A Journal of Conservation Biogeography

Diversity and Distributions

BIODIVERSITY VIEWPOINT

Moving beyond static species distribution models in support of conservation biogeography

Janet Franklin

School of Geographical Sciences and Urban Planning and School of Life Sciences, Arizona State University, Tempe, AZ, USA

ABSTRACT

Aim To demonstrate that multi-modelling methods have effectively been used to combine static species distribution models (SDM), predicting the geographical pattern of suitable habitat, with dynamic landscape and population models to forecast the impacts of environmental change on species' status, an important goal of conservation biogeography.

Methods Three approaches were considered: (1) incorporating models of species migration to understand the ability of a species to occupy suitable habitat in new locations; (2) linking models of landscape disturbance and succession to models of habitat suitability; and (3) fully linking models of habitat suitability, habitat dynamics and spatially explicit population dynamics.

Results Linking species–environment relationships, landscape dynamics and population dynamics in a multi-modelling framework allows the combined impacts of climate change (affecting species distribution and vital rates) and land cover dynamics (land use change, altered disturbance regimes) on species to be predicted. This approach is only feasible if the life history parameters and habitat requirements of the species are well understood.

Main conclusions Forecasts of the impacts of global change on species may be improved by considering multiple causes. A range of methods are available to address the interactions of changing habitat suitability, habitat dynamics and population response that vary in their complexity, realism and data requirements.

Keywords

Climate change, disturbance, landscape dynamics, metapopulation model, species distribution model, species migration.

Correspondence: Janet Franklin, School of Geographical Sciences and Urban Planning, Arizona State University P.O. Box 875302, Tempe, AZ 85287-5302, USA.
E-mail: Janet.Franklin@asu.edu

INTRODUCTION

Species distribution modelling (SDM) has exploded in recent years in the literature and in practice (Scott *et al.*, 2002; Guisan *et al.*, 2006; Elith & Leathwick, 2009; Franklin, 2009). SDM extrapolates species location data in space based on correlations of species occurrence with environmental variables thought to influence habitat suitability. The modelling framework can be a statistical (in the broadest possible sense) or rule-based model, and a spatially explicit prediction of species' distribution based on SDM results in a predictive map (Franklin, 1995). The modelling process can be quite complex in terms of the size of the datasets involved, the geographical extent they represent and the decisions that must be made about data quality, sample design, assembly and derivation of mapped environmental predictors, modelling methods, model parameterization and selection, assessment of model

performance and evaluation of spatial predictions (Wintle *et al.*, 2005; Elith & Leathwick, 2009; Franklin, 2009). Nonetheless, these are static, correlative models that rely on the assumptions that species location data used for modelling are representative of its true distribution, that observed species distributions are in equilibrium with environmental factors that limit those distributions, and that the correct environmental predictors have been included in the model (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005).

Advances in conservation biogeography (sensu Whittaker *et al.*, 2005) should support conservation practice though improved methods for reserve design, ecological restoration, invasive species management, species reintroductions and predicting the potential impacts of global environmental change on biogeographical patterns (Richardson & Whittaker, 2010). Species distribution modelling has been deployed in support of each of these worthy practices (Franklin, 2009). And

yet, SDM is also strongly criticized for being limited in its ability to project species patterns over time and space into 'non-analog' environments, that is, novel combinations of environmental factors (Pearson *et al.*, 2006), specifically because it is correlative and does not incorporate dynamic ecological processes.

The static approach used in SDM is particularly effective at spatial interpolation, filling in the geographical gaps in species distributions known only from sparse observations available from biological surveys and natural history collections. However, SDM is increasingly used for spatio-temporal extrapolation, predicting species distributions in a new place or time. Notably, SDM is used to predict the impacts of anthropogenic climate change, land use change and other dynamic processes on biotic distributions (Pearson *et al.*, 2004; Thomas *et al.*, 2004) and to predict the risk of spread of invasive species, including pathogens, in new places (Peterson, 2003; Kueppers *et al.*, 2005; Richardson & Thuiller, 2007; van Wilgen *et al.*, 2009). Because of the limitations of this correlative approach, the results have sometimes been controversial (Thuiller *et al.*, 2004a; Akçakaya *et al.*, 2006; Carmel & Flather, 2006; Kueppers *et al.*, 2006; Botkin *et al.*, 2007) and have even been satirized (Lozier *et al.*, 2009). Specifically, when applying models to new places (Randin *et al.*, 2006) or time periods (with changed climate and land cover), novel combinations of climatic and other environmental factors – those without contemporary analogues – may occur in the future, as they have in the past (Williams & Jackson, 2007). This situation is particularly confounding to correlative models (e.g. Thuiller *et al.*, 2004b; Guisan *et al.*, 2006). Further, rigorous validation of models predicting changing species distributions in response to climate change is challenging and rarely done (Araújo *et al.*, 2005).

