

# Improving species distribution models for climate change studies: variable selection and scale

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## Abstract

Statistical species distribution models (SDMs) are widely used to predict the potential changes in species distributions under climate change scenarios. We suggest that we need to revisit the conceptual framework and ecological assumptions on which the relationship between species distributions and environment is based. We present a simple conceptual framework to examine the selection of environmental predictors and data resolution scales. These vary widely in recent papers, with light inconsistently included in the models. Focusing on light as a necessary component of plant SDMs, we briefly review its dependence on aspect and slope and existing knowledge of its influence on plant distribution. Differences in light regimes between north- and south-facing aspects in temperate latitudes can produce differences in temperature equivalent to moves 200 km polewards. Local topography may create refugia that are not recognized in many climate change SDMs using coarse-scale data. We argue that current assumptions about the selection of predictors and data resolution need further testing. Application of these ideas can clarify many issues of scale, extent and choice of predictors, and potentially improve the use of SDMs for climate change modelling of biodiversity.

## Keywords

Climate change, climate envelope modelling, generalized additive modelling, realized niche, refugia, resolution, solar radiation, species distribution modelling.

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## INTRODUCTION

The use of statistical species distribution models (SDMs) to predict the potential changes in species distributions under climate change scenarios is now commonplace. There is, however, rising concern at how SDMs are being used to predict the impact of climate change on biodiversity (Heikkinen *et al.*, 2006; Beale *et al.*, 2008; Jeschke & Strayer, 2008; Luoto & Heikkinen, 2008; Morin & Lechowicz, 2008; Pöyry *et al.*, 2008; Randin *et al.*, 2009; Willis & Bhagwat, 2009). Assumptions criticized include: the expectation of equilibrium conditions (Schröder & Seppelt, 2006), ignoring the effects of evolutionary adaptation and limitations on dispersal (Dormann, 2007; Jeschke & Strayer, 2008), and ignoring the acclimatization and persistence ability of species (Willis & Bhagwat, 2009). Other concerns are the disregard of appropriate scales for plant–environment and biotic interactions (Luoto & Heikkinen, 2008; Randin *et al.*, 2009), the lack of modern analogues of future climates (Heikkinen *et al.*, 2006), and the absence of

ecophysiological and experimental confirmation of models (Dormann, 2007; although see Austin *et al.*, 2009 for an exception). While many of these issues require substantial research, we suggest that, by re-examining a simple conceptual framework and considering common ecological assumptions, improvements in the use of SDMs for climate change predictions can be made.

Early influential studies of species distributions used only climatic variables, for example the mean temperature of the coldest month, growing degree-days, and an index of annual moisture availability and species presence–absence data (Huntley *et al.*, 1995; Sykes *et al.*, 1996). Subsequent authors have often adopted this approach of using only climate predictors and a resolution of 10 × 10 km or 50 × 50 km pixel SDMs to explore a variety of methodological comparisons focused on SDM (e.g. Araújo *et al.*, 2006; Thuiller *et al.*, 2006; Pöyry *et al.*, 2008) and ecological issues (e.g. Luoto *et al.*, 2006; Svenning *et al.*, 2008). Araújo & Guisan (2006, pp. 1681–1682) state that the ‘use of automated solutions to predictor selection ... should

not be seen as a substitution for preselecting sound ecophysiological predictors based on deep knowledge of the biogeographical and ecological theory', and that 'when predicting the likely impact of climate change on species distributions, across large regions, one can reasonably assume that using climate predictors alone should prove sufficient to assess the main changes in distribution'. However, see Araújo & Luoto (2007) for a statement in which they call for more stringent evidence in support of the idea that purely climate-based modelling is sufficient to quantify the impact of climate change on species distributions.

We focus on two aspects of assuming that climate variables are sufficient in climate change studies, as follows. (1) How important are non-climatic variables? (2) What is the appropriate resolution for incorporating biophysical and biotic interactions for successful modelling? It is necessary to test these assumptions because they are often inconsistent with available ecological information (Dormann, 2007).

We use a conceptual framework to explore the choice and scale of environmental predictors currently being used in SDMs. We use light as an example of a predictor that is highly dependent on local topography, requiring the use of high-resolution data. We suggest that application of these ideas clarifies problems of the choice of environmental predictors, as well as of the data scale, resolution and extent, which can potentially improve how SDMs can be used for climate change modelling.

