

Projecting climate change impacts on species distributions in megadiverse South African Cape and Southwest Australian Floristic Regions: Opportunities and challenges

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Abstract Increasing evidence shows that anthropogenic climate change is affecting biodiversity. Reducing or stabilizing greenhouse gas emissions may slow global warming, but past emissions will continue to contribute to further unavoidable warming for more than a century. With obvious signs of difficulties in achieving effective mitigation worldwide in the short term at least, sound scientific predictions of future impacts on biodiversity will be required to guide conservation planning and adaptation. This is especially true in Mediterranean type ecosystems that are projected to be among the most significantly affected by anthropogenic climate change, and show the highest levels of confidence in rainfall projections. Multiple methods are available for projecting the consequences of climate change on the main unit of interest – the species – with each method having strengths and weaknesses. Species distribution models (SDMs) are increasingly applied for forecasting climate change impacts on species geographic ranges. Aggregation of models for different species allows inferences of impacts on biodiversity, though excluding the effects of species interactions. The modelling approach is based on several further assumptions and projections and should be treated cautiously. In the absence of comparable approaches that address large numbers of species, SDMs remain valuable in estimating the vulnerability of species. In this review we discuss the application of SDMs in predicting the impacts of climate change on biodiversity with special reference to the species-rich South West Australian Floristic Region and South African Cape Floristic Region. We discuss the advantages and challenges in applying SDMs in biodiverse regions with high levels of endemism, and how a similar biogeographical history in both regions may assist us in understanding their vulnerability to climate change. We suggest how the process of predicting the impacts of climate change on biodiversity with SDMs can be improved and emphasize the role of field monitoring and experiments in validating the predictions of SDMs.

Key words: biodiversity hotspot, climate change risk assessment, Mediterranean type ecosystem, species distribution modelling.

INTRODUCTION

Evidence for warming of the Earth's climate continues to accumulate with observations of global increases in average air and ocean temperatures, widespread melting of snow and ice, and rising average sea level. It is very likely that most of the increase in global temperatures since the mid 20th century is due to human activities, which have elevated concentrations of greenhouse gases in the global atmosphere. Continued

greenhouse gas emissions at or above the current rates are very likely to cause further warming and changes to the Earth's climate system. Reducing or stabilizing emissions will slow global warming, but past emissions will continue to contribute to unavoidable warming and sea level rise for more than a century (IPCC 2007). Because of this inevitability, governments and communities are beginning to address the causes of climate change by reducing greenhouse gas emissions, and at the same time implement strategies to adapt to the unavoidable impacts of climate change.

It has long been recognized that climate is a fundamental determinant of where organisms can establish,

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grow and reproduce. It is also well understood that in the Earth's past, climate changed significantly and rapidly on timescales of decades to millennia, and in response species' geographic ranges have expanded, or contracted and fragmented. It is therefore anticipated that future climate change will have a significant impact on the distribution of many, if not most, species. Indeed global analyses show that recent climate change is already affecting species and ecosystems and will continue to do so. Changes in the phenology, distribution and abundance of plants and animals are occurring for all well-studied, but mainly northern hemisphere marine, freshwater and terrestrial groups. These changes are consistently in the directions expected under global warming, and include earlier timing of spring events such as leaf unfolding, egg laying and migration, as well as poleward and upward shifts in species ranges (Parmesan 2006; Fischlin *et al.* 2007; Rosenzweig *et al.* 2008). With further climate change expected, credible scientific predictions of future impacts on biodiversity will have to underpin conservation planning and adaptation. This is particularly challenging because predicting the effects of novel conditions is very difficult and subject to considerable uncertainty.

There are multiple methods available to ecologists for predicting the consequences of climate change, with each method having its own strengths and weaknesses (Sutherland 2006). All methods involve a trade-off between reality and tractability, and between specificity and generality. Where they can be conducted at appropriate spatial and temporal scales, experiments provide the most realistic predictions, often yielding unexpected responses as a result of complex interactions (Suttle *et al.* 2007). The problem is that, for many systems, experiments become intractable and almost impossible to fund and carry out with acceptable replication at sufficiently large scales, over long enough time periods. For example, it may be possible to manipulate rainfall and temperature in grassland ecosystems at appropriate spatial and temporal scales, but this seems near impossible in forest ecosystems. Furthermore, long-term experiments set up now may not deliver results in time to inform urgent climate change adaptation policy. Manipulating distributions across climate gradients with transplant experiments may provide a more tractable approach to understand how species will respond to climate change (see later discussion). Ultimately, however, all forecasts of climate change impacts will have to be based on models, be they verbal, statistical or simulation models.

In the last decade there have been substantial advances in process-based models of the impacts of climate change on global patterns of vegetation and ecosystem functions such as carbon cycling. These process-based models are supported by reasonably

well-known empirical relationships and theory, but it is currently still very difficult to apply them to understanding species and biodiversity responses (Thuiller *et al.* 2008). Yet it is this level of understanding that is required for conservation strategies to be developed, especially in jurisdictions such as the Cape Floristic Region (CFR) of South Africa and the South West Australian Floristic Region (SWAFR; *sensu* Hopper & Gioia 2004), which are internationally recognized for their high plant species diversity (Myers *et al.* 2000). Indeed, conservation agencies and planners are seeking to determine how effectively current protected area systems protect future patterns of biodiversity; identifying areas that will become important; and managing the matrix between protected areas to facilitate range movement in the face of climate change (Hannah *et al.* 2002a,b).

In the last two decades correlative species distribution models (SDMs) have been increasingly used in conservation planning and more recently have become the most commonly used tool for predicting the impacts of climate change on biodiversity (Thomas *et al.* 2004; Guisan & Thuiller 2005; Botkin *et al.* 2007). These models have a number of advantages. They are spatially explicit, relatively straightforward, and can utilize occurrence records from large museum and herbarium collections, and can be rapidly deployed for simultaneous assessments of large numbers of species (e.g. Thomas *et al.* 2004). Different scenarios of climate and land-use change can be incorporated explicitly (Araújo & New 2006), and their predictions can inform adaptation policy and management immediately. A main disadvantage of SDMs is that extrapolating current correlations between species distributions and the environment into the future may lead to seriously biased predictions. To date, SDMs have been used to predict the impacts of climate change on the ranges of vascular plants, butterflies, amphibians, reptiles, birds and mammals across continents in both hemispheres (Table 1). But how well do SDMs encompass the factors limiting the distribution of species, and how reliable are the predictions for areas such as the CFR and SWAFR which share geo-historical contexts that differ from many other parts of the world?

The Cape Floristic Region and South West Australian Floristic Region

The CFR and the SWAFR have Mediterranean climates characterized by marked cool, wet winters and hot, dry summers with fire being a recurring disturbance and driver of ecosystem dynamics (Cowling *et al.* 2005). In both regions, the floras are characterized by moderate to high diversity within habitats and among adjacent habitats, with extraordinarily rapid

Table 1. Examples of taxonomic groups and regions for which species distribution models have been used to predict the impacts of climate change on biodiversity

Taxonomic group	Location	Study
Vascular plants	South Africa	Midgley <i>et al.</i> 2002, 2003; Bomhard <i>et al.</i> 2005; Broennimann <i>et al.</i> 2006; Pearson <i>et al.</i> 2006; Thuiller <i>et al.</i> 2006b
	Europe	Bakkenes <i>et al.</i> 2002; Thuiller 2003, 2004; Skov & Svenning 2004; Thuiller <i>et al.</i> 2005
	USA	Box <i>et al.</i> 1993, 1999; Crumpacker <i>et al.</i> 2001
	Britain and Ireland	Berry <i>et al.</i> 2002
	New Zealand	Leathwick <i>et al.</i> 1996
	Australia	Hughes <i>et al.</i> 1996; Fitzpatrick <i>et al.</i> 2008
Butterflies	Australia	Beaumont & Hughes 2002; Beaumont <i>et al.</i> 2005
	Europe	Hill <i>et al.</i> , 1999, 2001, 2002
Birds	Canada	Peterson <i>et al.</i> 2004
	Mexico	Peterson <i>et al.</i> 2002a,b
	Europe	Huntley <i>et al.</i> 2006
Mammals	USA	Peterson 2003
	Britain	Araújo <i>et al.</i> 2005a,b
	Mexico	Peterson <i>et al.</i> 2002a,b
	Western Hemisphere	Lawler <i>et al.</i> 2006
Amphibians	Australia	Brereton <i>et al.</i> 1995
	Africa	Thuiller <i>et al.</i> 2006a
Reptiles	Europe	Araújo <i>et al.</i> 2006
Vertebrates	Europe	Araújo <i>et al.</i> 2006
	Australia	Williams <i>et al.</i> 2003; Meynecke 2004

turnover of species across the landscape (Cowling *et al.* 1994; Cowling *et al.* 1996, references cited within Hopper & Gioia 2004; Mucina *et al.* 2006; Rebelo *et al.* 2006). For example in Kwongan shrublands in the Mt Leseuer region of the SWAFR, quadrats on the same landform 1 km apart may have up to a 60% difference in species composition (Hopkins & Griffin 1984). A significant consequence of this turnover is that local endemism is prominent in both regions.

These patterns are most likely a consequence of the special geo-historical contexts of both regions. These include exceptional opportunities for continuous evolution over very long periods, previous climate variability and change particularly throughout the Quaternary, mosaics of old highly weathered infertile soils, recurrent fire, poor dispersal, novel genetic systems and intricate webs of species interactions (Hopper & Gioia 2004). Present species and ecosystem distributions are correlated with climate gradients at macro-ecological scales as are landforms and soils at regional and local scales (Beard 1990; Gioia & Pigott 2002; Gibson *et al.* 2004; McKenzie *et al.* 2004; Mucina & Rutherford 2006; Rebelo *et al.* 2006). It is therefore expected that current and future climate change will affect most species and ecosystems directly through changes to temperature, rainfall and the frequency of extreme events, and indirectly through altering factors such as stream flow, groundwater levels, fire regimes and the nature and intensity of existing biodiversity threats. However, current distributions of species in both regions may be as much a product of poor dispersal, historical biogeography and processes

operating in deep evolutionary time (Hopper & Gioia 2004; Byrne 2007; Yates *et al.* 2007). Such factors should be taken into account when interpreting the predictions of SDMs.

Climates are predicted to become warmer and drier in both regions. In the SWAFR there has been an increase in temperatures, and since the 1970s a marked decline in rainfall particularly in the early months of the winter wet season. This decline is largely a consequence of changes to synoptic patterns and changes in sea level atmospheric pressure, which are likely to be due at least in part to increases in greenhouse gases arising from human activities (Cai & Cowan 2006; Hope *et al.* 2006; Bates *et al.* 2008; CSIRO 2007). In the CFR there has been significant warming, and a decline in rainfall in the western part of the region, together with a shift towards later winter precipitation (Hewitson & Crane 2006; MacKellar *et al.* 2007). The consensus among Global Climate Models (GCMs) is that rainfall in south-west Western Australia and in the CFR will continue to decline (Hewitson & Crane 2006; CSIRO 2007).