Many authors have urged that to meet the needs of conservation biogeography, we need to move beyond static SDM predictions to incorporate key dynamic processes determining species distributions (Guisan & Thuiller, 2005; Araújo & Guisan, 2006; Heikkinen *et al.*, 2006; Thuiller *et al.*, 2008; Zurrell *et al.*, 2009). I added my voice to this recommendation in the tenth and final chapter of my recently completed book on species distribution modelling (Franklin, 2009). Therefore, I am grateful for the timely opportunity to contribute this essay, an eleventh chapter of sorts (I will not say 'chapter eleven' which has a negative connotation in American financial slang), highlighting some excellent examples of promising approaches to this problem that have already been developed and that I hope will become more widely adopted. This is by no means a comprehensive review, but rather I hope to show that linking SDMs to process-based models of species dynamics has already been demonstrated to be feasible and informative.

Guisan & Thuiller (2005) suggested a modelling framework whereby SDMs based on multiscale environmental variables can predict the realized distribution of a species by including not only broad-scale climatic factors limiting species ranges, but also finer scale factors related to distribution of required resources, barriers to dispersal, and risk or history of disturbance. Although there are numerous examples of these finer scale factors or their surrogates being incorporated as static predictor maps into SDM (reviewed in Franklin, 2009), these authors also noted that modellers have begun linking SDMs to more dynamic models of dispersal and species migration, disturbance (landscape dynamics) and demographic processes (population dynamics).

In fact, researchers have been coupling SDMs with process models for more than a decade, as will be shown in the following sections. These studies start with the static spatial predictions from SDMs and then use them in spatially explicit simulation models of the non-equilibrium dynamics of populations, communities or landscapes. This strategy can be used to explore the interactions among habitat shifts, landscape structure and population demography (Fig. 1). In this essay, I will discuss three strategies of increasing complexity: models of species migration, models of community dynamics and models of population viability. Models of migration explicitly account for species dispersal and establishment in some way, but may not account for interactions with other species or for demographic processes of birth and death. Models of community dynamics can address both spatially explicit dispersal and competition among species. Models of population viability tend to be single-species focused but can take into account both dispersal and competition, and are detailed in terms of their treatment of demographic processes, accounting for population structure and age-specific vital rates. I will focus particularly on the application of these strategies in studies forecasting the potential impacts of anthropogenic climate change (global warming), as well as land use change and disturbance regimes, on the geographical distribution, and indeed the persistence, of species and ecological communities.

DISPERSAL AND MIGRATION

Evidence of species range changes resulting from the effects of anthropogenic climate change has already been observed in nature (Root *et al.*, 2003; Araújo *et al.*, 2005; Parmesan, 2006). To forecast the potential impacts of continued global warming on species distributions and persistence, a number of studies, some quite impressive in their scope (thousands of species, spanning continents, considering numerous climate change scenarios), model current species distribution with respect to bioclimatic and other environmental factors, and project future geographical distributions based on future climate maps from global or regional climate simulations (e.g. Thomas *et al.*, 2004; Thuiller *et al.*, 2005; Lawler *et al.*, 2009). Potential impacts of range shifts (changes in the distribution of suitable habitat) are assessed in terms of habitat area that is stable (overlapping present and future predicted distributions), lost or gained, or in terms of numbers of species expected to persist in a location. This approach does not account for the most fundamental limiting process, the species' ability to move on the landscape: dispersal of individual organisms and migration

Figure 1 Schematic example of shifting distribution of suitable habitat for a species (butterfly symbol), from the present configuration of patches (T1; open polygons), to future (T2, patches with diagonal pattern), as suitable habitat moves north and upslope because of climate change, for example. A) Black polygon is overlapping current and future suitable habitat; B) a new patch of habitat easily within the species' dispersal distance, C) patches that may be big enough to support viable subpopulations but that are in a location at risk of too frequent disturbance (e.g. fire) and perhaps too distant from present habitat for likely dispersal; D) a habitat patch at risk of loss because of land use change (e.g. urbanization), as well as distant from current habitat.

of species to newly suitable habitat (Pitelka *et al.*, 1997; Higgins *et al.*, 2003).

Studies that have used SDM to project climate change impacts typically acknowledge the limitation of not considering a species ability to reach new suitable habitat, and one strategy to address this has been to compare the extreme cases of 'all versus nothing' migration into new habitat (e.g. Araújo *et al.*, 2006; Thuiller *et al.*, 2006). 'All' assumes that there are no barriers or distance-related dispersal limitations and all new habitat becomes occupied by the species, while 'nothing' assumes that any intervening unsuitable habitat represents a dispersal barrier, and only new habitat that overlaps with the original distribution of habitat or is contiguous with it can be occupied (e.g. Bomhard *et al.*, 2005). However, these best versus worst case scenarios can result in very wide error bounds.

While projecting the redistribution of suitable habitat is a perfectly logical place to start, when trying to predict the impact of a complex and dynamic climate system on complex and dynamic ecological communities, it is only a start. Akçakaya *et al.* (2006) argued that the responses of most species to climate change are still too poorly understood (e.g. Austin, 1992) to estimate extinction risk solely from SDMs applied to environmental change scenarios. It has been suggested that adding more realism about dispersal or species' migration to the empirical SDM might be an effective step towards improving forecasts about climate impacts on species distributions and persistence (Thuiller *et al.*, 2008). A simple and straightforward approach has been to assume a fixed migration rate for the species studied (Midgley *et al.*, 2006; Fitzpatrick *et al.*, 2008), for example, 5 or 10 km per year, perhaps based on rates inferred from studies of post-glacial migration of similar taxa (Clark, 1998). However, this approach does not incorporate dynamic, mechanistic models of movement.