## CONCEPTUAL FRAMEWORK FOR SPECIES DISTRIBUTION MODELLING

Textbooks conventionally present plant growth and distribution as being controlled by both environmental and biological variables:

$$\text{species abundance} = f(\text{light, temperature, nutrients, water, CO}_2, \text{disturbance, biota}). \quad (1)$$

Each of these variables can be defined as either a direct or a resource variable *sensu* Austin (1980). That is, they have a direct effect on plants, for example temperature, or are consumed by plants in order for them to grow, for example nitrogen. (Note that here we focus on plants, but similar arguments can be advanced for animals.)

Improvement of SDMs requires an explicit statement of why predictors have been selected, what ecophysiological process they are intended to represent, and what assumptions have been made about non-included variables. Many predictors used in SDMs have no direct effect on growth (Austin, 1980), being surrogates for more biologically relevant variables, for example elevation for temperature. An advantage of equation (1) is that it focuses simply on the direct variables affecting plant growth.

A biologically relevant variable must also have a data resolution that is consistent with the scale at which the ecophysiological processes show greatest variation. Some hierarchical frameworks recommend critical scales for different

environmental characteristics but assume the use of coarse-scale data for large areas and fine-scale data for small areas (e.g. Pearson & Dawson, 2003). This is not necessarily appropriate, as local topographic factors may modify the climatic impact, particularly when studies are applied to very large areas (see Austin & Van Niel, 2010). Suitable conceptual models of the use of predictors have been presented (Franklin, 1995; Guisan & Zimmermann, 2000) but are often ignored in climate change studies. We suggest that equation (1) or a similar expression should be used to explicitly structure the selection of environmental predictors based on known ecophysiological processes, choice of data resolution, and arguments for the inclusion or exclusion of variables.

## An early approach

Perring, in a series of three papers (Perring, 1958, 1959, 1960), provided a very clear example of the explicit reasoning that could be used for the selection of predictors, based on Major's (1951) suggestion of applying Jenny's functional factorial approach in soil development (Jenny, 1941) to vegetation:

$$v = f(cl, p, r, o, t), \quad (2)$$

where *cl* is the regional climate, *p* is the parent material, *r* is the topography, *o* is the biotic factor and *t* is time.

The topographic and climatic gradients were analysed for individual plant species in chalk grasslands in England and northern France using graphical techniques (Perring, 1958). The study examined variation in regional climates (*cl*) by stratification, sampling four regions with different rainfall and temperature regimes, and a range of topographic conditions (*r*) within each region. Parent material (*p*) was controlled for by sampling only chalk substrates. Species displayed a range of distinctive distributions in relation to slope and aspect (Perring, 1959), and the patterns changed in a consistent manner when compared across climatic regions (Perring, 1960). A strong interaction between regional climate and local topography was critical in influencing the distribution of chalk grassland species. The influence of rainfall and temperature was shown to be conditional on local topography, owing to modification of the local climate by differences in radiation resulting from differences in topographic exposure and aspect. This outcome is significant for SDMs assessing the effects of climate change, as it underlines the importance of local topography in understanding species distributions.

While the conceptual framework presented has serious weaknesses of definition, the absence of a consistent framework for choosing environmental predictors in SDMs makes it difficult to compare models used in climate change predictions (Elith & Leathwick, 2009; Franklin, 2009).

## Current approaches

Araújo & Guisan (2006) recognize the challenge of understanding how geographical extent and resolution affect the

selection of predictor variables and model performance. Implicit in this recognition is the need for functionally relevant predictors (Elith & Leathwick, 2009). Rather than provide a review, we have selected papers published over the last 20 years in order to display the range of ways in which variables are selected and expressed.

### Choice of predictors

Franklin (2009) provides an illustrative table (table 10.3) of the number and types of environmental predictors used in SDMs based on 28 studies. The range in data resolution for the 19 plant studies is from 0.000625 to 2500 km<sup>2</sup>. The number of predictors used ranges from 3 to 36. Climate variables are used in all 19 studies, while substrate predictors are used in only 11 (numbers of predictors range from 1 to 22).