Both the CFR and SWAFR occur on the western and southern margins of their continents and are adjacent to arid zones. The SWAFR especially is a cooler and wetter continental refuge on the edge of a dry arid continent. Both regions have contrasting topographies. The SWAFR, with the exception of the Stirling Ranges which are just 1109 m a.s.l., is of low relief offering limited scope for altitudinal migration into montane refuges, whereas the CFR has significant montane topography in addition to coastal plains. Under

projected climate change, warmer and more arid conditions are expected to shift southwards and westwards in both regions and upwards in the CFR, and there is a possibility, especially in the relatively flat SWAFR, that the coolest and wettest climate zones on the south coast, containing many relictual and mesothermic phylogenetic lineages may disappear.

Early estimates of the potential impacts of anthropogenic climate change with SDMs in the CFR show that the Fynbos biome could exhibit between 51% and 65% loss of area (depending on the particular future climate scenario), and that up to one third of species of Proteaceae may need to migrate to completely novel geographic ranges in order to persist (Midgley *et al.* 2002). In a more detailed analysis of 28 species of Proteaceae, Midgley *et al.* (2003) predicted that 17 species may contract in range, and five species lose all bioclimatically suitable range by 2050. Similarly, in the SWAFR, in a study of 100 *Banksia* species, Fitzpatrick *et al.* (2008) predict that 66 species may contract in range, with between 5 and 25 species predicted to lose all bioclimatically suitable range by 2080 depending mainly on the future climate scenario.

In this review we discuss the application of SDMs in predicting the impacts of climate change on biodiversity with special reference to the species-rich SWAFR and CFR. We discuss the advantages and shortcomings of SDM, and how the biogeographical history of both regions may affect the vulnerability of their biota and predictions of the models. We suggest how the process of predicting the impacts of climate change can be improved and the role of monitoring and experiments in validating forecasts.

WHAT ARE SPECIES DISTRIBUTION MODELS AND HOW ARE THEY USED TO PREDICT THE EFFECTS OF CLIMATE CHANGE ON SPECIES RANGES?

There are many different SDM methods (see below), but all share a common underlying approach. The models relate the known occurrences of species to climate variables (taken as surrogates for physiologically relevant variables), and other factors such as soil and land-cover, to define the abiotic conditions within which populations can exist. In turn, the modelled environmental domains of species are projected onto a geographic space under current and predicted future climate scenarios, allowing the distribution of suitable conditions for each species to be predicted and mapped, and risk analysis undertaken.

Most models use two simple dispersal scenarios, unlimited or no dispersal, to estimate the percentage gain or loss of suitable climate space for a species. The unlimited dispersal scenario assumes species can track their shifting climate envelopes, and the future distri-

bution of species will mirror the spatial extent of their new climate envelopes. The no dispersal scenario assumes species will persist only in areas where the predicted current and future climate envelopes overlap. In cases where there is no overlap, species are assumed to become extinct. While some efforts have been made to incorporate lags in population migration due to dispersal and demographic limitations, these are seldom implemented, and are virtually untested. This is despite the abundant test systems available such as observed range shifts in indigenous species, and the range occupation rates of invasive alien species.

Modelling methods and approaches – different data requirements

Many SDM methods can be used to predict the impact of climate change on species' potential geographic distributions (Guisan & Thuiller 2005). Explanations of the SDM methods can be found in Elith *et al.* (2006), Heikkinen *et al.* (2006) and papers cited therein. Briefly, models can be broadly categorized into climatic envelope range – (e.g. BIOCLIM), statistical – (e.g. regression-based Generalized Linear Models, GLM; Generalized Additive Models, GAM; Multivariate Adaptive Regression Splines, MARS) or machine learning – techniques (e.g. GARP; MaxEnt; Classification and Regression Trees, CART) (Guisan & Zimmermann 2000; Elith *et al.* 2006). The techniques vary in the way they fit the response variable, allow for use of continuous and categorical predictive environmental variables, select variables and allow for interactions. Recently, Bayesian approaches have also been developed using the unusually complete sampling data offered by the Protea Atlas Database (e.g. Gelfand *et al.* 2006).

A major difference between the methods is the type of species occurrence data used. Some models have been designed to model presence-only data (e.g. BIOCLIM, GARP, MaxEnt) while others are typically used for presence/absence data (GLM, GAM, CART). This distinction is important for the application of bioclimatic models to conservation planning and climate change. In regions where species occurrence data have been collected systematically and absences from areas can be prescribed with reasonable certainty (e.g. Protea Atlas in South Africa), modellers have favoured the presence/absence techniques such as GLM, GAM, and CART, because these seem to give better predictions than techniques designed for presence-only data (Midgley *et al.* 2003; Pearson *et al.* 2006). Implicit in the use of absence data is the assumption that absence is due to a climatically induced inability to persist in the location rather than a factor that can't be quantified in the predictor

variables. Factors might include dispersal or competitive limitation (see later discussions on range equilibrium with climate and other factors and species interactions).

For most regions the great majority of species occurrence data have not been collected with species range modelling in mind, and these data are presence-only records in herbarium and museum databases (Elith *et al.* 2006; Pearce & Boyce 2006). To date, the choice of models that could be applied to such data has been restricted to apparently lesser performing techniques. However, recent developments in modelling presence-only data are encouraging, and extend to adaptation of methods that have previously only been used for presence-absence data. Elith *et al.* (2006) compared the performance of 16 correlative modelling methods in predicting the ranges of 226 species from five continents. Presence-only data were used to fit the models, and independent presence/absence data to evaluate them. They found that data were effective for modelling the distributions of many species across regions. Several novel techniques, a computational method borrowed from statistical mechanics, and a regression-based method, boosted regression trees, consistently outperformed more established methods such as BIOCLIM and GARP (Elith *et al.* 2006).

Do models and data which successfully predict current species distributions also provide robust predictions of future distributions under climate change?

Although SDM's are increasingly used to forecast the impacts of climate change on species distributions, their evaluation (validation) remains problematic, because there are seldom suitable data against which predictions of future ranges can be tested. Consequently, evaluation of models is usually restricted to how well they predict current distributions (but see Araújo *et al.* 2005a). Evaluations of current distributions preferably use an independent dataset, but in reality most often use data re-substitution or data splitting, whereby a portion of the data are used to train the model and a portion withheld to validate it. Two measures of classification accuracy are commonly used, the Kappa statistic and the area under the curve of a receiver operating characteristic plot (Guisan & Zimmermann 2000; Guisan & Thuiller 2005; Heikkinen *et al.* 2006). The Kappa coefficient measures the correctly classified presences and absences after the probability of chance agreement has been removed. The area under the curve of the receiver operating characteristic plot reports whether predictions are well ranked (i.e. predictions for presence sites being higher than predictions for absence sites) over all possible threshold levels. Other more subjective methods can

also be used to evaluate models, including expert interpretation of the model to check its consistency with knowledge of the species (Austin 2002).

Predictive accuracy may vary considerably among different modelling methods applied to the same dataset (Thuiller 2003, 2004; Araújo *et al.* 2005a; Elith *et al.* 2006; Lawler *et al.* 2006; Pearson *et al.* 2006). However, because the models are correlative, strong performance of any method in the present climate does not guarantee similar performance under future climates (Thuiller 2004, see discussion below), especially as biotic interactions may change due to species within current communities responding differently to climate change (Davis *et al.* 1998; Pearson & Dawson 2003).

One method of testing the robustness of different model predictions under future climate scenarios is to compare predictions from different modelling methods using a common dataset. Where this has been done, considerable variability among model predictions is reported. For example, Pearson *et al.* (2006) applied nine widely accepted bioclimatic modelling techniques to four South African plant species, and compared consistency in predictions of changes in range size under a future climate scenario. They showed significant differences in predictions among models, with changes in range size varying in both magnitude and direction. For one species, predicted changes in range size varied from a 92% loss to a 322% gain, and similarly wide variation in range changes were predicted for the other three species. This variation was in part explained by the data input requirements of the models (presence-only v presence/absence occurrence data), and assumptions made by each algorithm when extrapolating beyond the range of the data used to build the models. Similar variations in intermodel predictions of range shifts under future climate scenarios are reported for European plants (Thuiller 2003, 2004), amphibians and reptiles (Araújo *et al.* 2006), British birds (Araújo *et al.* 2006) and western hemisphere mammals (Lawler *et al.* 2006).

One conclusion from these studies is that the type of model used in a study will have a substantial effect on predicted range shifts, and because of this uncertainty, the common practice of using one method of forecasting may have limitations for conservation planning. This has led some authors to suggest that an ensemble of modelling methods should be used in forecasting potential changes in species distributions under climate change (Thuiller 2004; Araújo *et al.* 2005a; Araújo & New 2006). While this has merit, we suggest that there is also value in understanding why there are differences in predictions among methods. Substantial progress in reducing methodological uncertainty might result from rigorous theoretical analyses of the way different methods will perform in scenarios where they are extrapolating outside the range of the training data. For example, envelope methods based on

climatic profiles will predict 'unsuitable' outside the environmental space of the training data, whereas a GLM fitted with one variable and a positive linear gradient will predict increasingly suitable habitat as the value of the explanatory variable increases. Assessing methods in relation to their known properties is likely to provide important *a priori* information to aid decisions about which methods are most realistic ecologically, or how to adjust existing methods to make them behave in sensible ways.

Another methodological uncertainty lies within implementations of any given method. For example, a 'GLM' can be fitted in many different ways (with linear or quadratic fitted functions or splines; with or without interactions; via stepwise model selection routines or more recent shrinkage techniques), and these will have substantial impact on the resulting predictions, particularly under extrapolation. One way to respond to this type of model uncertainty is to test predictive performance under current climate (e.g. with independent data or resampling methods) and to explore the impacts of the different model formulations on prediction.

Another aspect of model development that affects the ability of models to successfully predict current and future distributions is the environmental data that are available as predictors. If key variables are missing, the model will try to describe the distribution with the available predictors, either making unnecessarily complex relationships with some predictors or predicting averaged patterns in areas that contain unquantified environmental variation. The former is particularly problematic when extrapolating into changed environmental conditions. In both the SWAFR and CFR, soils, landforms and hydrogeology are also major determinants of floristic and vegetation patterns at regional and local scales (Gioia & Pigott 2002; Gibson *et al.* 2004; Groom 2004; McKenzie *et al.* 2004; Mucina *et al.* 2006; Rebelo *et al.* 2006). Many plant species are restricted to particular edaphic environments and have specialized morphology and physiology that may be maladaptive in other edaphic environments (Cowling *et al.* 1994; Poot & Lambers 2008). Similarly, many species are restricted to particular locations on hydro-geological gradients (Groom 2004). Spatially explicit soil and hydrogeology data are not available at scales that are relevant to species distributions and this must be taken into account when interpreting the predictions of SDMs.

