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Meeting report

Integrating bioclimate with population models to improve forecasts of species extinctions under climate change

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Climate change is already affecting species worldwide, yet existing methods of risk assessment have not considered interactions between demography and climate and their simultaneous effect on habitat distribution and population viability. To address this issue, an international workshop was held at the University of Adelaide in Australia, 25–29 May 2009, bringing leading species distribution and population modellers together with plant ecologists. Building on two previous workshops in the UK and Spain, the participants aimed to develop methodological standards and case studies for integrating bioclimatic and metapopulation models, to provide more realistic forecasts of population change, habitat fragmentation and extinction risk under climate change. The discussions and case studies focused on several challenges, including spatial and temporal scale contingencies, choice of predictive climate, land use, soil type and topographic variables, procedures for ensemble forecasting of both global climate and bioclimate models and developing demographic structures that are realistic and species-specific and yet allow generalizations of traits that make species vulnerable to climate change. The goal is to provide general guidelines for assessing the Red-List status of large numbers of species potentially at risk, owing to the interactions of climate change with other threats such as habitat destruction, overexploitation and invasive species.

Keywords: global warming; species distribution model; population viability analysis; extinction risk; IUCN Red List

1. INTRODUCTION

Climate change poses a major threat to biodiversity, owing to its all-encompassing reach and the speed at which human-driven changes are taking place in already heavily modified systems (IPCC 2007), with impacts on species' ranges, phenology and physiology already widely documented (Brook *et al.* 2008). However, transferring observed impacts and range shift projections to predictions of increased extinction risk at the species level has proved difficult, with most current methods only considering climate-driven changes in the quantity of suitable habitat (Akçakaya *et al.* 2006). Recent work has aimed to move beyond climate-envelope models to incorporate the mechanisms and interactions that drive species distribution and abundance—a 'whole ecology' approach to risk assessment under global change.

Results from workshops hosted by Imperial College London in 2007, and the Museum of Natural Sciences Madrid in 2008, have shown that extinction risk under climate change is subject to complex dependencies between species life history, distribution patterns and landscape processes. This leads to some apparently paradoxical outcomes, such as rapid declines and range contractions in some currently widespread species, while other species that are currently restricted remain relatively stable or even expand their distributions (Keith *et al.* 2008). Evidence also emerged that populations at the core of a species range respond differently to those at the margin, and that those at the trailing margin of a shifting distribution may lag relative to those at the leading edge of the range (Anderson *et al.* 2009). A significant finding was that species persistence under climate change can be influenced by interactions with other processes such as disturbance regimes.

A workshop held at the University of Adelaide, Australia, 25–29 May 2009, built on these ideas and methodologies using Australian plants as a case study.

2. WORKSHOP METHODS

(a) *Downscaled global climate model ensembles*

Many attempts to model climate change impacts on biodiversity have used only a single global climate model (GCM) and greenhouse gas emissions scenario as a basis for forward projection. Yet, because of alternative GCM structures and a range of plausible possibilities for future carbon mitigation efforts, a preferred approach is to use ensemble climate modelling to account for this uncertainty. The method introduced at this workshop was to simulate a dynamic climate by synthesizing an annual time series of climate layers from multiple GCMs and emissions scenarios, and incorporating this into an annual environmental suitability map.

First, MAGICC/SCENGEN 5.3 (<http://www.cgd.ucar.edu/cas/wigley/magicc>)—a coupled gas-cycle/aerosol/climate model, calibrated against 20 different atmosphere/ocean general circulation models used in the IPCC Fourth Assessment Report (IPCC 2007)—forecasts global seasonal and monthly temperature and precipitation change at a projection scale of

250 km². Second, a smoothed linear interpolation of GCM grid cells reduces the projection scale to 50 km². Third, a thin-plate spline model fitted to meteorological weather station and elevation data is overlain on the GCM projections to produce a 1 km² 'downscaled' projections of regional climate change. The impact of landscape change (e.g. forestry and agriculture) can also be projected, using Landsat imagery, dynamic vegetation models and expert advice.

(b) *Single bioclimate envelopes versus ensembles*

Projections of species distributional shifts are sensitive to the initial conditions (ICs), model classes (MCs), parameters (MPs) and boundary conditions (BCs) used for model calibration (Araújo & New 2007). Two approaches currently exist to incorporate this uncertainty: single model versus ensemble forecasting. The single model approach is based on the premise that empirical examination of MPs and outputs is sufficient to allow experts to make informed judgements about model performance (Elith *et al.* 2006). However, when models are used for making future projections of climate change impacts, it is difficult to ascertain what a good model is. Ensemble forecasting assumes that predictive performance of models cannot be assessed *a priori* and that plausible multiple hypothesis can be proposed and compared simultaneously. With sufficiently large numbers of simulations across ICs, MCs, MPs and BCs, the frequency distribution of forecasts yields a probability density function.

Both approaches provide useful insights, and discussions in the workshop suggested that they need not be opposed. A careful examination of parameters is critical for modelling because even large ensembles are sensitive to poor model design, thoughtless selection of variables and overfitting of models. But it is clear that single models are unlikely to represent the breadth of possible outcomes that might arise from running equally plausible MCs and MPs (Araújo & New 2007).

