THE UTILITY OF BIOCLIMATIC MODELS FOR PROJECTING FUTURE CHANGES IN THE DISTRIBUTION OF BIRDS IN RESPONSE TO CLIMATE CHANGE

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Abstract.—Bioclimatic models, especially climatic envelope models, are a widely-used approach to assessing the likely future impacts of current rapid climatic change on species abundance and distribution. We describe the uses to which such models can be put, especially in the context of bird conservation. Most conservation applications involve setting of priorities for which species to allocate most conservation resources to, in which areas and deciding upon types of management which might alleviate negative effects of climatic change. Projections based upon climatic envelope models are expected to be reliable for some species, but not others, and be realized at markedly different rates, depending upon the mechanism by which climatic change alters the species' demographic rates. Precautions are suggested for guarding against inappropriate conservation applications of bioclimatic models and prospects for more detailed models that incorporate demographic mechanisms are described. *Received 20 June 2011, accepted 8 July 2011.*

Huntley, B., and R. E. Green. 2011. The utility of bioclimatic models for projecting future changes in the distribution of birds in response to climate change. *In* R. T. Watson, T. J. Cade, M. Fuller, G. Hunt, and E. Potapov (Eds.). Gyrfalcons and Ptarmigan in a Changing World. The Peregrine Fund, Boise, Idaho, USA. http://dx.doi.org/10.4080/gpcw.2011.0111

Key words: Climatic envelope, projected potential distribution, climatic change, conservation applications, priority setting.

The practice of conservation of biodiversity needs to be adapted to allow for rapid global climatic change (Green and Pearce-Higgins 2010). In addition to the negative anthropogenic pressures on species' distributions from conversion of natural and semi-natural habitats to human land uses, alien invasive species, overexploitation and pollution, rapid climatic change now imposes a new layer of threat, which interacts with all the others. The relative priorities given by conservation agencies to species, habitats, areas and different types of conservation action need to be informed by projections of how ecosystems, and the species within them, will be affected by climatic change. In this paper, we assess the utility of bioclimatic models, particularly climatic envelope models, of the geographical distribution of species for this purpose, with emphasis on applications to bird conservation.

WHAT ARE CLIMATIC ENVELOPE MODELS?

Climatic envelope models have been widely used to describe species' distributions during a particular period in terms of climatic variables measured during the same period. Observations of presence and, where possible, absence of species from spatial units, such as map grid cells, are used, in combination with climatic variables for the same units, to fit a statistical model of the distribution in which a species' probability of occurrence in a grid cell is some function of the variables. The climatic variables are usually averages of a particular quantity over a long period, often several decades. However, they can also be measures of short-term variability or frequencies of extreme events. Some modelers use modeling approaches that select from a long list of candidate climatic variables so as to produce a model that best fits the observed species' distribution, but this approach runs the risk of data dredging, i.e., producing models founded upon spurious correlations that are bound to emerge if a sufficiently large number of explanatory variables and their combinations is considered. An alternative is to define a short list of bioclimatic variables that can be derived from meteorological data, designed using prior knowledge to reflect processes of physiological or ecological relevance to the organisms being studied. A good example of a bioclimatic variable is the ratio of actual to potential evapotranspiration that reflects the availability of soil water to terrestrial plants.

A climatic envelope model is a means for calculating a species' expected probability of occurrence for grid cells for which the relevant climatic variables are available. These probabilities can then be used to generate simulated potential distributions under climatic conditions obtained from General Circulation Model (GCM) simulations of past or future climates, or from recent or historic climatic data. Such potential distributions depict the area that would be occupied if the species occurred only in those cells having the same climatic characteristics as those it occupied during the epoch for which the data used to fit the model were obtained.

HOW CAN CONSERVATIONISTS USE CLIMATIC ENVELOPE MODELS?

The most appropriate use of climatic envelope models in conservation is in setting priorities for conservation action. Considerable effort has already gone into the identification of species requiring special conservation efforts to allow them to persist in the face of continuing loss and degradation of habitat because of human land use, into designing the networks of protected habitat required to support them and into identifying unfilled gaps in such networks (Gaston et al. 2008). Nearly all previous efforts of this kind have assumed that the potential geographical range and habitat requirements of species remain constant, but this may not be the case during a period of rapid climatic change. Species prioritization for conservation action therefore needs to consider information on the potential impacts of projected future climatic change. Currently, the only practical way to achieve this for a large number of species is to make and apply climatic envelope models that describe current distributions (Huntley et al. 2007) or abundance (Huntley et al. 2011) in relation to climate. Each species' model can then be used, in combination with a projection of future climate, to predict the location of the species' future potential range, on the assumption that it will continue to occupy the same part of the potentially available climatic space. It is therefore relatively straightforward to model distributions of large numbers of species in terms of a limited number of readily available explanatory climatic variables, whose future average values can be projected using GCMs and emissions scenarios, and then rank those species according to the extent of projected range changes. For example, some species might be projected to become rarer or more narrowly distributed, whilst others are expected to maintain or increase their distribution and abundance. Species might also be projected to need to accomplish large shifts in their geographical range in order to maintain its extent.