Climate models may also contribute to uncertainty in predictions of species distribution models

Global climate models are the principal tools for projecting future climate (Randall *et al.* 2007). These are

numerical representations of the physical processes and interactions between the Earth's atmosphere, oceans and land-surface. There are many GCMs in operation, each with different assumptions and parameterizations. As a consequence, various GCMs display marked differences with respect to future climate projections. Similarly, because society may respond in different ways to climate change, the magnitude of future greenhouse gas emissions is unknown. To this end the IPCC (2000) developed a number of alternative emission scenarios (SRES markers) for use in forecasting. To derive a projection of future climate, a GCM is forced with a change in atmospheric chemistry prescribed by an emission scenario (Mackellar *et al.* 2007). Whether the IPCC scenarios encompass the emissions that are actually likely to occur is debated. Currently, greenhouse gas emissions are exceeding the IPCC (2000) most pessimistic highest emission scenario (Raupach *et al.* 2007). Uncertainties about GCMs and future emission will contribute to uncertainties in predicting the impacts of climate change on species distributions. Recent guidelines on forecasting and climate change risk assessment recommend using multiple GCMs and emission scenarios to specify the full range of uncertainties in future climate (CSIRO 2007), but note that the IPCC scenarios do not capture the full range of uncertainty about future emissions. It may therefore be most appropriate to use multiple GCMs with the one or two most pessimistic emission scenarios in risk analysis. To date most SDM studies use the climate projections from one GCM and one emission scenario in their predictions of future species geographic ranges (but see Thuiller 2004; Fitzpatrick *et al.* 2008).

Because there are a large number of GCMs, species distribution modellers are faced with using all available GCMs, or choosing a subset that encompasses the range of predictions for the region. As previously discussed for SDM types, using an ensemble of GCM models may result in a range of projections which is larger due to the inclusion of a 'mediocre' model that does not represent the climate of a region very well. Perkins *et al.* (2007) have suggested the evaluation of the 'skill' of individual GCMs to simulate the historical climate variables of interest in the study region may be a way of overcoming this problem. These authors have evaluated the skill of GCMs in reproducing historical daily minimum and maximum temperatures and precipitation for 12 regions in Australia including the SWAFR. They found variation between GCMs in skill at predicting each of the climate variables. Some models were more skilful at predicting temperature compared with precipitation and the converse. Ideally for SDM, GCMs would be chosen that have the greatest skill in predicting the climate variable that has the most influence on a species distribution, but this is rarely known.

Although GCMs can predict historical climate with reasonable skill, their spatial resolution remains problematic for predicting the impacts of climate change on biodiversity. The resolutions of GCM outputs have improved significantly, as the models have become more refined, but they are still very coarse, with horizontal grid spacing ranging from 125 to 400 km. Within this spatial scale there will be underlying climatological gradients and land surface heterogeneity (e.g. mountains and vegetation cover) affecting local climates and species distribution patterns (Hewitson & Crane 2006). In the highly diverse floras of the SWAFR and CFR there is rapid turnover of species across the landscape and a large number of geographically restricted species that have ranges which fall well within the spatial scale of even the highest resolution GCM. Except for the most widespread and common species, the input climate scenarios in SDMs may be too crude in spatial scale to provide accurate patterns of distributional changes for many endemics in both regions. Regional or mesoscale climate models and downscaling of GCMs can help resolve this problem. The method used to downscale a GCM will also impact on predictions. Many studies do not describe how GCM data are downscaled for use in SDMs, but techniques vary from simple linear interpolation to more complex dynamic and statistical (empirical) techniques (Hewitson & Crane 2006; Beaumont *et al.* 2007; Charles *et al.* 2007). Empirically downscaled climate data are available for the CFR (Hewitson & Crane 2006), but not for the SWAFR. Collaborations between biologists and climate scientists would help to resolve this issue and improve the predictions of SDMs.

How do we respond to the methodological uncertainty in models to produce more reliable estimates of biodiversity risk under global climate change?

One solution to the problem of methodological uncertainty is to utilize multiple bioclimatic modelling methods coupled with different emission scenarios (an ensemble) to define a 'bounding box' or generate a 'consensus' forecast (Thuiller 2004; Araújo *et al.* 2005b; Araújo & New 2006). The underlying logic of the ensemble approach is that ensembles of models will generate a broader variability of forecasts that is a better reflection of uncertainty, and that the combined forecasts will yield lower mean error than any of the constituent individual forecasts (Araújo & New 2006). The 'bounding box' approach uses the range in forecasts from the ensemble members to identify the areas where at least one or all models predict species presence in the future. The 'consensus' forecast approach calculates a measure of the central tendency (e.g.

mean or median) from the ensemble of forecasts, and for example, using the median identifies areas where at least half the models predict species presence (Araújo & New 2006). An ensemble approach will be computationally demanding with multiple permutations of climate scenarios and modelling methods for large numbers of species. Although ensemble forecasting provides a means of incorporating methodological uncertainty into risk analysis, the confidence limits of the predictions will still be dependent on how reliable the model predictions are. As discussed earlier, if the models are a poor representation in the first place then it does not matter how many different methods are used to calculate a range or average (Araújo & New 2006).

Undoubtedly, there is merit in using multiple SDM methods in ensembles to quantify associated uncertainty in predictions. However, the use of multiple SDM's in ensembles without some *a priori* assessment of their ecological relevance (see earlier discussion above) may result in 'pseudo-precision'. We suggest that there is merit in identifying a smaller subset of ecologically realistic approaches that can be validated against observations rather than to rely on a 'consensus of the mediocre'. In the same way, using a subset of the GCM's that capture likely scenarios for the CFR and SWAFR seems a sensible strategy. Tests against range shifts in real world species would provide a way forward (for example Foden *et al.* 2007).

BIOLOGICAL UNCERTAINTY IN BIOCLIMATIC MODELS

Uncertainties in future species distributions arising from variation in predictions among different SDM methods, GCMs and emission scenarios can at least be quantified and incorporated into a range of conditional probabilities. More problematic are uncertainties in model predictions arising from the genetic, life-history, ecological and historical factors, which, in addition to climate, influence species distributions (Lewis 2006). The question of why species are present in some places and absent from others is one of the oldest in ecology, and has significant practical consequences when predicting the impacts of climate change on species distributions (Krebs 2001). Species distributions are influenced by environmental history (previous climate change, disturbance regimes), migration ability, behaviour, other species (predation, parasitism, disease, competition and mutualisms), and their tolerances to the physical and chemical factors affecting resources and conditions. In addition, genetic variation and natural selection may change the tolerances of species (Davis & Shaw 2001). Many studies have experimentally analysed the influence of one or other of these factors, but in no case have all factors

been studied completely for a species. Consequently, there is considerable uncertainty about which factors most limit species distribution and how this varies among species and between regions (Krebs 2001; Gaston 2003).

With the exception of recent Bayesian models most SDMs assume species are at equilibrium with the present climate, and most use just bioclimatic variables to predict the present and future distributions of species under climate change. As a consequence SDMs have been criticized for not including key processes affecting species distributions, and have been seen as overly simple, yielding misleading predictions (Hampe 2004; Pearson & Dawson 2004; Lewis 2006). In the next sections we review the assumptions underlying SDMs with particular reference to the biology of species in the CFR and SWAFR.

Are species geographic ranges in equilibrium with climate?

Species distribution models rely on the assumption that a species is currently at equilibrium with the present climate and the models extrapolate this equilibrium assumption into the future to generate potential range forecasts. This is problematic because past events (e.g. climate at the Last Glacial Maximum LGM), together with the migration ability of species, will influence their present distribution (Svenning & Skov 2007). Species with limited migration ability or whose ranges are restricted by physical barriers to migration may take a long time to reach a new future equilibrium with climate (e.g. Leathwick 1998), and for all species that are not at equilibrium with climate (e.g. because they are still in a phase of expansion since the LGM), correlative range distribution forecasts will inevitably be biased. In this case any methods of consensus/ensemble forecasting will only summarize these biased projections.

In both the SWAFR and CFR, many plant lineages show phylogeographic patterns consistent with repeated expansion and contraction of ranges in response to Pleistocene glacial-interglacial conditions and oscillations (Hopper & Gioia 2004; Midgley *et al.* 2005; Byrne 2007). Currently, there is mixed evidence as to whether species are at equilibrium with climate. In the SWAFR the present distributions of some plant taxa cannot be adequately explained by ecological factors alone (Latimer *et al.* 2005; Byrne 2007; Yates *et al.* 2007). Their distributions are better explained by Pleistocene climate oscillations with associated fragmentation, contraction and persistence of populations in suitable habitats and recovery of range from these areas limited because of poor migration capacity (Latimer *et al.* 2005; Byrne 2007; Yates *et al.* 2007; Byrne *et al.* 2008). Transplant

experiments across climate gradients also reveal that species will grow beyond their bioclimatically modelled distributions (Witkowski & Lamont 2006; Latimer *et al.* 2009).

In the CFR, however, the extent to which 37 species of Proteaceae fill their potential range (as estimated by bioclimatic models) could be explained by mechanistically derived estimates of colonization and persistence ability, but was shown to be independent of the evolutionary age of a species (Schurr *et al.* 2007). This suggests that post-speciation expansion did not limit their current distributions and that these species may currently be at a dynamic equilibrium with climate. Yet, this example also shows that projections of future ranges have yet to account for interspecific differences in dispersal and colonization ability.

To deal with the equilibrium assumption associated with correlative bioclimatic models, we have to fit process-based models of range dynamics to distribution data. A first step in this direction has been taken by Wikle (2003), although the simple model used in this study does not consider environmental covariates. Clearly, the statistical fitting of process-based models poses challenges to both data quality and statistical methodology: for instance, we may need spatio-temporal data rather than 'simple' spatial data, and we may need to use Hierarchical Bayesian rather than frequentist approaches (Thuiller *et al.* 2008). An alternative approach using physiologically motivated mechanistic models also shows promise (Kearney *et al.* 2008).

Interspecific interactions and bioclimatic envelope (niche) conservatism

All species exist within a web of mutualistic and antagonistic interactions with other species, and numerous studies have demonstrated how the presence or absence of one species can affect the population and range dynamics of another (Connell 1961; Davis *et al.* 1998; Leathwick & Austin 2001). An acknowledged shortcoming of single-species SDMs is that they do not explicitly account for the effects of biotic interactions on species distributions. Negative interactions (e.g. interspecific competition), positive interactions (e.g. mutualisms) and meta-population source-sink dynamics may alter species distributions (Hutchinson 1957; Shmida & Ellner 1984; Araújo & Guisan 2006). Thus what appears to be a climatic limit to a species range may be a biotic interaction with, for example a competing species. This may not be a weakness for predicting species distributions under present conditions. Indeed, many SDMs utilizing only bioclimatic variables predict present species distributions reasonably well. However, neglecting interspecific interactions may result in incorrect predictions of

future distributions if biotic interactions change (Davis *et al.* 1998; Pearson & Dawson 2003), and this will be influenced by the stability of assemblages of interacting species.