We use a similar illustrative table (Table 1) to explore the use of predictors, structured using the conceptual framework presented in equation (1). It is clear that each study has an implicit conceptual model, but there is little consistency between them. No study includes predictors for all six conceptual variables, although the category 'other predictors' may provide surrogates for them. The total number of predictors ranges from 5 to 38. The number of predictors used for each conceptual variable varies greatly; for example, for water Pearman *et al.* (2008) used one variable while Coudon *et al.* (2006) used ten. All studies in the table include temperature- and water-related predictors but only six include light. No two studies have identical predictors for temperature or water. This raises the question of how to assess the comparative value of models when no two studies measure the conceptual variables in the same way.

The illustrative table (Table 1) is in our opinion representative of the predictors currently used in SDMs and of the way in which they are expressed. We suggest that as much attention needs to be given to the choice of environmental predictors and their estimation from biophysical process models as is given to comparing statistical methods for SDMs. While the choice of predictors depends on available data, failure to incorporate an influential predictor reduces both model performance and the relevance of model outcomes.

### Data resolution

Plot size in the papers varied from 16 m<sup>2</sup> to 2500 km<sup>2</sup> (Table 1). The larger grid cell sizes reflect the interest in climate change, and, importantly, the availability of distribution data at a grid cell size of 50 × 50 km. The assumption that only climate variables are important when the extent of a study is very large leads to the corollary that local environmental heterogeneity can be ignored in large-area studies. Since these assumptions were recognized (Huntley *et al.*, 1995), they do not appear to have been explicitly tested, although see Coudon *et al.* (2006). Local heterogeneity is important for light (see below) and for soil properties such as nutrients.

Soil properties vary with lithology and along topographic gradients from ridge to gully. The magnitude of these local differences in soils will equal or exceed that between 50-km grid cells. Coudon *et al.* (2006) explicitly tested whether including soil nutrient variables with climate variables improved a model predicting the distribution of the tree *Acer campestre* across the whole of France. It did. Such soil heterogeneity may define local refugia for species, confounding predictions of distribution under climate change.

### Environmental predictors: light as a critical example

We use light as an example of how we suggest that each variable should be considered.

Careful logical consideration of the biophysical processes associated with light should determine the level of resolution required to model the impact of light on species (Grace, 1987; Franklin, 2009). For all the variables in equation (1), knowledge exists concerning the distributions and biological responses of species to the variables, and there is an understanding of the biophysical processes linking plants to direct and indirect predictors. A careful collation of this knowledge is needed when selecting predictors. Light expressed as solar radiation has long been known to influence plant distribution (e.g. Boyko, 1947) based on known biophysical processes (e.g. Austin, 1972). There is now an extensive literature on the calculation of radiation models (see Wilson & Gallant, 2000) and their use in SDMs (Franklin, 2009, table 5.1), and ecophysiological studies have demonstrated the influence that radiation has on thermal, photosynthesis, photomorphogenesis and mutagenesis effects on plants (Jones, 1992).

Grace (1987) examined the climate tolerance of plants, drawing attention to species distributions that may be limited by low summer temperatures. *Cirsium acaule*, near its northern limits in the UK, occurs mainly on south-facing slopes. Failure to set seed appears to be the main limitation to northern expansion, and reproductive success can be improved experimentally. Grace quotes long-term results from Rorison *et al.* (1986) that the summer mean temperature (at 20 mm above soil surface) was 3 °C higher on a south-facing slope than on a north-facing slope for a similar community in the Derbyshire Dales, a difference equivalent to a latitudinal shift of several hundred kilometres. Rorison *et al.* (1986) recorded differences of 12 °C in maximum air temperature between north- and south-facing slopes for April. The magnitude of these differences implies that local topographic variability results in extreme differences in growing conditions for plants.

Authors treat radiation very differently, namely as a direct variable or as a component in a water-balance model, or they ignore it (Table 1). This is despite the ready availability of biophysical process models used to create variables representing light, providing proximal direct predictors for SDMs (Franklin, 1998; Leathwick, 1998; Coudon *et al.*, 2006; Randin *et al.*, 2006; Guisan *et al.*, 2007). Only two papers (Franklin, 1998; Randin *et al.*, 2006) use global solar radiation locally

**Table 1** Illustrative examples of environmental predictors and data resolution used in species distribution models (SDMs).