Studies of potential impacts of invasive species also need to account for dispersal ability or species migration rates, and some of the fundamental spatial modelling work on this problem has been done in the context of invasive species or pathogen spread (Higgins & Richardson, 1996). A dispersal kernel describes the distribution of offspring as a function of distance (and perhaps direction) from the parent (Higgins *et al.*, 2003). Maps of potential habitat based on SDMs have been combined with dispersal kernels to determine the importance of dispersal constraints to the spread of invasive plant species (Williams *et al.*, 2008) and forest pathogens (Meentemeyer *et al.*, 2008). Dispersal kernels could also be applied in the case of shifting habitat under climate change.

Several studies have used a cellular automata (CA) modelling framework for spatially explicit simulations of species migration in response to climate change effects on habitat distribution. CA models are matrix simulations that apply rules to each cell in a grid, rules that are based on the values of the eight neighbouring cells, to determine the value or identity of each grid cell in the subsequent time step. Carey (1996) projected the impact of climate change on a plant species in Great Britain by modelling the fate of its population in each grid cell as a function of changing climate suitability and dispersal from neighbouring cells using a CA model called DISPERSE. CA modelling was also used recently to predict colonization (as a function of dispersal) and extinction (as a function of habitat suitability) during climate change-induced range expansion for a simulated species (Wilson *et al.*, 2009). Ostendorf *et al.* (2001) developed a CA model that imposed spatial constraints on the transition of a grid cell to a new community type under climate change based on proximity to forest types in the Australian Wet Tropics, leading to as much as a 27% difference in vegetation transitions when compared to assuming unlimited ability of communities to migrate.

Iverson and colleagues also implemented a CA model, called SHIFT, to simulate migration of tree species under future climate change in North America. The probability of new suitable habitat (predicted from an SDM) being colonized by a species was modelled as a function of that species abundance in neighbouring cells, forest density and distance; an inverse power function was used to describe the distance decay of seed dispersal (Iverson *et al.*, 2004a,b). The proportion of new suitable habitat that was likely to be colonized was generally < 15% what was available for most species, and the abundance of the species near the boundary between currently occupied and newly suitable habitat drove migration. Rare long-distance dispersal events did not 'rescue' migration (did not greatly improve the occupancy of newly suitable habitat).

Recently, a CA model called MigClim has been developed to simulate plant migration in the presence of climate change and habitat fragmentation (Engler & Guisan, 2009). Sharing qualities with both Carey's DISPERSE model (Carey, 1996) and the population models described below (Population Dynamics), MigClim simulates dispersal, colonization, growth and extirpation of populations within each cell in the grid as a function of dispersal distance from occupied cells and also takes into account barriers to dispersal and gaps in the distribution of suitable habitat. Another grid-based plant spread simulator, similar to the CA models already discussed, was developed to explore the relative effects of climate change, dispersal and other factors on upward shifts in treeline with global warming (Dullinger *et al.*, 2004). Because this model incorporated demographic parameters (fecundity, growth, mortality) that were a function of (changing) climate, it is, like MigClim, also related to population modelling approaches discussed below. In this study, colonization by trees above present treeline was predicted to occur more slowly than would be expected based on climate alone (availability of newly suitable habitat) because of the dispersal limitations, long generation time and slow growth of the species (*Pinus mugo*).

LANDSCAPE DISTURBANCE AND COMMUNITY DYNAMICS

Habitat is dynamic at the landscape spatial extent and at decadal time scales as a result of both anthropogenic disturbance (land use and land cover change) and natural disturbance regimes. Disturbance leads to altered biophysical conditions on a site and results in community succession. Further, climate change, land use change and other human activities can affect the frequency, location, extent and intensity of disturbance (fire, hurricanes, flooding). Landscape modelling of plant community dynamics requires spatially explicit information on the initial distribution of key species or functional types comprising the community (He & Mladenoff, 1999; Mladenoff & Baker, 1999). Often this information is derived from SDMs (Franklin, 2002; Franklin *et al.*, 2005), although these baseline maps can also be derived from inventory data (e.g. dense forest data, He *et al.*, 1998; Ohmann & Gregory, 2002) through spatial interpolation.

These maps provide initial conditions for simulation models that predict the impacts of natural and anthropogenic disturbance on ecological communities at large spatial scales (Gustafson *et al.*, 2004; Franklin *et al.*, 2005; Scheller *et al.*, 2005). For example, fire, logging and climate change may synergistically affect the distribution of late-successional forest communities on the landscape (Xu *et al.*, 2007; Scheller *et al.*, 2008). Urban growth in conjunction with spatially varying human impacts on fire frequency can lead to declines in key plant functional types (Syphard *et al.*, 2006, 2007). The initial distribution of species' habitat predicted from an SDM can also be modified using a landscape simulation model to provide dynamic habitat information to a population model (Akcakaya, 2001; Larson *et al.*, 2004), as discussed in the next section. This is particularly useful for understanding the effect of landscape dynamics on species that are dependent on habitat at a certain successional stage, e.g. early seral or old growth habitat (Akçakaya *et al.*, 2004, 2005).