Although the distribution of species assemblages can often be predicted by environmental variables, the fossil record indicates that in many areas these assemblages may not be stable in geological time. Species apparently respond idiosyncratically to climate change, because of differential persistence, dispersal rates and substrate affinities. As a consequence novel species assemblages and interactions will develop in the future. A question which arises from the foregoing is: how will a new community context affect the population and range dynamics of a species or, put another way, how stable are modelled niches in the face of changing species assemblages? Species distribution models assume niche conservatism. Some authors argue that rearrangements of species interactions will have effects on population and range dynamics far greater than those arising directly from the influence of climate change on species physiological tolerances (Davis *et al.* 1998). Other authors argue that bioclimatic envelopes remain stable through time (Peterson *et al.* 2005; Martínez-Meyer & Peterson 2006). The reality probably lies somewhere in between. There are a growing number of experimental and empirical studies which demonstrate that climate change can affect the strength and direction of existing interspecific interactions and so profoundly affect the population dynamics of species and alter the composition of ecosystem (Suttle *et al.* 2007). The legacy of long-lived species with adult stages that can persist, but are unable to recruit as the climate changes, may prevent colonizing species from establishing. Currently, SDMs cannot forecast the lagged impacts of altered higher order species interactions that will govern the trajectory of ecosystems. More systems oriented approaches will be necessary to elucidate these responses (Suttle *et al.* 2007).

Fire regimes and extreme events shaping species distributions and vegetation

In both the CFR and the SWAFR fire is a major factor influencing population and ecosystem dynamics, and fire regimes have a profound influence on the composition and structure of vegetation (Bond & van Wilgen 1996; Bradstock *et al.* 2002; Abbott & Burrows 2003). Little attention has been paid to the influence of fire regimes on the stability of the modelled environmental niche, but Bond *et al.* (2004) provided evidence that global vegetation patterns are shaped by landscape-level fire regimes, as well as climate. At more regional scales it is also evident that fire regimes influence the composition and structure of vegetation (Bowman

2000). In the SWAFR very long fire intervals appear to be responsible for the tree *Allocasuarina huegeliana* encroaching into Kwongan shrublands in isolated fragments of native vegetation (Maher 2007). Similar patterns have been reported in South Africa where afro-montane forest species invade Fynbos communities during long fire-free periods (Manders & Richardson 1992; Bond & van Wilgen 1996).

Fuel loads, ignition and fire weather are all influenced by climate. Therefore predicted hotter and drier conditions will affect fire regimes in the CFR and SWAFR. Increase in frequency, scale or intensity of fire will differentially affect the population and range dynamics of species depending on their fire life-histories. Non-sprouting serotinous species are very prevalent among geographically restricted species in the diverse Fynbos and Kwongan communities of the CFR and SWAFR (Cowling *et al.* 1994; Yates *et al.* 2003). Fire return times are very important for the persistence of these species. This group will be particularly threatened if very short fire intervals become frequent (Bond & van Wilgen 1996). Yet on the other hand, the dispersal and colonization rates of non-sprouters may be higher than those of sprouters (Schurr *et al.* 2007; Higgins *et al.* 2008). Increases in the size of fires may reduce barriers to long-distance dispersal and establishment, and increases in fire frequency may reduce generation times thereby speeding up ecological and evolutionary responses to climate change. These changes in the fire regime may be more favourable for migration of non-sprouters allowing them to escape climate change more easily than sprouters.

Extreme weather events may also affect apparent equilibrium of species distributions with climate. It is likely that extreme episodic events play a significant role in shaping species distributions through effects on both mortality and recruitment. Thus, current distributions may be in part a legacy of previous extreme events. The importance of these extreme events in shaping future species ranges is likely to be missed using SDMs because they typically use means and trends in climatic variables and do not address the role of past extremes in shaping observed distributions, or changes in the frequency of extreme conditions (e.g. extended droughts, cyclonic summer rainfall) under future climates in producing new distributions. This is a problem because extreme conditions may have a greater impact than changes in the mean values of climate variables. Extreme events can result in complete reorganization of systems and communities (e.g. Brown *et al.* 1997; Breshears *et al.* 2005) and may provide important opportunities for and limitations to plant recruitment. For example, In the CFR and SWAFR many of the effects of fires on seedling recruitment are related to temperature and rainfall patterns before and during the year after the event

(event dependent) rather than the long-term averages (Bond & van Wilgen 1996). The reason that SDMs do not include these more relevant data is not that the models are incapable of it, but rather that the data are not available. Summaries of climate data that focus on extreme events could be a valuable addition.

Similarly, changes in the frequency of extreme events may affect the abundance and spread of pathogens. In the SWAFR 2284 species are considered susceptible and 800 species highly susceptible to the plant pathogen *Phytophthora cinnamomi* (Shearer *et al.* 2004). Episodic heavy summer rainfall events associated with ex-tropical cyclones moving across the region provide ideal conditions for the spread of *P. cinnamomi* and are linked with the widespread death of susceptible species (McDougall 1996). Increases in the frequency of these events associated with predicted increase in cyclone and monsoonal activity in north-western Australia may facilitate the spread of the pathogen.

Increasing atmospheric CO₂

An important, but not widely acknowledged shortcoming of using SDMs to predict climate change impacts on species distributions, is that they cannot explicitly account for the physiological responses of plants to increases in the atmospheric CO₂ concentration. Yet, elevated CO₂ has been shown to have significant impacts on plant performance, albeit with considerable variation in the responses of different species, functional types and ecosystems (Körner 2003; Ainsworth & Long 2005). One of the reported effects of elevated CO₂ appears to be a reduction in stomatal conductance (Wand *et al.* 1999; Ainsworth & Long 2005), resulting in increased soil moisture beneath plants (Niklaus *et al.* 1998).

Because SDMs do not currently include the effects of elevated CO₂ water savings, they may underestimate the amount of suitable bioclimatic habitat available for some species (Shafer *et al.* 2001). Model simulations of vegetation distribution through the last glacial maximum and pre-industrial era indicate that, during periods of higher atmospheric CO₂ concentrations, grasses and trees were able to establish with much lower rainfall than it was possible under lower CO₂ conditions (Crucifix *et al.* 2005).

The incorporation of elevated CO₂ effects into species specific SDMs is hampered by the complexity of the observed responses. Detailed predictions of elevated CO₂ effects on plant performance are difficult because they appear to be taxon specific and strongly interactive with soil type and climate (Spinnler *et al.* 2002; Körner 2003; Bradley & Pregitzer 2007; Fischlin *et al.* 2007). If these could be estimated, they could be added as predictor variables in SDMs.

Collaborations between physiologists and spatial modellers might enable some development in this area.

What effect will life-history traits and adaptive genetic variation have on species range dynamics?

In the face of climate change, species may persist *in situ*, adapt *in situ* over generations, migrate or go extinct (Hewitt & Nichols 2005; Midgley *et al.* 2005). Palynological records (Dodson & Macphail 2004), phylogeography (Byrne 2007), present day distributions and population level studies integrating phylogeny, life-history and ecology (Yates *et al.* 2007) provide evidence for all of the above responses in both the SWAFR and CFR since the late Pliocene (Hopper & Gioia 2004; Midgley *et al.* 2005).

Species distribution model studies investigating the impacts of climate change, do not explicitly account for persistence, adaptation and migration in any realistic way (Thuiller *et al.* 2008). This is acknowledged as a major limitation in most SDM studies. These factors are important because the interplay of longevity, breadth of climate tolerance, dispersal ability and mode of reproduction varies greatly among species, and will ultimately determine their range dynamics. For example, clonal plant species with low sexual reproduction rates, and no means of dispersal, will have to persist *in situ* (Witkowski & Lamont 2006). The life-history characteristics of some species may allow them to persist in the landscape long after suitable climate conditions have changed (Midgley *et al.* 2005). This can be achieved either through high levels of tolerance and longevity in adult stages, or through dormancy and longevity of propagules (Bond & Midgley 2001). Indeed a comparative study of serotinous CFR Proteaceae suggests that – for a given colonization ability – more persistent species (sprouters) fill more of their bioclimatic potential range (Schurr *et al.* 2007). Despite this, most studies assume time lags in responses to climate change are relatively short and that species are at immediate risk even though they may persist for several decades (Fitzpatrick *et al.* 2008). In the SWAFR and CFR this may be a reasonable assumption for the many short to moderately lived shrub non-sprouting species which are killed by fire. However, in both regions there are many long-lived sprouting species and in the SWAFR a number of long-lived tree species. If the adult life stages of these species are relatively drought tolerant, or have access to regional aquifers that are buffered against rainfall declines, they may form a substantial legacy effect. These characteristics may allow the species to persist for considerable periods of time as the climate dries. Similarly, a combination of adult longevity and a very high tolerance to drought may have allowed *Verticordia*

staminosa ssp. *staminosa* to persist on a granite outcrop through multiple climate oscillations in the Pleistocene (Yates *et al.* 2007).

It should, however, be noted that persistent species are by no means safe from climate change. If climate change precludes the establishment of seedlings, even species with high adult persistence will have to migrate. Trade-offs between persistence and migration ability may even cause persistent species to be at greater risk from climate change. In migration simulations parameterized with empirical data on reproduction and seed dispersal of CFR Proteaceae, Higgins *et al.* (2008) found that sprouters have substantially lower migration ability than non-sprouters, even though they are competitively superior. In the long run, these persistent species may thus be more threatened by the consequences of rapid climate change.

Species distribution models treat species as genetically invariant across their ranges. This is unrealistic, because spatial variation in adaptive traits among populations has been documented for most species investigated (Davis & Shaw 2001), notably among plants (Bradshaw 1972). Such information is generally unavailable for most species across their entire geographic range. This information is currently lacking for species in the CFR and SWAFR. Nonetheless, spatial genetic variation in physiological and demographic properties may affect SDM predictions of species range changes with climate change.

Additionally, SDMs assume that the magnitude and rate of climate change will be beyond the ability of species to adapt over multiple generations *in situ* (Pearson & Dawson 2003). Two factors will be important in determining whether species can evolve rapidly enough to keep pace with climate change: first, the amount of functional genetic variation within species; and second, the frequency of opportunities for intergenerational selection. For example, some species which have endured previous cycles of climate change may have sufficient adaptive variation in their genomes to survive future climate change (Hewitt & Nichols 2005). This may be particularly relevant to the CFR and SWAFR where a number of plant lineages may have persisted through Pleistocene climate oscillations (Byrne *et al.* 1999; Coates & Hamley 1999; Coates 2000; Coates *et al.* 2003; Linder 2003; Linder & Hardy 2004; Yates *et al.* 2007), but there are extenuating circumstances. For example, Midgley *et al.* (2005) argued that persistence through Pleistocene climates may not equip CFR species to deal with projected anthropogenic climate change because Pleistocene climates were very different. Glacial conditions dominated the Pleistocene especially in the last 400 ka BP. At a global scale, glacial climates have been interpreted as relatively dry and cold. However, there is some evidence that the west coast of South Africa and its adjacent interior experienced an increase in rainfall

out of phase with the rest of the world. If this is the case, then many species within the CFR may have spent the greater part of their evolutionary history under colder and wetter conditions, and predicted increases in temperature and declines in rainfall may be beyond their physiological limits and adaptive capacity (Midgley *et al.* 2005). In the SWAFR, palynological evidence for the Quaternary is scarce, however, on the current evidence the last glacial maximum (18 ka BP) was much drier across all of southern Australia. In addition, in contrast to the east coast of Australia the mid Holocene in south-west Western Australia may also have been drier than present (Pickett *et al.* 2004). Although there is no palynological evidence from south-west Western Australia, evidence from palynological studies in eastern Australia show that previous glacial periods during the Quaternary were drier and colder than present (Kershaw *et al.* 1994). How this will equip species to deal with warmer and drier conditions is unknown. Investigations of the physiological phenotypic plasticity, adaptive genetic variation and tolerable limits to changes in temperature and rainfall across species ranges in both regions should clarify whether they will be able to persist and adapt to climate change. Studies in the CFR indicate that projected increases in temperature may be beyond the physiological tolerances of a number of species (Musil *et al.* 2005).

