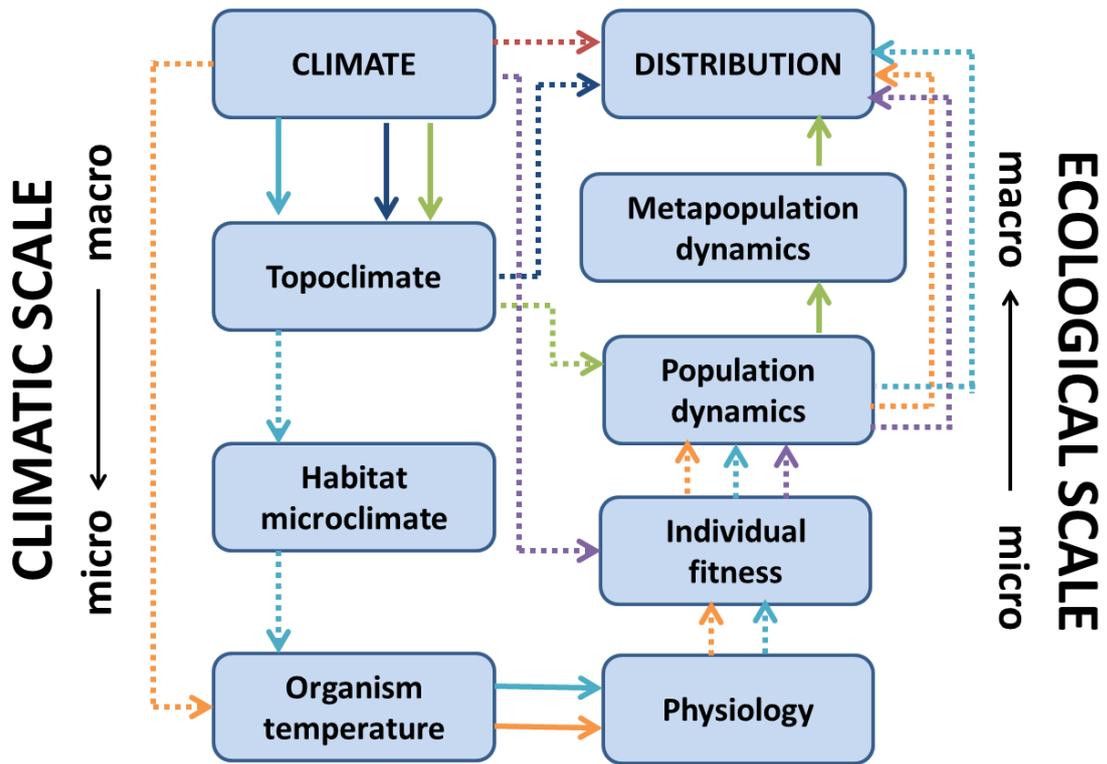
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Figure 1: Climatic and ecological scaling in species distribution models (SDMs). The aim of an SDM is to predict a species' distribution from a set of environmental (including climatic) variables. Most SDMs apply a statistical relationship directly between climate and distribution at a coarse scale. Alternative approaches taken by selected key studies is shown by arrows; solid arrows show explicit representation of processes between scales (for example multiple microclimates modelled within a climate grid square, multiple populations modelled within a metapopulation), dashed lines represent mean field approximations (for example fitness of an individual scaled to population dynamics).

CLIMATIC SCALE   macro ↑ micro ↓

ECOLOGICAL SCALE   macro ↑ micro ↓

CLIMATE

Topoclimate

Habitat microclimate

Organism temperature

DISTRIBUTION

Metapopulation dynamics

Population dynamics

Individual fitness

Physiology

Most SDMs
Ashcroft *et al.*, 2008

Crozier and Dwyer 2006
Buckley 2008

Kearney and Porter 2004
Bennie *et al.*, 2013