Such projections can be used to make assessments of the probable future status of a species which vary throughout a large geographical area, enabling conservation priorities to be modified in different parts of the area (Hole et al. 2011). Suppose that the combined present and future potential range of a hypothetical species spans several countries or other administrative units. The species' potential future range is likely to remain of similar size to the present range, but to shift location substantially. Thus in large areas where the species does not occur at present, the climate is projected to become suitable for it in future, whereas climatic conditions in much of the present range are projected to become unsuitable in future and in only a small proportion of the present range are they expected to remain suitable in the long term. The projections are thought to be reliable, but the species is a poor disperser inhabiting a patchily distributed habitat, and therefore is unlikely easily to occupy the whole of the newly suitable parts of its potential future range. The influence of the climatic impact projection on conservation management priorities and objectives should differ in the three parts of the range. If the species' status can be improved by the designation of existing critical habitats as protected areas and management, regardless of climatic change, then expanding the extent and quality of such habitat in the part of the current range which is expected to remain climatically suitable is the highest priority. This will increase the population in the area most secure against effects of future climatic change and is a "no regrets" option. This will also increase the flow of potential colonists to those areas not currently occupied but projected to become climatically suitable in future. In these areas, the extent of potentially suitable habitat should be surveyed, particularly in areas close to the current range boundary and, if scarce, should be increased. If the prime habitat is patchily distributed, consideration should be given to improving the permeability of the matrix between habitat patches to aid dispersal. Even in parts of their current range where species are predicted to disappear they should not necessarily be removed from the list of conservation priorities. Because projections of climatic change remain uncertain, monitoring of the species and its habitats should be carried out to assess whether the predicted deterioration in status caused by climatic change is really occurring. If it is, consideration should be given to special management within existing sites holding the species or expansion of protected habitat. Several options for such management are frequently available. These include counteracting management, which seeks to prevent or reduce the negative effects of climatic change on the species' demographic rates, and compensating management, which accepts the negative effect of climatic change, but seeks to improve demographic rates by other means to compensate for it (Green and Pearce-Higgins 2010). Even if the species eventually declines to extinction in this part of the area, maintaining its population and hence maximizing production of colonists in the short to medium term will promote dispersal to other parts of the range, assisting especially in the colonization of newly suitable areas.

Although decisions about priorities are currently most often made at national levels, the process outlined above argues for the projected future international importance of the country for each species to play a part in priority-setting, which requires species and protected area management to be coordinated internationally over large areas to a greater extent than at present (Hole et al. 2011).

WHY ARE SOME PROJECTIONS FROM CLIMATIC ENVELOPE MODELS LIKELY TO BE UNRELIABLE?

Appropriate translation of these projected changes in distribution into conservation priorities depends upon several factors, particularly the degree of confidence associated with the predictions. At extensive spatial scales and coarse grain, climatic envelope models can provide good descriptions of current geographical range, especially for small-bodied species without special habitat requirements and without a history of extensive range restriction by human persecution and exploitation (Huntley et al. 2007). However, models may fit the current distribution less well, and/or be misleading for projecting future changes, for several reasons. The observed distribution which is used to fit the climatic envelope model may have been modified by factors unrelated to climate, such as persecution by humans, exploitation or pollution. Conversion to human land use of large continuous tracts of natural habitats such as wetlands and forest may also render areas unsuitable for a species. This can make the fitted model less reliable because some current range boundaries are determined by factors unrelated to climate, and it can also make projections of future potential range expansion inaccurate because an apparently climatically suitable area in future may lack the species' required habitat. These problems are more likely to occur for large-bodied than small-bodied species because the former are more likely to be hunted for food and to require large tracts of suitable habitat than the latter. Natural factors such as a requirement for patchily distributed and uncommon resources, such as cliffs for nesting, can also render model fits and projections unreliable for similar reasons.

Model projections of future changes can also be misleading for reasons associated with the choice of modeling approach and domain. Many modeling approaches that have been used to fit climatic envelope models make inappropriate assumptions about the underlying form of the relationship between a species' probability of occurrence and the climatic variables (e.g., Gaussian), or about the nature of the interactions between the two or more variables that are the principal determinants of the species' range (e.g., uniform throughout climatic space). Where the projections for future climatic conditions require some extrapolation of the model into regions of climatic space not represented in the data to which the model was fitted, different modeling approaches can give very different results. Projections potentially can also be misleading in cases where the geographical region from which data were used to fit the model does not encompass the entire species' range. Whether or not a model fitted to only part of a species' geographical range will give misleading projections, however, depends not upon how much of the geographical range is excluded but upon how completely the species' range, and especially range limits, in climatic space are represented in that part of its geographical range.