How important will migration capacity be in the face of climate change?

Species that lack stress tolerance or the ability to evolve rapidly will need to migrate to keep pace with shifting suitable climate conditions. Migration capacity is an acknowledged source of uncertainty in the predictions of SDMs (Midgley *et al.* 2007). In reality the migration capacity of most species will be somewhere on a continuum between the two dispersal extremes (zero *vs.* universal) used by most models.

In the CFR and SWAFR, knowledge of migratory capacity, including the scale and frequency of dispersal events is rudimentary at best for most plant species, and this is an impediment to realistic estimates of dispersal in models. Generic mechanistic models of seed dispersal may provide a means of overcoming this problem (Schurr *et al.* 2005), and estimates of colonization ability derived from these models explain a substantial part of interspecific variation in current biogeographical distributions (Schurr *et al.* 2007). Some authors argue that the relative climatic and landscape stability and the extremely nutrient deficient soils of the CFR and SWAFR compared with northern hemisphere continents has selected for persistence traits rather than dispersal traits and cite the low prevalence of morphological mechanisms for long dispersal

as evidence (Hopper & Gioia 2004). However, recent research on long-distance seed dispersal indicates that seeds of most species are moved by multiple dispersal processes and that dispersal syndromes based on morphological classifications may reveal little about the mechanisms and frequency of long-distance dispersal (Higgins *et al.* 2003a). Recent investigations into seed dispersal in SWAFR have revealed that common generalist herbivores such as *Dromaius novaehollandiae* (emu) may disperse seeds over long distances regardless of apparent mechanisms for dispersal (Calviño-Cancela *et al.* 2006). A better understanding of dispersal may improve our capacity to predict the effects of climate change on species ranges, but long-distance dispersal as a rare event is difficult to study and better knowledge may only marginally narrow the confidence intervals of current rate of spread predictions (Higgins *et al.* 2003b).

The migratory capacity of a species also depends on opportunities for seed germination and seedling establishment, and many species only recruit seedlings following episodic events related to infrequent weather or disturbance. For example, in fire prone ecosystems such as those found in the CFR and SWAFR, recruitment of many species occurs predominantly in the first few years following a fire, and very rarely in inter-fire periods, and is affected by rainfall in those years (Bond & van Wilgen 1996, Keith *et al.* 2002). In the semi-arid and arid ecosystems cradling the two regions many species rely on infrequent years of high rainfall for recruitment (Milton 1995; Wiegand *et al.* 1995). A combination of poor dispersal and reliance on episodic recruitment opportunities could mean that many plant species are unable to track the expanding margins of their climate envelopes. For these species the full dispersal scenario used currently in SDMs is probably overly optimistic.

Migration capacity can be incorporated into SDMs in relatively simple ways by estimating a migration rate per unit of time based on the mode of dispersal (but see discussion above on dispersal syndromes) and opportunities for recruitment (e.g. fire) of the selected species (Williams *et al.* 2005; Fitzpatrick *et al.* 2008). More complex and realistic approaches would couple mechanistic models of seed dispersal with SDMs (Schurr *et al.* 2005; Thuiller *et al.* 2008). The extent to which migration capacity will improve predictions in SDMs may be in part dependent on the impacts that climate change is likely to have on species distributions. For species with ranges that are predicted to shift or increase in size, more realistic estimates of migration capacity should improve the accuracy of predictions. This may be particularly important for arid zone and weed species moving into the CRF and SWAFR. For species with ranges that are predicted to contract, inclusion of migration capacity may not substantially improve predictions unless their

habitat is patchily distributed in space (see below). In the CFR the extensive mountain ranges provide opportunities for species ranges to shift upwards. In the flat SWAFR, options are more limited and range contraction and fragmentation may be the most common response of plant species to climate change (Byrne 2007; Byrne *et al.* 2008; Fitzpatrick *et al.* 2008). For species for which range contraction is predicted, determining the location of refuges may be more important than better estimates of migration capacity.

Yet the migration capacity of a species is determined not only by its dispersal characteristics but also by the structure of the landscape the organisms lives in. For species which must migrate to survive climate change, habitat must be available where they are now, will be in the future and in the intervening areas they must traverse (Lewis 2006). Two factors that may be particularly relevant to modelling the migration capacity of plant species in the SWAFR and CFR are complex soil mosaics and habitat fragmentation. In both regions species distributions are strongly influenced by edaphic factors and complex soil mosaics affect regional patterns of diversity (Gibson *et al.* 2004; McKenzie *et al.* 2004; Rebelo *et al.* 2006). Species that have specialized morphology or physiology for growing on particular substrates that are patchily distributed may not be able to disperse to suitable habitat as climate changes because they are unable to grow on soils in intervening areas (Latimer *et al.* 2009). For many species past and continuing habitat destruction and fragmentation has created or will create significant barriers to dispersal (Midgley *et al.* 2005; Neilson *et al.* 2005; Bacles *et al.* 2006; Lewis 2006).

In the SWAFR the broad-scale conversion of native vegetation to agricultural land between the 300 and 600 mm isohyets has created a major barrier to migration across the region's climate gradient. In this area which encompasses c.75% of the SWAFR and covers 205 000 km², some 74% of the native vegetation has been cleared and the regional biodiversity is now restricted to isolated remnants of bushland surrounded by croplands (Hobbs & Saunders 1993; Yates & Hobbs 1997; McKenzie *et al.* 2004). In the CFR the extent of clearing and habitat fragmentation is not as great but none the less is an issue in some parts of the region (Kemper *et al.* 1999; Donaldson *et al.* 2002). Moreover, habitat transformation does not have to affect a large area to limit seed dispersal: for instance, roads may act as efficient dispersal barriers for the secondary wind dispersal of Cape Proteaceae (Schurr *et al.* 2005).

In the CFR and SWAFR habitat fragmentation can also affect the fecundity of species and opportunities for recruitment thereby further reducing species migration capacity (Donaldson *et al.* 2002; Hobbs & Yates 2003; Higgins *et al.* 2003c; Yates & Ladd 2005; Yates *et al.* 2007). In both regions but particularly the

SWAFR, regional analyses of the impacts of climate change on species distributions will need to include land-cover.

How important are micro-refuges for species persistence through climate change?

New evidence is emerging globally that species have persisted as isolated populations in micro-climatic refuges when regional climates were unsuitable (Moritz *et al.* 2000; Hewitt 2004; McGlone & Clark 2005; Byrne 2007; Byrne *et al.* 2008). A recent review of phylogeographic patterns in the Australian arid zone shows that as the climate became drier, many species contracted to dispersed refuges across the landscape (Byrne *et al.* 2008).

The scale of the environmental data which are used in bioclimatic models is likely to be too coarse to incorporate micro-refugia, the result being overly pessimistic predictions in extinction risk from climate change (Pearson 2006). Research to identify areas that will act as refuges as the climates become warmer and drier in the CFR and SWAFR will be particularly relevant. In both regions water gaining sites on and around the extensive systems of granite inselbergs may be particularly important. In the CFR seepage zones in the heavily metamorphosed and fractured sandstones in the Cape Fold belt will also be important.

CONCLUSIONS

Many factors contribute to uncertainty in predictions of species range changes using SDMs. Yet these models remain one of the few spatially explicit tools available for investigating the potential impacts of climate change, and are therefore attractive especially in regions such as the CFR and SWAFR where there are thousands of species that will be impacted. In both regions atlas data and large herbarium datasets are available now for modelling. Like all models, SDMs are simplified representations of reality, but this should not preclude their use in predicting the impacts of climate change. Advocates see the models as useful heuristic tools which do not provide a definitive answer, but rather give a sense of the nature and extent of range shifts that need to be accounted for when planning for climate change. We concur with this view and contend that even the simplest models may yield important insights. For example Fitzpatrick *et al.* (2008) found that including a simple estimate of migration capacity in SDMs did not significantly improve predictions because most species ranges were predicted to contract. This insight has at least two useful implications for adaptation; first further research effort may be best directed at identifying

refuges; and second that investing in corridors may be of little value for these species.

Modellers will undoubtedly continue to develop better parameterized and more realistic SDMs, with better estimates of uncertainty, as well as emphasizing models as a starting point in vulnerability assessments and paying more attention to validating and probing their predictions. Despite the large number of SDM studies forecasting the impacts of climate change on species distributions, attempts to validate the predictions are rare (but see Foden *et al.* 2007). Substantial gains could be made through targeted monitoring and experiments that seek to identify how populations will behave and establish the physiological thresholds of species across their ranges. It will be essential to empirically validate the predictions of models through monitoring and demographic studies of representative species (Abbott & le Maitre 2009). Spatial gradients in climate which serve as proxies for temporal climate change may provide a means for studying population dynamics and population viability under future climate scenarios, and allow for testing of SDM predictions. In both the SWAFR and CFR where there are strong temperature and rainfall gradients with a number of species spanning some part of the gradient, there is an opportunity to understand how their population and range dynamics will be affected by climate factors, particularly rainfall change, through demographic monitoring and transplant experiments along gradients. The recent investigation of population and range dynamics in the Namib Desert tree *Aloe dichotoma* coupled with species distribution modelling has yielded useful insights into what might be expected (Foden *et al.* 2007). However, this study could be extended to gain many more insights. Manipulative experiments that encompass the range in projected changes in climate and investigate physiological thresholds in species will also be important, especially in the SWAFR and CFR where the current locations of species may not reflect their climate tolerances.

Our review and others highlight the need for the development of more realistic dynamic SDMs that integrate disturbance, dynamic population processes, species interactions and transient climates (Crick 2004; Guisan & Thuiller 2005; Keith *et al.* 2008; Thuiller *et al.* 2008). The mega diverse floras of the SWAFR and the CFR continue to pose a challenge for biodiversity risk assessments. Some of the limitations of SDMs could be overcome with more ecologically relevant predictor variables, including summaries of extreme climate events and atmospheric CO₂. As models better integrate the array of processes that limit the distributions of species, the demands for detailed data on each species will increase and extensive model fitting/analyses to quantify the uncertainty of the projections will be required. It seems unlikely that the resources necessary for doing this will be available in

the near future in either the SWAFR or the CFR. One option will be to focus research effort on a small number of species for which there are already sound and extensive data. If results of these detailed studies can be related to attributes of the target species (such as functional or life-history traits, range size or population abundance), we may be able to generalize the detailed studies to a larger number of species. This is a perennial challenge in ecology and conservation biology, generalizing from the specific and one that is particularly relevant in biodiversity hotspots such as the CFR and SWAFR.