	Eucalypt	Plants	Trees	Shrubs	Trees	Proteas
Light	Mean annual radiation (used slope, aspect, location and rainfall)	–	–	1. Clear-day potential solar radiation, spring 2. Ditto winter	1. Mean annual solar radiation 2. June radiation (adjusted for correlation)	–
Temperature	Mean annual temperature	1. Mean annual temperature 2. Minimum temperature of coldest month 3. Growing degree-days >5 °C	1. Mean annual temperature 2. Minimum temperature of coldest month	1. Mean minimum temperature of coldest month 2. Mean maximum temperature of warmest month	1. Mean annual temperature 2. July minimum temperature (adjusted for correlation)	1. Mean minimum temperature of coldest month 2. Heat units annual $\sum$ daily temperatures >18 °C
Water	1. Mean annual rainfall 2. Rainfall seasonality	1. Mean annual precipitation 2. Mean summer precipitation 3. Mean winter precipitation 4. Potential evapotranspiration	1. Mean annual precipitation 2. Precipitation December–March 3. Precipitation June–August	Mean annual precipitation	1. Soil water deficit (used water balance model including precipitation, temperature, radiation, soil texture and rooting depth) 2. lowest mean monthly humidity	1. Annual potential evaporation 2. Winter soil moisture days 3. Summer soil moisture days
Nutrients	‘Nutrient index’	–	–	–	–	Soil fertility
Disturbance	–	–	–	–	–	–
Biota	–	–	–	–	–	–
Other predictors	1. Lithology 2. Topographic position	–	–	1. Slope 2. Northing 3. Easting	1. Geology 2. Site drainage	1. Soil sand content 2. Soil clay content
Number of predictors	7	7	5	8	8	8
Purpose	Use of SDMs for climate change modelling	Influence of data resolution on predicted extinction under climate change	Testing the ability of SDMs to predict past climate-change impacts	SDMs using climate and terrain	Are species in equilibrium with present environment?	Predicting extinction risk under climate change
Resolution	≤0.4 ha plot	Various 64 m <sup>2</sup> –2500 km <sup>2</sup>	2500 km <sup>2</sup>	10 × 10 m plot	0.04, 0.4 ha plots	1-minute grid
Region	SE New South Wales Australia	Europe & 2 Swiss regions	Europe	South-western California	New Zealand	Western Cape Floristic region South Africa
Author(s)	Austin (1992)	Randin <i>et al.</i> (2009)	Pearman <i>et al.</i> (2008)	Franklin (1998)	Leathwick (1998)	Keith <i>et al.</i> (2008)

**Table 1** Continued

	Trees	Trees	Trees	Plants	Trees	<i>Acer campestre</i>
Light	–	–	Potential clear-sky annual radiation	Summer solar radiation		Annual radiation
Temperature	1. Mean summer temperature 2. Temperature seasonality 3. Absolute minimum temperature 4. Growing degree-days >5 °C	1. Mean annual temperature 2. Mean winter temperature 3. Growing degree-days until April 4. Growing degree-days until August	1. Growing degree-days >0 °C 2. Mean temperature of coldest month 3. Summer frost frequency	Growing degree-days >0 °C	1. Mean annual temperature 2. Mean January temperature 3. Mean July temperature 4. Mean May–September temperature 5. Mean difference July and January temperatures	7 predictors including annual temperature, frost days, growing degree-days >6 °C
Water	8 predictors including annual precipitation and 4 other measures of precipitation 3 measures of water balance	Model A 1. Annual precipitation 2. Winter precipitation 3. Moisture index (equilibrium evapotranspiration-pre cipation) Model B (LPJ-GUESS) <sup>1</sup>	1. Summer precipitation days 2. Mean annual precipitation 3. Site water balance (used soil properties)	Summer moisture index (precipitation – potential evapotranspiration)	1. Annual precipitation 2. Mean May–September precipitation	10 predictors including annual rainfall, autumn rainfall, length of drought period, 3 measures of evapotranspiration, 4 measures of water balance
Nutrients	–	–	Nutrient index	–	Potential soil productivity	1. Calcium content 2. Magnesium content 3. Potassium content
Disturbance	–	–	–	–	Fragmentation index	–
Biota	–	–	1. Percentage broad-leaf cover 2. Percentage conifer cover	–	4 land cover classes	–
Other predictors	–	–	1. Slope 2. Topographic position 3. Bedrock	1. Slope 2. Snow cover (used climate variables adjusted for slope aspect and shade)	1. Slope 2. 5 measures of elevation 3. 9 soil classes 4. 10 soil properties	1. pH 2. Base saturation rate 3. C/N ratio
Number of predictors	12	A, 7 B, >100	13	5	38	24?