Modelling software, BioMove, has recently been developed that incorporates a grid-based landscape simulation model of plant community disturbance and succession (Midgley *et al.*, in press). BioMove was designed to simulate plant species range shifts in response to environmental change by linking this model of vegetation dynamics (based on plant functional types) to a population model for a focal species that is grid-based, age-structured and uses kernel seed dispersal. As with the other landscape models discussed in this section, SDMs for both the 'habitat' (plant functional types making up the vegetation community) and the target species are developed externally and then linked to BioMove. By integrating vegetation dynamics and demographic models, BioMove can directly address the effects of light competition on the target species, in contrast with the population modelling approaches discussed in the next section. However, no research using BioMove has yet been published.

POPULATION DYNAMICS

Population viability analysis (PVA) is a species-based modelling framework for assessing threats to species persistence, estimating extinction risk and ranking potential management options (Akçakaya & Burgman, 1995; Possingham *et al.*, 2001; Beissinger & McCullough, 2002). PVA has been widely used to predict the consequences of habitat loss as well as other threats for species of conservation concern (Brigham *et al.*, 2003; Henle *et al.*, 2004; Melbourne *et al.*, 2004). One model structure frequently used in PVA has been metapopulation modelling, where subpopulations occupy discrete patches of habitat, may move between them, and the spatial arrangement of the patches is defined (Akçakaya, 2000). When using metapopulation or other spatially explicit population model structures, PVA can make use of spatial information about the distribution of habitat (arrangement, size and quality of suitable habitat patches), derived using a SDM or by some other means. PVA can also incorporate changing carrying capacities of habitat patches through time in cases where

temporal variation in habitat suitability has population effects (Pulliam *et al.*, 1992; Lindenmayer & Possingham, 1996; Akçakaya & Atwood, 1997; Kindvall *et al.*, 2004).

Although the grid-based population models discussed in the previous sections also incorporated demographic parameters in a spatially explicit manner, the examples described in this section differ somewhat in that they are patch based instead of grid based and they tend to focus on threats to population persistence instead of species migration in response to environmental change. However, both approaches model population change based on demographic parameters in a spatially explicit way. Models based on these two data structures, raster versus vector, correspond to different geographical data models or conceptual views of real geography, the 'field' and the 'entity' (Goodchild, 1992, 1994). In the field view, geographical variables can be measured (have a value) at every location, and geography is a multivariate vector field, for example, a grid map of the likelihood of species occurrence or habitat suitability. In the entity view, there are discrete geographic objects scattered in geographical space that is otherwise empty, such as patches of suitable habitat with an associated carrying capacity or other attributes.

There are a number of well-established formulations for spatially explicit population viability modelling (reviewed by Akçakaya & Regan, 2002), and several of these have been coupled with models of habitat suitability (SDMs) and landscape dynamics to predict the impacts of environmental change on species persistence. For example, a patch occupancy or incidence function model predicts the presence or absence of a species in habitat patches (Hanski, 1994). Patch occupancy models have recently been used to predict a threshold effect of climate change-induced habitat loss on species viability (Travis, 2003) and to contrast the effects of habitat fragmentation versus range expansion under climate change (Wilson *et al.*, 2009).

While not a metapopulation model, PATCH (Schumaker, 1998), a spatially explicit individual-based model, has been used to study the impacts of landscape change on wildlife populations. PATCH was linked with SDMs and climate change scenarios to explore the relative impacts of climate change, logging and hunting on two carnivore species, showing synergistic effects of climate change-induced habitat shifts in combination with these other threats (Carroll, 2007). In another example, predicted changes in wildlife populations based on linked models were greater than those predicted from climate-induced changes in habitat suitability alone; both land use change and changes in vital rates resulting from climate change affected population trajectories (McRae *et al.*, 2008).

Structured metapopulation models incorporate population dynamics within each subpopulation, and while there are a number of implementations available, the RAMAS-GIS software (Akçakaya, 2002) has been widely used to explore the impacts of habitat change on species. In one case study, a coupled SDM-population modelling approach has shown that range expansion at the 'leading edge' (poleward range expansion) was faster, and range shrinkage at the southern range margin (trailing edge) was slower (the species was able to persist there longer) when dispersal was accounted for (Anderson *et al.*, 2009).

SDMs linked with landscape dynamics models described in the previous section (Landscape Disturbance and Community Dynamics) have been used to provide maps of suitable habitat at different time steps (Akçakaya *et al.*, 2004, 2005) when habitat suitability is linked to community dynamics driven by natural disturbance (Regan *et al.*, 2010). A PVA framework, using SDMs to characterize present and future habitat conditions, can be used to address the interactions among potential habitat shifts because of climate and land cover change, landscape structure (dispersal barriers caused by land use patterns, landscape patterning caused by altered disturbance regimes) and demography. When this approach is used for a range of species' functional groups, it can be used to assign degrees of threat to types of species (Keith *et al.*, 2008).

The study by Keith *et al.* (2008) is illustrative. They linked SDMs to models of spatially explicit metapopulation dynamics for over 200 plant species in the fynbos community of the Cape region of South Africa (a global plant diversity hotspot). Their models accounted for the demographic effects of fire frequency as well as climate change effects on habitat distribution. Increased fire frequency posed a risk to the species they studied, and while habitat loss because of climate change caused marked population declines for some species (especially those with widespread but contracting distributions), less frequent fire mitigated this effect in some functional types (fire-obligate seeders, those species with fire-cued seed germination).