Additional discussions focused on the choice of predictors. Studies examining climate change effects on species often use climate variables alone. Workshop participants expressed concern that exclusion of physiographic variables, such as soil type and slope, might reduce discriminatory ability. Adding such variables as covariates in the models is possible, but several models are additive so that once a variable is selected the remaining variables 'only explain what is left to explain' (Araújo & Guisan 2006). If the chosen variables do not change with climate, this constrains our ability to model climate change impacts. Conversely, exclusion of static variables, when these are causal, might cause over-prediction of climate change impacts. One solution is to use such variables to mask out climatically suitable areas that are locally unsuitable owing to non-climatic factors (e.g. Pearson *et al.* 2004). This strategy works when simple statements can be made about the relationship of species with their environment, but may be inadequate if more complex interactions between variables exist. Workshop participants concurred on the need to

further test ensembles versus single models and the contribution of static variables, so that general standards for modelling species distributional shifts under climate change are agreed upon.

(c) *Demographic models*

Demographic models of population and metapopulation dynamics used in this integrated approach incorporate processes of survival, growth, reproduction and dispersal (Akçakaya 2009). Each of these processes may change stochastically (e.g. weather-related fluctuations in survival rates) or deterministically (e.g. temporal trends in average survival rates because of climate change). They may be dependent on the age, size and/or sex of the individuals and on the size (density) of the population. In addition, dispersal is often dependent on the spatial context (e.g. the size, shape, location and number of populations), which can change in time as a result of shifting habitat suitability (bioclimate envelope). The integration of dynamic landscape models, habitat models and spatially explicit metapopulation models has previously been used to simulate the effects of landscape changes brought about by timber harvest, succession and natural disturbances (Akçakaya *et al.* 2004). Using a similar integration for climate change allows its impacts on species viability to be assessed through limited dispersal (leading to unoccupied suitable habitat), increased fragmentation (causing local extinctions owing to demographic and environmental stochasticity), increased fluctuations owing to increased frequency of extreme weather events and reduced vital rates.

For many species, direct effects of weather on vital rates are as important as the longer term relationship between climate and habitat suitability. For Australian plants, the focal taxon of the workshop, such effects included the dependence of survival and reproduction on fire, which in turn depends on weather. Two important aspects of this relationship are the expected increase in fire frequency as a result of climate change and the spatial correlation of fires. The demographic models can incorporate temporal trends in variability and spatial correlations of environmentally induced fluctuations (including fires). Estimating such parameters requires different approaches. For example, temporal trends in variability are estimated using the predicted variability of a single GCM under a single scenario (so as not to conflate it with model/scenario uncertainties), and spatial correlations are estimated from past weather data from a number of stations across the species' range.

3. OUTCOMES

(a) *Workshop results*

Participants selected a small sample of vascular plant species with a broad range of generation lengths (2–100 years), propagule dormancy types (serotiny, physiological), fire responses (resprouter, obligate seeder), range sizes (less than 100 to approx. 3000 km) and habitat types (temperate forests, grasslands and arid shrublands). Preliminary results suggest that single populations of some species are exposed to appreciable extinction risks over the next 100 years,

irrespective of climate change. A number of the study species may be sensitive to changes in moisture availability, particularly during episodes of regeneration. For example, annual rainfall proved to be a key predictor in the distribution model for *Banksia ericifolia*, one of the study species in which the success of post-fire seedling establishment is closely related to temporally variable soil moisture status (Bradstock & O'Connell 1988). Risks posed by existing pressures associated with land-use change, fire regimes and herbivory are likely to be exacerbated by their synergy with climate change (Brook *et al.* 2008).

The limited availability of demographic data imposed a significant constraint on the species that could be selected for analysis. This highlighted data deficiencies, which must be remedied to further improve the reliability of estimates of extinction risk under climate change and so gain a reasonable overview across the diverse range of taxa and habitats for which generalizations are sought. Workshop participants identified the estimation of vital rates across climatic gradients and dispersal profiles as being two of the most important priorities for future data collection.

(b) Outlook

The integrated bioclimate–population approach tested in these workshops has so far demonstrated the feasibility of linking spatial and demographic dynamics to assess vulnerability of species to climate change (Keith *et al.* 2008; Anderson *et al.* 2009). Future plans will involve applications to other taxonomic groups (e.g. amphibians, mammals), increasing the regional coverage to different parts of the globe, adding the effects of changing species interactions and using remote-sensed data to better define suitable areas for species.

One ultimate goal is to provide general rules for risk assessment of large numbers of species that may be threatened by the interactions of climate change (Akçakaya *et al.* 2006). Currently, the established systems for threatened species listing such as the current IUCN Red List Criteria (Mace *et al.* 2008) lack clarity and consistency about how to list species facing the impacts of climate change. Integrating the outcome of the work described here with the current IUCN system will inform new guidelines, based on a meta-analysis of the results of the application of the integrated model to several taxonomic groups and geographical regions. Covering the range of life-history attributes exhibited by these groups will require demographic structures that are realistic and species-specific and yet generic in the sense that they apply to relatively large groups of functionally similar species, allowing generalizations of traits that make species vulnerable to climate change (Keith *et al.* 2008).

Another important advantage of the integrated approach is that it allows the simultaneous effects of multiple threats to be assessed. When assessing species vulnerability to climate change, it is very important not to ignore other threats, which may interact with, or supersede, climate change impacts. Many species

may be driven to extinction by habitat destruction, overexploitation or the effects of invasive species long before they are affected by climate change. Approaches that focus on climate change alone may therefore lead to underestimation of threats facing biodiversity.

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