**Table 1** Continued

	Trees	Trees	Trees	Plants	Trees	<i>Acer campestre</i>
Purpose	Possible existence of glacial refugia	Testing value of vegetation growth model LPG-GUESS in SDM predicting future distribution under climate change	Is SDM predictive success a function of species traits?	To test transferability of SDM between regions	Estimating potential habitat under six climate scenarios	Importance of soil nutritional factors for SDM
Resolution	2500 km <sup>2</sup>	2500 km <sup>2</sup>	0.01 km <sup>2</sup>	16 m <sup>2</sup> , 5–30 m <sup>2</sup> plots	400 km <sup>2</sup>	c. 400 m <sup>2</sup>
Region	Europe	Europe	Switzerland	Parts of Switzerland and Austria	Eastern United States	France
Author(s)	Svenning <i>et al.</i> (2008)	Rickebusch <i>et al.</i> (2008)	Guisan <i>et al.</i> (2007)	Randin <i>et al.</i> (2006)	Iverson <i>et al.</i> (2008)	Coudon <i>et al.</i> (2006)

<sup>1</sup>Process-based model of vegetation dynamics and biogeochemistry using parameters for 20 plant functional types.

adjusted for slope, aspect and shade (i.e. light cut-off owing to horizon effects). Rickebusch *et al.* (2008) examined the incorporation of various components of vegetation growth models in SDMs for predicting response to climate change. However, their standard SDM does not explicitly use a radiation variable for comparison, while their vegetation growth model uses latitude to estimate radiation from sunshine hours to calculate photosynthesis (Hickler *et al.*, 2009).

The importance of these local effects is supported by recent studies. A solar radiation model predicts that daily June radiation for a south-facing slope of 40° at latitude 36.5° S is 5% of that received by a similar north-facing slope (Kumar *et al.*, 1997, figure 9). Lassueur *et al.* (2006) showed that the indirect predictors slope and aspect improved species modelling using a high-resolution digital elevation model (DEM). They concluded that slope at a 100-m resolution and aspect at 20-m resolution maximized predictive power, and recommended their use for predicting potential refugia in climate change scenarios.

This review of light as a predictor indicates that it constitutes a critical influence on plant distribution. These effects will be greatest at a local scale but vary along climatic gradients (Boyko, 1947; Perring, 1960). It also highlights the need to consider an appropriate scale for predictions, as topographic complexity is degraded by the use of coarse-resolution DEMs. The value of including radiation predictors in SDMs at an appropriate scale (i.e. including both local and regional effects) needs to be tested.

## CONCLUSIONS

Elith & Leathwick (2009) in their review state that ‘we believe that a more wide-ranging approach to linking theory, data and models would bring substantial benefits’. A comparison of recent papers using the simple conceptual framework proposed in equation (1) demonstrates how inconsistent are the links being made between known ecological processes, environmental data and SDMs (Table 1). A consideration of biophysical models of solar radiation indicates that local variation in radiation will be greater than regional variation, leading to local climate refugia. Similar conclusions can be drawn from the known local variations in soil properties. This will have major implications for those climate change SDMs that use only regional climate predictors at a resolution of 100 km<sup>2</sup> or greater.

Knowledge of biophysical processes also suggests there is a natural scale of resolution for an SDM, namely that which maximizes the relevant environmental differences between plots. Tests of whether local or regional differences are of greater magnitude need to be made. We suggest that local topography may create critical climatic refugia for species that are important even in studies of very large areas. We conclude that the relative importance of climatic and non-climatic predictors is best tested at high resolution and large extent before it is assumed that climate predictors alone are ‘sufficient



to assess main changes in distribution' (Araújo & Guisan, 2006).

Numerous problems need to be addressed by species distribution modellers in order to improve predictions under future climates. Some progress can be made if there is consistency in the choice of variables and careful consideration of appropriate scales relative to the organism being studied.