In contrast, another recent study used the same framework of linked distribution and population viability models under scenarios of climate change, land use change and altered fire frequency for an obligate seeding shrub in the California Floristic Province (Lawson *et al.*, 2009); they concluded that dramatic habitat losses because of climate change (Fig. 2) may pose a greater risk to this species than future urbanization or altered fire frequency (e.g. Syphard *et al.*, 2007). This poorly dispersing species is projected to lose much of its existing habitat and gain no new habitat within its current range under climate change projections. The geographical range and prior land use history played an important role in projected future risk. Suitable habitat for this narrowly endemic species occurs within a highly urbanized area, resulting in a current distribution of subpopulations that is fragmented and isolated. Future urbanization would cause only limited further habitat loss because most areas suitable for urban development are already developed. Ironically, subpopulations can be 'protected' from too frequent fire by isolation of habitat fragments which decouples fire events across the landscape (Regan *et al.*, 2010).

Linking species distributions, landscape dynamics and populations allows the synergistic effects of climate-induced range shifts and land cover dynamics (land use change, disturbance regimes) on population persistence to be explored, and species extinction risk to be predicted (Brook *et al.*, 2009).
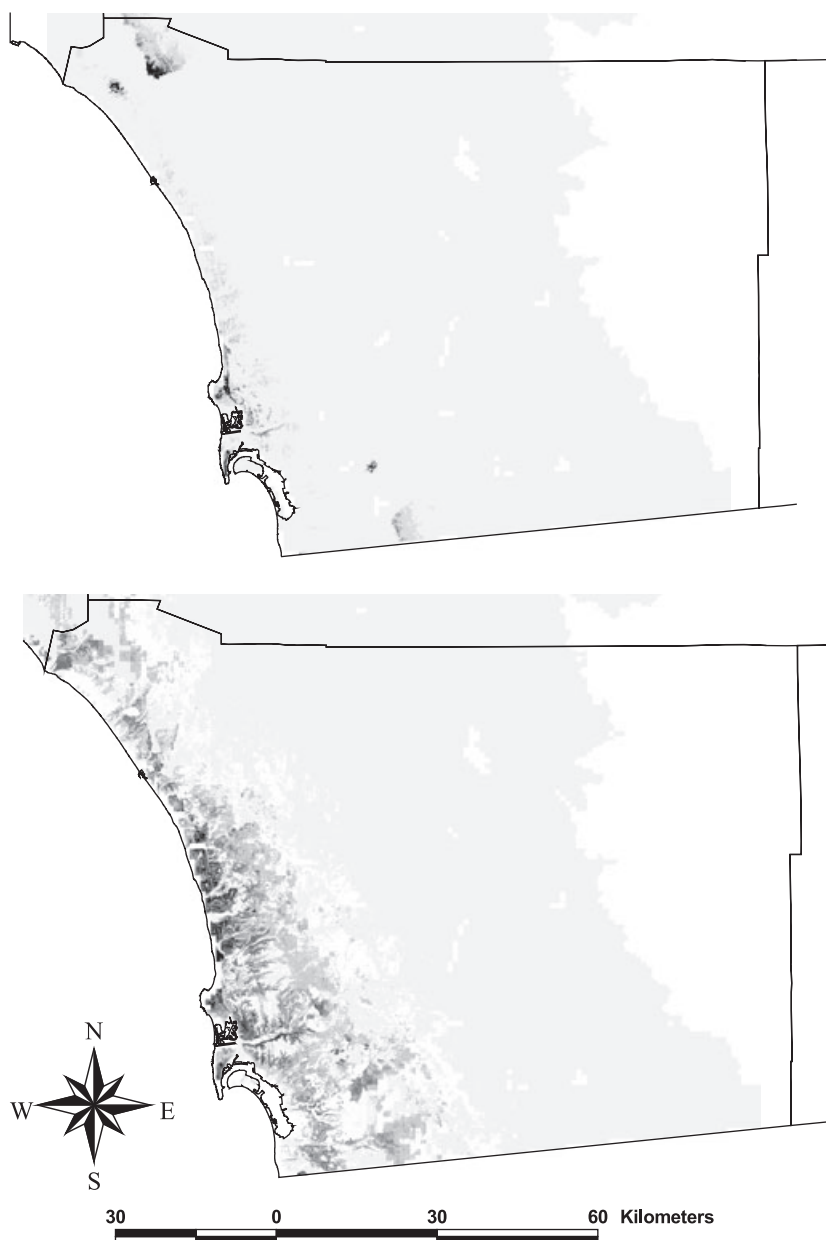
Figure 2 Example of shift in distribution of climatically suitable habitat shown for *Ceanothus verrucosus*, a narrowly endemic shrub found in the Southwest Ecoregion of the California Floristic Province (Lawson *et al.*, 2009), modelled using Maxent (Phillips & Dudík, 2008). Darker tones indicate higher habitat suitability. Future habitat suitability for 2100 shown for San Diego County, CA, USA (upper map), is based on downscaled temperature and precipitation prediction maps from the GFDC climate model and a high emissions scenario, predicting hotter, drier conditions (Cayan *et al.*, 2008), averaged for 2070-2099. Current habitat suitability modelled from current climate maps (as well as soil and terrain variables) is shown in the lower map. The actual current distribution of *C. verrucosus* is greatly restricted by extensive urban land cover, not shown.