In addition while a new generation of more realistic dynamic SDMs will increase confidence in some areas, new sources of uncertainty will inevitably arise. For example integrating a mechanistic model of migration capacity with an SDM will introduce a new set of model uncertainties. It remains to be seen whether increased realism will result in increased accuracy. Another option is to develop models that predict climate effects on the distribution of community attributes rather than single-species distributions. In theoretical ecology, there is a strong interest in such meta-community models (e.g. Hubbell 2001), whereas in biodiversity risk assessment community approaches are far less developed than single-species approaches (as evidenced by the focus on single-species approaches in this review). For mega-diverse systems, however, risk assessment based on community models and resilience may be worthwhile in addition to the generalization of single-species projections.

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REFERENCES

- Abbott I. & Burrows N. (2003) *Fire in Ecosystems of South-West Western Australia: Impacts and Management*. Backhuys Publishers, Leiden.
- Abbott I. & le Maitre D. (2009) Monitoring the impacts of climate change on biodiversity – the challenge of mega diverse Mediterranean climate ecosystems. *Aust. Ecol.* DOI: 10.1111/j.1442-9993.2009.02053.x
- Ainsworth E. A. & Long S. P. (2005) What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO₂. *New Phytol.* **165**, 351–72.
- Araújo M. B. & Guisan A. (2006) Five or so challenges for species distribution modelling. *Journal of Biogeography*. **33**, 1677–88.
- Araújo M. B. & New M. (2006) Ensemble forecasting of species distributions. *TREE* **22**, 42–7.
- Araújo M. B., Pearson R. G., Thuiller W. & Erhard M. (2005a) Validation of species-climate impact models under climate change. *Glob. Change Biol.* **11**, 1504–13.
- Araújo M. B., Whittaker R. J., Ladle R. J. & Erhard M. (2005b) Reducing uncertainty in projections of extinction risk from climate change. *Global. Ecol. Biogeogr.* **14**, 529–38.
- Araújo M. B., Thuiller W. & Pearson R. G. (2006) Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography*. **33**, 1712–28.
- Austin M. P. (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecol. Model.* **157**, 101–18.
- Bates B. C., Hope P., Ryan B., Smith I. & Charles S. (2008) Key findings from the Indian Ocean Climate Initiative and their impact on policy development in Australia. *Climate Change* **89**, 339–54.
- Bacles C. F. E., Lowe A. J. & Ennos R. A. (2006) Effective seed dispersal across a fragmented landscape. *Nature* **311**, 628.
- Bakkenes M., Alkemade J. R. M., Ihle F., Leemans R. & Latour J. B. (2002) Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Glob. Change Biol.* **8**, 390–407.
- Beard J. S. (1990) *Plant Life of Western Australia*. Kangaroo Press, Kenhurst, NSW.
- Beaumont L. J. & Hughes L. (2002) Potential changes in the distributions of latitudinally restricted Australian butterfly species in response to climate change. *Glob. Change Biol.* **8**, 954–71.
- Beaumont L. J., Hughes L. & Poulsen M. (2005) Predicting species distributions: use of climatic parameters in BIOCLIM and its impact on predictions of species' current and future distributions. *Ecol. Model.* **10**, 250–68.
- Beaumont L. J., Pitman A. J., Poulsen M. & Hughes L. (2007) Where will species go? Incorporating new advances in climate modelling into projections of species distributions. *Glob. Change Biol.* **13**, 1368–85.
- Berry P. M., Dawson T. P., Harrison P. A. & Pearson R. G. (2002) Modelling potential impacts of climate change on the bioclimatic envelope of species in Britain and Ireland. *Global. Ecol. Biogeogr.* **11**, 453–62.
- Bomhard B., Richardson D. M., Donaldson J. S. *et al.* (2005) Potential impacts of future land use and climate change on the Red List status of the Proteaceae in the Cape Floristic Region, South Africa. *Glob. Change Biol.* **11**, 1452–68.
- Bond W. J. & Midgley J. J. (2001) Ecology of sprouting in woody plants: the persistence niche. *TREE* **16**, 45–51.
- Bond W. J. & van Wilgen B. W. (1996) *Fire and Plants*. Chapman and Hall, London.
- Bond W. J., Woodward F. I. & Midgley G. F. (2004) The global distribution of ecosystems in a world without fire. *New Phytol.* **165**, 525–38.
- Botkin D. B., Saxe H., Sobel M. J. & Stockwell D. R. B. (2007) Forecasting the effects of global warming on biodiversity. *BioScience* **57**, 227–36.
- Bowman D. M. J. S. (2000) *Australian Rainforests: Islands of Green in A Land of Fire*. Cambridge University Press, Cambridge.
- Box E. O., Crumpacker D. W. & Hardin E. D. (1993) A climatic model for the location of plant species in Florida, USA. *Journal of Biogeography*. **20**, 629–44.
- Box E. O., Crumpacker D. W. & Hardin E. D. (1999) Predicted effects of climatic change on distribution of ecologically important native tree and shrub species in Florida. *Clim. Change* **41**, 213–48.

- Bradley K. L. & Pregitzer K. S. (2007) Ecosystem assembly and terrestrial carbon balance under elevated CO₂. *TREE* **22**, 538–47.
- Bradshaw A. D. (1972) Some of the evolutionary consequences of being a plant. *Evol. Biol.* **5**, 25–47.
- Bradstock R. A., Williams J. E. & Gill M. A. (2002) *Flammable Australia: The Fire Regimes and Biodiversity of A Continent*. Cambridge University Press, Cambridge.
- Brereton R., Bennett S. & Mansergh I. (1995) Enhanced greenhouse climate change and its potential effect on selected fauna of south-eastern Australia: a trend analysis. *Biol. Conserv.* **72**, 339–54.
- Breshears D. D., Cobb N. S., Rich P. M. *et al.* (2005) Regional vegetation die-off in response to global-change-type drought. *Proc. Natl Acad. Sci. USA* **102**, 15144–8.
- Broennimann O., Thuiller W., Hughes G., Midgley G. F., Alkemade J. R. M. & Guisan A. (2006) Do geographic distribution, niche property and life form explain plants' vulnerability to global change? *Glob. Change Biol.* **12**, 1079–93.
- Brown J. H., Valone T. J. & Curtin C. G. (1997) Reorganization of an arid ecosystem in response to recent climate change. *Proc. Natl Acad. Sci. USA* **94**, 9729–33.
- Byrne M. (2007) Phylogeography provides an evolutionary context for the conservation of a diverse and ancient flora. *Aust. J. Bot.* **55**, 316–25.
- Byrne M., Macdonald B. & Coates D. (1999) Divergence in the chloroplast genome and nuclear rDNA of the rare Western Australian plant *Lambertia orbifolia* Gardner (Proteaceae). *Mol. Ecol.* **8**, 1789–96.
- Byrne M., Yeates D. K., Joseph L. *et al.* (2008) Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota. *Mol. Ecol.* **17**, 4398–417.
- Cai W. & Cowan T. (2006) SAM and regional rainfall in IPCC AR4 models: Can anthropogenic forcing account for south-west Western Australian winter rainfall reduction. *Geophys. Res. Lett.* **33**, L24708.
- Calviño-Cancela M., Dunn R. R., van Etten E. & Lamont B. B. (2006) Emus as non-standard seed dispersers and their potential for long-distance dispersal. *Ecography* **29**, 632–40.
- Charles S. P., Bari M. A., Kitsios A. & Bates B. C. (2007) Effect of GCM bias on downscaled precipitation and runoff projections for the Serpentine Catchment, Western Australia. *Int. J. Climatol.* **27**, 1673–90.
- Coates D. J. (2000) Defining conservation units in a rich and fragmented flora: implications for the management of genetic resources and evolutionary processes in south-west Western Australian plants. *Aust. J. Bot.* **48**, 329–39.
- Coates D. J. & Hamley V. L. (1999) Genetic divergence and the mating system in the endangered and geographically restricted species *Lambertia orbifolia* Gardner (Proteaceae). *Heredity* **83**, 418–27.
- Coates D. J., Carstairs S. & Hamley V. L. (2003) Evolutionary patterns and genetic structure in localized and widespread species in the *Stylidium caricifolium* complex (Stylidiaceae). *Am. J. Bot.* **90**, 997–1008.
- Connell J. H. (1961) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* **42**, 710–32.
- Cowling R. M., Witkowski E. T. F., Milewski A. V. & Newbey K. R. (1994) Taxonomic, edaphic and biological aspects on narrow plant endemism on matched sites in Mediterranean South Africa and Australia. *J. Biogeogr.* **22**, 651–64.
- Cowling R. M., Rundel P. W., Lamont B. B., Arroyo M. K. & Arianoutsou M. (1996) Plant diversity in Mediterranean-climate regions. *TREE* **11**, 362–6.
- Cowling R. M., Ojeda F., Lamont B. B., Rundel P. W. & Lechmere-Oertel R. (2005) Rainfall reliability, a neglected factor in explaining convergence and divergence in plant traits in fire-prone mediterranean-climate ecosystems. *Global. Ecol. Biogeogr.* **14**, 509–19.
- Crick H. Q. P. (2004) The impact of climate change on birds. *Ibis* **146**, 48–56.
- Crucifix M., Betts R. A. & Hewitt C. D. (2005) Pre-industrial-potential and Last Glacial Maximum global vegetation simulated with a coupled climate-biosphere model: diagnosis of bioclimatic relationships. *Glob. Planet. Change* **45**, 295–312.
- Crumpacker D. W., Box E. O. & Hardin E. D. (2001) Implications of climatic warming for conservation of native trees and shrubs in Florida. *Conserv. Biol.* **15**, 1008–20.
- CSIRO (2007) Climate Change in Australia. Technical Report 2007. CSIRO, Australian Bureau of Meteorology, Australia.
- Davis M. B. & Shaw R. G. (2001) Range shifts and adaptive responses to Quaternary climate change. *Science* **292**, 673–9.
- Davis A. J., Jenkinson L. S., Lawton J. L., Shorrocks B. & Wood S. (1998) Making mistakes when predicting shifts in species range in response to global warming. *Nature* **391**, 783–6.
- Dodson J. R. & Macphail N. K. (2004) Palynological evidence for aridity events and vegetation change during the middle Pliocene, a warm period in southwestern Australia. *Glob. Planet. Change* **41**, 285–307.
- Donaldson J., Nänni I., Zachariades C. & Kemper J. (2002) Effects of habitat fragmentation on pollinator diversity and plant reproductive success in Renosterveld shrublands of South Africa. *Conserv. Biol.* **16**, 1267–76.
- Elith J., Graham C. H. & Anderson R. P. *et al.* (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29**, 129–51.
- Fischlin A., Midgley G. F. & Price J. T. *et al.* (2007) Ecosystems, their properties, goods and services. In: *Climate Change 2006: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds M. L. Parry, O. F. Canziani, J. P. Palutikof, P. J. van der Linden & C. E. Hanson) pp. 211–72. Cambridge University Press, Cambridge.
- Fitzpatrick M. C., Gove A. D., Sanders N. J. & Dunn R. R. (2008) Climate change, plant migration, and range collapse in a global biodiversity hotspot: the *Banksia* (Proteaceae) of Western Australia. *Glob. Change Biol.* **14**, 1–16.
- Foden W., Midgley G. F., Bond W. J. *et al.* (2007) A changing climate is eroding the geographical range of the Namib Desert tree *Aloe* through population declines and dispersal lags. *Divers. Distrib.* **13**, 645–53.
- Gaston K. J. (2003) *The Structure and Dynamics of Geographic Ranges*. Oxford University Press, Oxford, UK.
- Gelfand A. E., Silander J. A., Wu S. *et al.* (2006) Explaining species distribution patterns through hierarchical modeling. *Bayesian Anal.* **1**, 41–92.
- Gibson N., Keighery G. J., Lyons M. N. & Webb A. (2004) Terrestrial flora and vegetation of the Western Australian wheatbelt. *Rec. West. Aust. Mus. Suppl.* **67**, 139–89.
- Gioia P. & Pigott P. (2002) Biodiversity assessment: a case study in predicting richness from the potential distributions of plant species in the forest of south-western Australia. *J. Biogeogr.* **27**, 1065–78.
- Groom P. K. (2004) Rooting depth and plant water relations explain species distribution patterns within a sandplain landscape. *Funct. Plant Biol.* **31**, 423–8.