## REFERENCES

- Araújo, M.B. & Guisan, A. (2006) Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, **33**, 1677–1688.
- Araújo, M.B. & Luoto, M. (2007) The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography*, **16**, 743–753.
- Araújo, M.B., Thuiller, W. & Pearson, R.G. (2006) Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography*, **33**, 1712–1728.
- Austin, M.P. (1972) Models and analysis of descriptive vegetation data. *Proceedings of 12th Symposium British Ecological Society* (ed. by J.N.R. Jeffers), pp. 61–86. Blackwell Scientific Publications, Oxford.
- Austin, M.P. (1980) Searching for a model for use in vegetation analysis. *Vegetatio*, **42**, 11–21.
- Austin, M.P. (1992) Modelling the environmental niche of plants: implications for plant community response to elevated CO<sub>2</sub> levels. *Australian Journal of Botany*, **40**, 615–630.
- Austin, M.P. & Van Niel, K.P. (2010) Impact of landscape predictors on climate change modelling of species distributions: a case study with *Eucalyptus fastigata* in southern New South Wales, Australia. *Journal of Biogeography*, doi:10.1111/j.1365-2699.2010.02415.x.
- Austin, M.P., Smith, T.M., Van Niel, K.P. & Wellington, A.B. (2009) Physiological responses and statistical models of the environmental niche: a comparative study of two co-occurring *Eucalyptus* species. *Journal of Ecology*, **97**, 496–507.
- Beale, C.M., Lennon, J.L. & Gimona, A. (2008) Opening the climate envelope reveals no macroscale associations with climate in European birds. *Proceedings of the National Academy of Sciences USA*, **105**, 14908–14912.
- Boyko, H. (1947) On the role of plants as quantitative climate indicators and the geo-ecological law of distribution. *Journal of Ecology*, **35**, 138–157.
- Coudon, C., Gegout, J.-C., Piedallu, C. & Rameau, J.-C. (2006) Soil nutritional factors improve models of plant species distribution: an illustration with *Acer campestre* (L.) in France. *Journal of Biogeography*, **33**, 1750–1763.
- Dormann, C.F. (2007) Promising the future? Global change projections of species distributions. *Basic and Applied Ecology*, **8**, 387–397.
- Elith, J. & Leathwick, J.R. (2009) Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 677–697.
- Franklin, J. (1995) Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. *Progress in Physical Geography*, **19**, 474–499.
- Franklin, J. (1998) Predicting the distribution of shrub species in southern California from climate and terrain-derived variables. *Journal of Vegetation Science*, **9**, 733–748.
- Franklin, J. (2009) *Mapping species distributions: spatial inference and prediction*. Cambridge University Press, Cambridge.
- Grace, J. (1987) Climatic tolerance and the distribution of plants. *New Phytologist*, **106**(Suppl.), 113–130.
- Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.
- Guisan, A., Zimmermann, N.E., Elith, J., Graham, C.H., Phillips, S. & Peterson, A.T. (2007) What matters for predicting the occurrences of trees: techniques, data, or species' characteristics? *Ecological Monographs*, **77**, 615–630.
- Heikkinen, R.K., Luoto, M., Araújo, M.B., Virkkala, R., Thuiller, W. & Sykes, M.T. (2006) Methods and uncertainties in bioclimatic envelope modelling under climate change. *Progress in Physical Geography*, **30**, 751–777.
- Hickler, T., Fronzek, S., Araújo, M.B., Schweiger, O., Thuiller, W. & Sykes, M.T. (2009) An ecosystem model-based estimate of changes in water availability differs from water proxies that are commonly used in species distribution models. *Global Ecology and Biogeography*, **18**, 304–313.
- Huntley, B., Berry, P.M., Cramer, W.P. & McDonald, A.P. (1995) Modelling present and potential future ranges of some European higher plants using climate response surfaces. *Journal of Biogeography*, **22**, 967–1001.
- Iverson, L.R., Prasad, A.M., Mathews, S.N. & Peters, M. (2008) Estimating potential habitat for 134 eastern US tree species under six climate scenarios. *Forest Ecology and Management*, **254**, 390–406.
- Jenny, H. (1941) *Factors of soil formation: a system of quantitative pedology*. McGraw-Hill Book Company, New York, NY.
- Jeschke, J.M. & Strayer, D.L. (2008) Usefulness of bioclimatic models for studying climate change and invasive species. *Annals of the New York Academy of Sciences*, **1134**, 1–24.
- Jones, H.G. (1992) *Plants and microclimate: a quantitative approach to environmental plant physiology*, 2nd edn. Cambridge University Press, Cambridge.
- Keith, D.A., Akçakaya, H.R., Thuiller, W., Midgley, G.F., Pearson, R.G., Phillips, S.J., Regan, H.M., Araújo, M.B. & Rebelo, T.G. (2008) Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biology Letters*, **4**, 560–563.
- Kumar, L., Skidmore, A.K. & Knowles, E. (1997) Modelling topographic variation in solar radiation in a GIS environment. *International Journal of Geographical Information Science*, **11**, 475–497.
- Lassueur, T., Joost, S. & Randin, C.F. (2006) Very high resolution digital elevation models: do they improve models of