However, this approach is only practical if the life history parameters and habitat requirements of the species are well understood (Keith *et al.*, 2008).

SUMMARY

Species distribution modelling is a powerful tool for conservation biogeography (Franklin, 2009); however, is almost always a means to an end and rarely an end in itself. The limitations of this static, empirical modelling approach are well documented (McPherson *et al.*, 2004; Segurado & Araújo, 2004; Elith *et al.*, 2006). Specific suggestions for combining SDM with other data and approaches lead to improved methods for evaluating environmental change at large spatial scales. For example, Botkin *et al.* (2007) suggested that forecasts of the impacts of global change on biodiversity could be improved by considering multiple causes, exactly as the examples described in this paper have done.

Thuiller *et al.* (2008) reiterated a caveat that applies to all models: there will always be trade-offs between using complex, mechanistic versus simple, empirical models to forecast environmental change. I suggest the following strategy for employing SDMs in conjunction with other approaches to forecast risk to species from climate and landscape change:
1. At a minimum, forecasts of climate change impacts on the distribution of species should account for species migration rates determined in large part by the ability of individuals to disperse to newly suitable habitat. This will greatly reduce the

range of uncertainty than may exist between the 'all' and 'nothing' dispersal scenarios. Approaches, in order of complexity, can include:

 a. applying a single estimate of migration rate,

 b. using a dispersal kernel to account for dispersal distance from occupied map cells,

 c. developing a rule-based CA model that imposes constraints to species movement based on dispersal ability, barriers, and other factors, and

 d. developing a grid-based population model to investigate species migration as a function of abundance, dispersal ability, fecundity, longevity and mortality (if demographic data are available to support this).

2. At the other end of the modelling complexity spectrum are fully linked distribution, landscape dynamics and population models for species or functional types; this provides a powerful framework for understanding the potential interactions among multiple factors affecting species distributions and population persistence, including climate change, land use change and altered disturbance regimes (Fig. 1). These dynamic factors not only affect the geographical distribution of suitable habitat, they also can affect vital rates. However, good knowledge of species interactions, habitat requirements and life history is required, and so this approach may not be feasible in all cases.

The examples discussed here show that as a research community, we are already coupling correlative models of habitat suitability with spatially explicit models of community and population dynamics to understand processes affecting species' distributions in the face of environmental change. These studies have revealed that as we might have expected, when biological populations are subjected to multiple stressors, the combined effect can be more than the sum of the parts, and the responses may be non-linear. There are a range of possible approaches that vary in their complexity, realism and hunger for data that can be employed depending on the specific question being addressed and data available.

ACKNOWLEDGEMENTS

REFERENCES

Akcakaya, H.R. (2001) Linking population-level risk assessment with landscape and habitat models. *Science of the Total Environment*, **274**, 283–291.

Akçakaya, H.R. (2000) Viability analyses with habitat-based metapopulation models. *Population Ecology*, **42**, 45–53.

Akçakaya, H.R. (2002) *RAMAS GIS: linking landscape data with population viability analysis. Version 4.0.* Applied Biomathematics, Setauket, NY.

Akçakaya, H.R. & Atwood, J.L. (1997) A habitat based metapopulation model of the California gnatcatcher. *Conservation Biology*, **11**, 422–434.

Akçakaya, H.R. & Burgman, M. (1995) PVA in theory and practice. *Conservation Biology*, **9**, 705–707.

Akçakaya, R.H. & Regan, H.M. (2002) Population models: individual-based. *Ecological modeling in risk assessment: chemical effects on populations, ecosystems and landscapes*, (ed. by R.A. Pastorok, S.M. Bartell, S. Ferson and L.R. Ginzburg), pp. 83–95. Lewis Publishers, Boca Raton FL.

Akçakaya, H.R., Radeloff, V.C., Mlandenoff, D.J. & He, H.S. (2004) Integrating landscape and metapopulation modeling approaches: Viability of the sharp-tailed grouse in a dynamic landscape. *Conservation Biology*, **18**, 526–537.

Akçakaya, H.R., Franklin, J., Syphard, A.D. & Stephenson, J.R. (2005) Viability of Bell's Sage Sparrow (*Amphispiza belli* ssp. *belli*) under altered fire regimes. *Ecological Applications*, **15**, 521–531.

Akçakaya, H.R., Butchart, S.H.M., Mace, G.M., Stuart, S.N. & Hilton-Taylor, C. (2006) Use and misuse of the IUCN Red List Criteria in projecting climate change impacts on biodiversity. *Global Change Biology*, **12**, 2037–2043.

Anderson, B.J., Akcakaya, H.R., Araújo, M.B., Fordham, D.A., Martinez-Meyer, E., Thuiller, W. & Brook, B.W. (2009) Dynamics of range margins for metapopulations under climate change. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 1415–1420.

Araújo, M.B. & Guisan, A. (2006) Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, **33**, 1677–1688.

Araújo, M.B., Pearson, R.G., Thuiller, W. & Erhard, M. (2005) Validation of species-climate impact models under climate change. *Global Change Biology*, **11**, 1504–1513.