- Guisan A. & Thuiller W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.* **8**, 993–1009.
- Guisan A. & Zimmermann N. E. (2000) Predictive habitat distribution models in ecology. *Ecol. Model.* **135**, 147–86.
- Hampe H. (2004) Bioclimate envelope models: what they detect and what they hide. *Global. Ecol. Biogeogr.* **13**, 469–70.
- Hannah L., Midgley G. F., Lovejoy T. *et al.* (2002a) Conservation of biodiversity in a changing climate. *Conserv. Biol.* **16**, 264–8.
- Hannah L., Midgley G. F. & Millar D. (2002b) Climate change-integrated conservation strategies. *Global. Ecol. Biogeogr.* **11**, 485–95.
- Heikkinen R. K., Luoto M., Araujo M. B., Virkkala R., Thuiller W. & Sykes M. T. (2006) Methods and uncertainties in bioclimatic envelope modelling under climate change. *Prog. Phys. Geog.* **30**, 751–77.
- Hewitson B. C. & Crane R. G. (2006) Consensus between GCM climate change projections with empirical downscaling: precipitation downscaling over South Africa. *Int. J. Climatol.* **26**, 1315–37.
- Hewitt G. M. (2004) Genetic consequences of climatic oscillations in the Quaternary. *Philosophical Transactions of the Royal Society of London Series B* **359**, 183–95.
- Hewitt G. M. & Nichols R. A. (2005) Genetic and evolutionary impacts of climate change. In: *Climate Change and Biodiversity* (eds T. E. Lovejoy & L. Hannah) pp. 176–92. Yale University Press, New Haven & London.
- Higgins S. I., Nathan R. & Cain M. L. (2003a) Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? *Ecology* **84**, 1945–56.
- Higgins S. I., Clark J. S., Nathan R. *et al.* (2003b) Forecasting plant migration rates: managing uncertainty for risk assessment. *J. Ecol.* **91**, 341–7.
- Higgins S. I., Lavorel S. & Revilla E. (2003c) Estimating plant migration rates under habitat loss and fragmentation. *Oikos* **101**, 354–66.
- Higgins S. I., Flores O. & Schurr F. M. (2008) Costs of persistence and the spread of competing seeders and sprouters. *J. Ecol.* **96**, 679–86.
- Hill J., Thomas C. D. & Huntley B. (1999) Climate and habitat availability determine 20th century changes in butterfly's range margin. *Proc. R. Soc. Lond. B. Biol. Sci.* **266**, 1197–206.
- Hill J., Collingham Y. C., Thomas C. D. *et al.* (2001) Impacts of landscape structure on butterfly range expansion. *Ecol. Lett.* **4**, 313–21.
- Hill J., Thomas C. D., Fox R. *et al.* (2002) Responses of butterflies to twentieth century climate warmings: implications for future ranges. *Proc. R. Soc. Lond. B. Biol. Sci.* **269**, 2163–71.
- Hobbs R. J. & Saunders D. A. (1993) *Re-Integrating Fragmented Landscapes. Towards Sustainable Production and Nature Conservation*. Springer, New York.
- Hobbs R. J. & Yates C. J. (2003) Turner Review No. 7 Impacts of ecosystem fragmentation on plant populations: generalizing the idiosyncratic. *Aust. J. Bot.* **51**, 471–88.
- Hope P. K., Drosowsky W. & Nicholls N. (2006) Shifts in the synoptic systems influencing southwest Western Australia. *Clim. Dyn.* **26**, 751–64.
- Hopper S. D. & Gioia P. (2004) The Southwest Australian Floristic Region: evolution and conservation of a global hotspot of biodiversity. *Annu. Rev. Ecol. Syst.* **35**, 623–50.
- Hopkins A. J. M. & Griffin E. A. (1984) Floristic patterns. In: *Kwongan – Plant Life of the Sandplain* (eds J. S. Pate & J. S. Beard) pp. 69–83. University of Western Australia Press, Nedlands.
- Hubbell S. P. (2001) *The United Theory of Biodiversity and Biogeography*. Princeton University Press, New Jersey.
- Hughes L., Cawsey E. M. & Westoby M. (1996) Climatic range sizes of *Eucalyptus* species in relation to future climate change. *Global. Ecol. Biogeogr. Lett.* **5**, 23–9.
- Huntley B., Collingham Y. C., Green R. E., Hilton G. M., Rahbek C. & Willis S. G. (2006) Potential impacts of climatic change upon geographical distributions of birds. *Ibis* **148**, 8–28.
- Hutchinson G. E. (1957) Concluding remarks. *Cold Spring Harb. Symp. Quant. Biol.* **22**, 145–59.
- IPCC (2000) Emissions Scenarios. In: *Special Report of the Intergovernmental Panel on Climate Change* (eds N. Nakicenovic & R. Swart) pp. 570. Cambridge University Press, Cambridge.
- IPCC (2007) Summary for policy makers. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds S. Solomon, D. Qin, M. Manning *et al.*) pp. 1–18. Cambridge University Press, Cambridge and New York.
- Kearney M., Phillips B. L., Tracy C. R., Christian K. A., Betts G. & Porter W. P. (2008) Modelling species distributions without using species distributions: the cane toad in Australia under current and future climates. *Ecography* in press, doi: 10.1111/j.0906-7590.2008.05457.x.
- Keith D. A., McCaw W. L. & Whelan R. J. (2002) Fire regimes in Australian heathlands and their effects on plants and animals. In: *Flammable Australia: The Fire Regimes and Biodiversity of A Continent* (eds R. A. Bradstock, J. E. Williams & A. M. Gill) pp. 199–237. Cambridge University Press, Cambridge.
- Keith D. A., Akçakaya H. R., Thuiller W. *et al.* (2008) Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biol. Lett.* doi: 10.1098/rsbl.2008.0049.
- Kemper J., Cowling R. M. & Richardson D. M. (1999) Fragmentation of South African renosterveld shrublands: effects on plant community structure and conservation implications. *Biol. Conserv.* **90**, 103–11.
- Kershaw A. P., Martin H. A. & Mason J. R. C. M. (1994) The neogene: a period of transition. In: *The History of the Australian Vegetation: Cretaceous to Recent* (ed. R. S. Hill) pp. 299–327. Cambridge University Press, Cambridge.
- Körner C. (2003) Ecological impacts of atmospheric CO₂ enrichment on terrestrial ecosystems. *Phil. Trans. R. Soc. Lond. A.* **361**, 2023–41.
- Krebs C. J. (2001) *Ecology: The Experimental Analysis of Distribution and Abundance*, 5th edn. Benjamin Cummings, San Francisco.
- Latimer A. M., Silander J. A. & Cowling R. M. (2005) Neutral ecological theory reveals isolation and rapid speciation in a biodiversity hotspot. *Science* **309**, 1722–5.
- Latimer A. M., Silander J. A., Rebelo A. G. & Midgley G. F. (2009) Experimental biogeography: the role of environmental gradients in the high geographic diversity of Cape Proteaceae. *Oecologia* **160**, 151–62.
- Lawler J. L., White D., Neilson R. P. & Blaustein A. R. (2006) Predicting climate-induced range shifts: model differences and model reliability. *Glob. Change Biol.* **12**, 1568–84.
- Leathwick J. R. (1998) Are New Zealand's Nothofagus species in equilibrium with their environment? *J. Veg. Sci.* **9**, 719–32.