- plant species distribution? *Ecological Modelling*, **198**, 139–153.
- Leathwick, J. (1998) Were New Zealand's *Nothofagus* species in equilibrium with their environment? *Journal of Vegetation Science*, **9**, 719–732.
- Luoto, M. & Heikkinen, R.K. (2008) Disregarding topographical heterogeneity biases species turnover assessments based on bioclimatic models. *Global Change Biology*, **14**, 483–494.
- Luoto, M., Heikkinen, R.K., Pöyry, J. & Saarinen, K. (2006) Determinants of the biogeographical distribution of butterflies in boreal regions. *Journal of Biogeography*, **33**, 1764–1778.
- Major, J. (1951) A functional, factorial approach to plant ecology. *Ecology*, **32**, 392–412.
- Morin, X. & Lechowicz, M.J. (2008) Contemporary perspectives on the niche that can improve models of species range shifts under climate change. *Biology Letters*, **4**, 573–576.
- Pearman, P.B., Randin, C.F., Broennimann, O., Vittoz, P., van der Knaap, W., Engler, R., Le Lay, G., Zimmermann, N.E. & Guisan, A. (2008) Prediction of plant species distributions across six millennia. *Ecology Letters*, **11**, 357–369.
- Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, **12**, 361–371.
- Perring, F. (1958) A theoretical approach to a study of chalk grassland. *Journal of Ecology*, **46**, 665–679.
- Perring, F. (1959) Topographical gradients of chalk grassland. *Journal of Ecology*, **47**, 447–481.
- Perring, F. (1960) Climatic gradients of chalk grassland. *Journal of Ecology*, **48**, 415–442.
- Pöyry, J., Luoto, M., Heikkinen, R.K. & Saarinen, K. (2008) Species traits are associated with the quality of bioclimatic models. *Global Ecology and Biogeography*, **17**, 403–414.
- Randin, C.F., Dirnbock, T., Dullinger, S., Zimmermann, N.E., Zappa, M. & Guisan, A. (2006) Are niche-based species distribution models transferable in space? *Journal of Biogeography*, **33**, 1689–1703.
- Randin, C.F., Engler, R., Normand, S., Zappa, M., Zimmermann, N.E., Pearman, P.B., Vittoz, P., Thuiller, W. & Guisan, A. (2009) Climate change and plant distribution: local models predict high-elevation persistence. *Global Change Biology*, **15**, 1557–1569.
- Rickebusch, S., Thuiller, W., Hickler, T., Araujo, M.B., Sykes, M.T., Schweiger, O. & Lafourcade, B. (2008) Incorporating the effects of changes in vegetation functioning and CO<sub>2</sub> on water availability in plant habitat models. *Biology Letters*, **4**, 556–559.
- Rorison, I.H., Sutton, F. & Hunt, R. (1986) Local climate topography and plant growth in Lathkill Dale NNR: a twelve-year summary of solar radiation and temperature. *Plant, Cell and Environment*, **9**, 49–56.
- Schröder, B. & Seppelt, R. (2006) Analysis of pattern–process interactions based on landscape models—Overview, general concepts and methodological issues. *Ecological Modelling*, **199**, 505–516.
- Svenning, J., Normand, S. & Kageyama, M. (2008) Glacial refugia of temperature trees in Europe: insights from species distribution modelling. *Journal of Ecology*, **96**, 1117–1127.
- Sykes, M.T., Prentice, I.C. & Cramer, W. (1996) A bioclimatic model for the potential distributions of North European tree species under present and future climates. *Journal of Biogeography*, **23**, 203–233.
- Thuiller, W., Lavorel, S., Sykes, M.T. & Araújo, M.B. (2006) Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe. *Diversity and Distributions*, **12**, 49–60.
- Willis, K.J. & Bhagwat, S.A. (2009) Biodiversity and climate change. *Science*, **326**, 806–807.
- Wilson, J. & Gallant, J. (2000) *Terrain analysis: principles and applications*. John Wiley & Sons, New York.

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Editor: Mark Bush