Araújo, M.B., Thuiller, W. & Pearson, R.G. (2006) Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography*, **33**, 1712–1728.

Austin, M.P. (1992) Modelling the environmental niche of plants: some implications for plant community response to elevation CO_2 levels. *Australian Journal of Botany*, **40**, 615–630.

Beissinger, S.R. & McCullough, D.R. (2002) *Population viability analysis*, University of Chicago Press, Chicago.

Bomhard, B., Richardson, D.M., Donaldson, J.S., Hughes, G.O., Midgley, G.F., Raimondo, T., Rebelo, A.G., Rouget, M. & Thuiller, W. (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. *Global Change Biology*, **11**, 1452–1468.

Botkin, D.B., Saxe, H., Araújo, M.B., Betts, R., Bradshaw, R.H.W., Cedhagen, T., Chesson, P., Dawson, T.P., Etterson, J.R., Faith, D.P., Ferrier, S., Guisan, A., Hansen, A.S., Hilbert, D.W., Loehle, C., Margules, C., New, M., Sobel, M.J. &

Stockwell, D.R.B. (2007) Forecasting the effects of global warming on biodiversity. *BioScience*, **57**, 227–236.

Brigham, C.A. & Thomson, D.M. (2003) Approaches to modeling population viability in plants: an overview. *Population Viability in Plants: Conservation, Management, and Modeling of Rare Plants* (ed. by C.A. Brigham and M.W. Schwartz), pp. 145–171. Springer-Verlag, Berlin.

Brook, B.W., Akçakaya, R.H., Keith, D.A., Mace, G.M., Pearson, R.G. & Araújo, M.B. (2009) Integrating bioclimate with population models to improve forecasts of species extinctions under climate change. *Biology Letters*, **5**, 723–724.

Carey, P.D. (1996) DISPERSE: a cellular automaton for predicting the distribution of species in changed climates. *Global Ecology and Biogeography Letters*, **5**, 217–226.

Carmel, Y. & Flather, C.H. (2006) Constrained range expansion and climate change assessments. *Frontiers in Ecology and the Environment*, **4**, 178–179.

Carroll, C. (2007) Interacting effects of climate change, landscape conversion, and harvest on carnivore populations at the range margin: Marten and Lynx in the northern Appalachians. *Conservation Biology*, **21**, 1092–1104.

Cayan, D.R., Maurer, E.P., Dettinger, M.D., Tyree, M. & Hayhoe, K. (2008) Climate change scenarios for the California region. *Climatic Change*, **87**, S21–S42.

Clark, J.S. (1998) Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *American Naturalist*, **152**, 204–224.

Dullinger, S., Dirnböck, T. & Grabherr, G. (2004) Modelling climate change-driven treeline shifts: relative effects of temperature increase, dispersal and invasibility. *The Journal of Ecology*, **92**, 241–252.

Elith, J. & Leathwick, J. (2009) Conservation prioritisation using species distribution modelling. *Spatial conservation prioritization: quantitative methods and computational tools*, (ed. by A. Moilanen, K.A. Wilson and H. Possingham), pp. 70–93. Oxford University Press, Oxford, UK.

Elith, J., Graham, C.H., Anderson, R.P. *et al.* (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**, 129–151.

Engler, R. & Guisan, A. (2009) MigClim: predicting plant distribution and dispersal in a changing climate. *Diversity and Distributions*, **15**, 590–601.

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. *Global Change Biology*, **14**, 1337–1352.

Franklin, J. (1995) Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. *Progress in Physical Geography*, **19**, 474–499.

Franklin, J. (2002) Enhancing a regional vegetation map with predictive models of dominant plant species in chaparral. *Applied Vegetation Science*, **5**, 135–146.

Franklin, J. (2009) *Mapping species distributions: spatial inference and prediction*, Cambridge University Press, Cambridge, UK.

Franklin, J., Syphard, A.D., He, H.S. & Mladenoff, D.J. (2005) The effects of altered fire regimes on patterns of plant succession in the foothills and mountains of southern California. *Ecosystems*, **8**, 885–898.

Goodchild, M.F. (1992) Geographical data modeling. *Computers & Geosciences*, **18**, 401–408.

Goodchild, M.F. (1994) Integrating GIS and remote sensing for vegetation analysis and modeling: methodological issues. *Journal of Vegetation Science*, **5**, 615–626.

Guisan, A. & Thuiller, W. (2005) Predicting species distributions: offering more than simple habitat models. *Ecology Letters*, **8**, 993–1009.

Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.

Guisan, A., Lehmann, A., Ferrier, S., Austin, M., Overton, J.M.C., Aspinall, R. & Hastie, T. (2006) Making better biogeographical predictions of species' distributions. *The Journal of Applied Ecology*, **43**, 386–392.

Gustafson, E.J., Zollner, P.A., Sturtevant, B.R., He, H.S. & Mladenoff, D.J. (2004) Influence of forest management alternatives and land type on susceptibility to fire in northern Wisconsin, USA. *Landscape Ecology*, **19**, 327–341.

Hanski, I. (1994) A practical model of metapopulation dynamics. *Journal of Animal Ecology*, **63**, 151–162.

He, H.S. & Mladenoff, D.J. (1999) Spatially explicit and stochastic simulation of forest-landscape fire disturbance and succession. *Ecology*, **80**, 81–90.