- Leathwick J. R. & Austin M. P. (2001) Competitive interactions between tree species in New Zealand's old-growth indigenous forests. *Ecology* **82**, 2560–73.
- Leathwick J. R., Whitehead D. & Mcleod M. (1996) Predicting changes in the composition of New Zealand's indigenous forests in response to global warming: a modelling approach. *Environ. Softw.* **11**, 81–90.
- Lewis O. T. (2006) Climate change, species-area curves and the extinction crisis. *Phil. Trans. R. Soc. Lond. B. Biol. Sci.* **361**, 163–71.
- Linder H. P. (2003) The radiation of the Cape flora, southern Africa. *Biol. Rev.* **78**, 597–638.
- Linder H. P. & Hardy R. C. (2004) Evolution of the species-rich Cape flora. *Phil. Trans. R. Soc. Lond. B. Biol. Sci.* **359**, 1623–32.
- McDougall K. L. (1996) Vegetation patterns in the northern jarrah forest of Western Australia in relation to dieback history and the current distribution of *Phytophthora cinnamomi*. PhD Thesis, Murdoch University, Western Australia.
- MacKellar N. C., Hewitson B. C. & Tadross M. A. (2007) Namaqualand's climate: recent historical changes and future scenarios. *J. Arid Environ.* **70**, 604–14.
- McKenzie N. L., Gibson N., Keighery G. J. & Rolfe J. K. (2004) Patterns in the biodiversity of terrestrial environments in the Western Australian wheatbelt. *Rec. WA. Mus. Suppl.* **67**, 293–355.
- Maher K. A. (2007) Encroachment of sandplain heathland (Kwongan) by *Allocasuarina huegeliana* in the Western Australian wheatbelt: the role of herbivores, fire and other factors. PhD Thesis, Murdoch University, Western Australia.
- Manders P. T. & Richardson D. M. (1992) Colonisation of Cape Fynbos communities by forest species. *For. Ecol. Manage.* **48**, 277–93.
- Martínez-Meyer E. & Peterson A. T. (2006) Conservation of ecological niche characteristics in North American plant species over the Pleistocene-to-recent transition. *J. Biogeogr.* **33**, 1779–89.
- McGlone M. & Clark J. (2005) Microrefugia and macro ecology. In: *Climate Change and Biodiversity* (eds T. E. Lovejoy & L. Hannah) pp. 157–9. Yale University Press, New Haven & London.
- Meynecke J. O. (2004) Effects of global climate change on geographic distributions of vertebrates in North Queensland. *Ecol. Model.* **174**, 347–57.
- Midgley G. F., Hannah L., Millar D., Rutherford M. C. & Powrie L. W. (2002) Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Global. Ecol. Biogeogr.* **11**, 445–51.
- Midgley G. F., Hannah L., Millar D., Thuiller W. & Booth A. (2003) Developing regional and species-level assessments of climate change impacts on biodiversity in the Cape Floristic Region. *Biol. Conserv.* **112**, 87–97.
- Midgley G. F., Reeves G. & Klak C. (2005) Late Tertiary and Quaternary climate change and centres of endemism in the southern African flora. In: *Phylogeny and Conservation* (eds A. Purvis, J. L. Gittleman & T. Brooks) pp. 230–42. Cambridge University Press, Cambridge.
- Midgley G. F., Thuiller W. & Higgins S. I. (2007) Plant species migration as a key uncertainty in predicting future impacts of climate change on ecosystems: progress and challenges. In: *Terrestrial Ecosystems in A Changing World* (eds J. G. Canadell, D. E. Pataki & L. F. Pitelka) pp. 129–37. Springer, Berlin.
- Milton S. J. (1995) Spatial and temporal patterns in the emergence and survival of seedlings in arid Karoo shrubland. *J. Appl. Ecol.* **32**, 145–56.
- Moritz C., Patton J. L., Schneider C. J. & Smith T. B. (2000) Diversification of rainforest faunas: an integrated molecular approach. *Annual Review of Ecology and Systematics* **31**, 533–63.
- Mucina L., Jürgens N., le Roux A. *et al.* (2006) Succulent Karoo biome. In: *The Vegetation of South Africa, Lesotho and Swaziland* (eds L. Mucina & M. C. Rutherford) Strelitzia 19, pp. 221–323. South African National Biodiversity Institute, Pretoria.
- Mucina L. & Rutherford M. C. (eds) (2006) The vegetation of South Africa, Lesotho and Swaziland. *Strelitzia* **19**. South African National Biodiversity Institute.
- Musil C. F., Schmiedel U. & Midgley G. F. (2005) Lethal effects of experimental warming approximating a future climate scenario on Southern African quartz-field succulents: a pilot study. *New Phytol.* **165**, 539–47.
- Myers N., Mittermeier R. A., Mittermeier C. G., da Fonseca G. A. B. & Kent J. (2000) Biodiversity hot spots for conservation priorities. *Nature* **403**, 803–8.
- Neilson R. P., Pitelka L. F., Solomon A. F. *et al.* (2005) Forecasting regional to global plant migration in response to climate change. *BioScience* **55**, 749–59.
- Niklaus P. A., Spinnler D. & Körner C. (1998) Soil moisture dynamics of calcareous grassland under elevated CO₂. *Oecologia* **117**, 201–8.
- Parmesan C. (2006) Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* **37**, 637–9.
- Pearce J. L. & Boyce M. S. (2006) Modelling distribution and abundance with presence-only data. *J. Appl. Ecol.* **43**, 405–12.
- Peterson A. T. (2003) Projected climate change effects on Rocky Mountain and Great Plain birds: generalities on biodiversity consequences. *Glob. Change Biol.* **9**, 647–55.
- Peterson A. T., Ball L. G. & Cohoon K. P. (2002a) Predicting distributions of Mexican birds using ecological niche modelling methods. *Ibis* **144**, 27–32.
- Peterson A. T., Ortega-Huerta M. A., Bartley J. *et al.* (2002b) Future projections for Mexican faunas under global climate change scenarios. *Nature* **416**, 626–9.
- Peterson A. T., Martínez-Meyer E., González Salazar C. & Hall P. W. (2004) Modelled climate change effects on distributions of Canadian butterfly species. *Can. J. Zool.* **82**, 851–8.
- Peterson A. T., Tian H., Martínez-Meyer E., Soberon J., Sanchez-Cordero V. & Huntley B. (2005) Modeling distributional shifts of individual species and biomes. In: *Climate Change and Biodiversity* (eds T. E. Lovejoy & L. Hannah) pp. 211–28. Yale University Press, New Haven & London.
- Pearson R. G. (2006) Climate change and the migration capacity of species. *TREE* **21**, 111–13.
- Pearson R. G. & Dawson T. P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful. *Global. Ecol. Biogeogr.* **12**, 361–71.
- Pearson R. G. & Dawson T. P. (2004) Bioclimate models what they detect and what they hide – response to H (2004). *Global. Ecol. Biogeogr.* **13**, 469–70.
- Pearson R. G., Thuiller W., Araújo M. B. *et al.* (2006) Model-based uncertainty in species range prediction. *J. Biogeogr.* **33**, 1704–11.
- Perkins S. E., Pitman A. J., Holbrook N. J. & McAneney J. (2007) Evaluation of climate models' simulated daily maximum temperature, minimum temperature, and precipitation over Australia using probability density functions. *J. Clim.* **20**, 4356–76.
- Pickett S. E., Pitman A. J., Holbrook N. J. & McAneney J. (2004) Evaluation of the AR4 model's simulated daily maximum

- temperature, minimum temperature, and precipitation over Australia using probability density functions. *J. Clim.* **20**, 4356–76.
- Poot P. & Lambers H. (2008) Shallow-soil endemics: adaptive advantages and constraints of a specialized root-system morphology. *New Phytol.* **178**, 371–81.
- Randall D. A., Wood R. A., Bony S. *et al.* (2007) Climate models and their evaluation. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group 1 to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds S. Solomon, D. Qin, M. Manning *et al.*) pp. 589–662. Cambridge University Press, Cambridge and New York.
- Raupach M. R., Marland G., Ciais P., Le Quéré C., Canadell J. G., Klepper G. & Field C. B. (2007) Global and regional drivers of accelerating CO₂ emissions. *Proc. Nat. Acad. Sci.* **104**, 10288–10293.
- Rebello A. G., Boucher C., Helme N., Mucina L. & Rutherford M. C. (2006) Fynbos biome. In: *The Vegetation of South Africa, Lesotho and Swaziland* (eds L. Mucina & M. C. Rutherford) Strelitzia 19, pp. 220–99. South African National Biodiversity Institute, Pretoria.
- Rosenzweig C., Karoly D., Vicarellio M. *et al.* (2008) Attributing physical and biological impacts to anthropogenic climate change. *Nature* **453**, 353–7.
- Schurr F. M., Bond W. J., Midgley G. F. & Higgins S. I. (2005) A mechanistic model for secondary seed dispersal by wind and its experimental validation. *J. Ecol.* **93**, 1017–28.
- Schurr F. M., Midgley G. F., Rebello A. G., Reeves G., Poschod P. & Higgins S. I. (2007) Colonization and persistence ability explain the extent to which plant species fill their potential range. *Global. Ecol. Biogeogr.* **16**, 449–59.
- Shafer S. L., Bartlein P. J. & Thompson R. S. (2001) Potential changes in the distributions of western North America tree and shrub taxa under future climate scenarios. *Ecosystems* **4**, 200–15.
- Shearer B. L., Crane C. E. & Cochrane A. (2004) Quantification of the susceptibility of the native flora of the South-West Province, Western Australia to *Phytophthora cinnamomi*. *Aust. J. Bot.* **52**, 435–43.
- Shmida A. & Ellner S. (1984) Coexistence of plant species with similar niches. *Vegetatio* **58**, 29–55.
- Skov F. & Svenning J. C. (2004) Potential impact of climatic change on the distribution of forest herbs in Europe. *Ecography* **27**, 366–80.
- Spinnler D., Egli P. & Körner C. (2002) Four-year growth dynamics of beech-spruce model ecosystems under CO₂ enrichment on two different forest soils. *Trees: Struct. Funct.* **16**, 423–36.
- Sutherland W. J. (2006) Predicting the ecological consequences of environmental change: a review of the methods. *J. Appl. Ecol.* **43**, 599–16.
- Suttle K. B., Thomsen M. A. & Power M. E. (2007) Species interactions reverse grassland responses to changing climate. *Science* **315**, 640–2.
- Svenning J. C. & Skov F. (2007) Could the tree diversity pattern in Europe be generated by post glacial dispersal limitation. *Ecol. Lett.* **10**, 453–60.
- Thomas C. D., Cameron A., Green R. E. *et al.* (2004) Extinction risk from climate change. *Nature* **427**, 145–8.
- Thuiller W. (2003) BIOMOD – optimizing predictions of species distributions and projecting potential future shifts under global change. *Glob. Change Biol.* **9**, 1353–62.
- Thuiller W. (2004) Patterns and uncertainties of species' range shifts under climate change. *Glob. Change Biol.* **10**, 2020–7.
- Thuiller W., Lavorel S., Araujo M. B., Sykes M. T. & Prentice I. C. (2005) Climate change threats to plant diversity in Europe. *Proc. Natl Acad. Sci. USA* **102**, 8245–50.
- Thuiller W., Broennimann O., Hughes G., Alkemade J. R. M., Midgley G. F. & Corsi F. (2006a) Vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions. *Glob. Change Biol.* **12**, 424–40.
- Thuiller W., Midgley G. F., Hughes G. *et al.* (2006b) Endemic species and ecosystem sensitivity to climate change in Namibia. *Glob. Change Biol.* **12**, 759–76.
- Thuiller W., Albert C., Araújo M. B. *et al.* (2008) Predicting global change impacts on plant species' distributions: future challenges. *Perspect. Plant Ecol. Evol. Syst.* **9**, 137–52.
- Ward S. J. E., Midgley G. F., Jones M. H. & Curtis P. S. (1999) Responses of wild C4 and C3 grass (Poaceae) species to elevated atmospheric CO₂ concentration: a meta-analytic test of current theories and perceptions. *Glob. Change Biol.* **5**, 723–41.
- Wiegand T., Milton S. J. & Wissel C. (1995) A simulation model for a shrub ecosystem in the semiarid Karoo, South Africa. *Ecology* **76**, 2205–21.
- Wikle C. K. (2003) Hierarchical Bayesian models for predicting the spread of ecological processes. *Ecology* **84**, 1382–94.
- Williams P., Hannah L., Anelman S. *et al.* (2005) Planning for climate change: identifying minimum-dispersal corridors for the Cape Proteaceae. *Conserv. Biol.* **19**, 1063–74.
- Williams S. E., Bolitho E. E. & Fox S. (2003) Climate change in Australian tropical rainforests: an impending environmental catastrophe. *Proc. R. Soc. Lond. B. Sci.* **270**, 1887–92.
- Witkowski E. T. F. & Lamont B. B. (2006) Resilience of two *Banksia* species to global change: comparing results of climate modelling, demographic and translocation studies. *Int. J. Biodivers. Sci. Manage.* **2**, 59–72.
- Yates C. J. & Hobbs R. J. (1997) Temperate eucalypt woodlands: a review of their status, processes threatening their persistence and techniques for restoration. *Aust. J. Bot.* **45**, 949–73.
- Yates C. J. & Ladd P. G. (2005) Relative importance of reproductive biology and establishment ecology for persistence of a rare shrub in a fragmented landscape. *Conserv. Biol.* **19**, 239–49.
- Yates C. J., Abbott I., Hopper S. D. & Coates D. J. (2003) Fire as determinant of rarity in the south-west Australian global biodiversity hotspot. In: *Fire in Ecosystems of South-West Western Australia: Impacts and Management* (eds I. Abbott & N. Burrows) pp. 395–420. Backhuys Publishers, Leiden.
- Yates C. J., Ladd P. G., Coates D. J. & McArthur S. (2007) Hierarchies of cause: understanding rarity in an endemic shrub *Verticordia staminosa* (Myrtaceae) with a highly restricted distribution. *Aust. J. Bot.* **55**, 194–205.