Beale et al. (2008) suggested that the reliability of climate envelope models should be assessed by significance tests of the degree to which they fit observed static distributions, but we regard the only stringent tests of reliability to be those that either involve the independent prediction of species distribution in a different region to that in which the model was fitted (e.g., Beerling et al. 1995) or, better still, predictions or retrodictions of change in distribution or abundance during a period of rapid climatic change using a model fitted during a period of little or no climatic change. Few tests of these kinds have been carried out. A correlation between observed and predicted abundance changes of birds at the edge of their geographical range in the UK in the last few decades provides support for the validity of this approach (Green et al. 2008), as does a Europe-wide analysis of abundance changes of common European breeding birds over a similar period (Gregory et al. 2009).

Most climatic envelope modeling for large numbers of species is carried out at extensive spatial scales (sub-continental to continental) and coarse grains (>2500 km^2). Although excluding non-climatic variables is often criticized on the grounds that this reduces the realism of the models in describing current distributions, this generally only becomes an issue when models are fitted at finer grains (Luoto et al. 2007). As Huntley and Baxter (2003) illustrate, the ability of models to predict the fine-scale features of species' distributions could certainly be improved by including the effects of non-climate variables that are unaffected by socio-economic factors, such as soil type and topography. However, the inclusion of variables that are influenced by human land use, such as the availability of particular habitats, introduces large and unquantifiable uncertainty about future values of these variables that results from the considerable uncertainties associated with predictions of future land-use changes.

As a rough guide to the current reliability of climate envelope projections of future range changes to assess conservation status, we suggest that projections for species' groups with artificial gaps in the distribution data used to obtain the climate envelope model should be regarded with caution. This includes species whose recent geographical range have been extensively modified by human activities such as overexploitation, persecution, habitat destruction and pollution, principally birds of prey and other large-bodied bird species (Newton 1979). For these species, other sources of information are required to assess their likely vulnerability to climatic change, such as from ecological knowledge, or other studies of climatic change impacts. Projections derived from models fitted to domains that do not encompass the species' entire geographical range should also be treated with caution, as especially should those made using models that were fitted using inappropriate assumptions and/or using 'data dredging' techniques. Even for those species for which a change in distribution is forecast accurately, there is currently no well-tested way to predict how rapidly it will happen. The range of mechanisms by which climatic change can influence species' abundance and distribution is vast and the nature of the mechanism has implications for how rapidly it will occur. To take extreme contrasting examples: suppose that the winter survival of a bird species is negatively affected by the duration of periods of snow cover, which restricts access to its food supply. Climatic change leading to progressively less frequent long periods of snow cover in an area currently outside the species' range may allow it to colonize this new area rapidly. On the other hand, another species whose potential range is also projected by a climatic envelope model to expand, may require a particular functional type of tree (e.g., temperate broadleaved summer-green trees, typified by many *Quercus* spp. (Oaks) or *Ulmus* spp. (Elms)) to be abundant because an ecologically similar closely-related species outcompetes it in forests dominated by trees of other functional types (e.g., evergreen needle-leaved gymnosperm trees, typified by *Picea* spp. (Spruces) or *Pinus* spp. (Pines)). Tree species, and hence functional type, composition is affected by climate and will eventually change to favor the bird species in the area that it is projected to colonize. However, because of the long generation time of trees, this change may take decades or even centuries to occur (Prentice et al. 1991, Sykes and Prentice 1996).

What can be done to Allow for Uncertainty in Projections?

The obvious but difficult solution is to develop more reliable models that allow for or avoid all of the various problems outlined above. We return to the prospects for this in the final section of the paper, but there are some steps that can be taken without new models.

It is likely that, over the next few years, there will be increasing evidence for the effects of climatic change on species abundances (e.g., Devictor et al. 2008), as well as distributions, which can be used to refine and update model projections. This may indicate the characteristics of species whose populations and distributions do or do not respond to climatic change in the way projected by climatic envelope models. To facilitate this approach, it is important to establish and maintain high quality monitoring programs to enable climate-related changes in populations to be rapidly identified and incorporated into decisions about priorities. The results of such monitoring should be used to validate and refine predictions, and provide an early warning of species declining as a result of climatic change.

FUTURE DEVELOPMENTS

Much current research effort is being devoted to developing models of species' responses to climatic change that incorporate information on species' abundance (Huntley et al. 2011), demographic rates and dispersal, and the direct and indirect effects of climate upon these (Huntley et al. 2010). Indirect effects of climatic change that act via effects on habitat (Midgley et al. 2010), predators, diseases and competitors can also be incorporated in such models where this is feasible. These models have the potential advantage that they can predict not only the eventual future distribution of a species, but also how long it will take to realize it, as well as changes in its population size and geographical variation in its density. However, in many cases the performance of such models is likely to be limited by the extent to which a species' habitat requirements, and the sensitivity of its demographic rates to climatic and habitat change, are understood.

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