He, H.S., Mladenoff, D.J., Radeloff, V.C. & Crow, T.R. (1998) Integration of GIS data and classified satellite imagery for regional forest assessment. *Ecological Applications*, **8**, 1072–1083.

Heikkinen, R.K., Luoto, M., Araújo, M.B., Virkkala, R., Thuiller, W. & Sykes, M.T. (2006) Methods and uncertainties in bioclimatic envelope modelling under climate change. *Progress in Physical Geography*, **30**, 751–777.

Henle, K., Lindenmayer, D.B., Margules, C.R., Saunders, D.A. & Wissel, C. (2004) Species survival in fragmented landscapes: where are we now? *Biodiversity and Conservation*, **13**, 1–8.

Higgins, S.I. & Richardson, D.M. (1996) A review of models of alien plant spread. *Ecological Modelling*, **87**, 249–265.

Higgins, S.I., Clark, J.S., Nathan, R., Hovestadt, T., Schurr, F., Fragoso, J.M.V., Aguiar, M.R., Ribbens, E. & Lavorel, S. (2003) Forecasting plant migration rates: managing uncertainty for risk assessment. *The Journal of Ecology*, **91**, 341–347.

Iverson, L.R., Schwartz, M.W. & Prasad, A.M. (2004a) How fast and far might tree species migrate in the eastern United States due to climate change? *Global Ecology and Biogeography*, **13**, 209–219.

Iverson, L.R., Schwartz, M.W. & Prasad, A.M. (2004b) Potential colonization of newly available tree-species habitat under climate change: an analysis for five eastern US species. *Landscape Ecology*, **19**, 787–799.

Keith, D.A., Akçakaya, H.R., Thuiller, W., Midgley, G.F., Pearson, R.G., Phillips, S.J., Regan, H.M., Araújo, M.B. &

Rebelo, T.G. (2008) Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biology Letters*, **4**, 560–563.

Kindvall, O. & Bergman, K.-O. (2004) Woodland brown butterfly (*Lopinga achine*) in Sweden: viability in a dynamic landscape maintained by grazing. *Species conservation and management: case studies* (ed. by R. Akcakaya, M.A. Burgman, O. Kindvall, C.C. Wood, P. Sjogren-Gulve, J.S. Hatfield and M.A. McCarthy), pp. 171–178. Oxford University Press, New York.

Kueppers, L.M., Snyder, M.A., Sloan, L.C., Zavaleta, E.S. & Fulfrost, B. (2005) Modeled regional climate change and California endemic oak ranges. *Proceedings of the National Academy of Sciences USA*, **102**, 16281–16286.

Kueppers, L.M., Zavaleta, E., Fulfrost, B., Snyder, M.A. & Sloan, L.C. (2006) Constrained range expansion and climate change assessments - The authors reply. *Frontiers in Ecology and the Environment*, **4**, 179–179.

Larson, M.A., Thompson, F.R., Millspaugh, J.J., Dijak, W.D. & Shifley, S.R. (2004) Linking population viability, habitat suitability, and landscape simulation models for conservation planning. *Ecological Modelling*, **180**, 103–118.

Lawler, J.J., Shafer, S.L., White, D., Kareiva, P., Maurer, E.P., Blaustein, A.R. & Bartlein, P.J. (2009) Projected climate-induced faunal changes in the Western Hemisphere. *Ecology*, **90**, 588–597.

Lawson, D.M., Regan, H.M., Zedler, P.H. & Franklin, J. (2009) Cumulative effects of land use, altered fire regime and climate change on persistence of *Ceanothus verrucosus*, a rare, fire dependent plant species. *Global Change Biology*, doi: 10.1111/j.1365-2486.2009.02143.x.

Lindenmayer, D.B. & Possingham, H.P. (1996) Modelling the inter-relationships between habitat patchiness, dispersal capability and metapopulation persistence of the endangered species, Leadbeater's possum, in south-eastern Australia. *Landscape Ecology*, **11**, 79–105.

Lozier, J.D., Aniello, P. & Hickerson, M.J. (2009) Predicting the distribution of Sasquatch in western North America: anything goes with ecological niche modelling. *Journal of Biogeography*, **36**, 1623–1627.

McPherson, J.M., Jetz, W. & Rogers, D.J. (2004) The effects of species' range sizes on the accuracy of distribution models: ecological phenomenon or statistical artefact? *The Journal of Applied Ecology*, **41**, 811–823.

McRae, B.H., Schumaker, N.H., McKane, R.B., Busing, R.T., Solomon, A.M. & Burdick, C.A. (2008) A multi-model framework for simulating wildlife population response to land-use and climate change. *Ecological Modelling*, **219**, 77–91.

Meentemeyer, R.K., Anacker, B.L., Mark, W. & Rizzo, D.M. (2008) Early detection of emerging forest disease using dispersal estimation and ecological niche modeling. *Ecological Applications*, **18**, 377–390.

Melbourne, B.A., Davies, K.F., Margules, C.R., Lindenmayer, D.B., Saunders, D.A., Wissel, C. & Henle, K. (2004) Species survival in fragmented landscapes: where to from here? *Biodiversity and Conservation*, **13**, 275–284.

Midgley, G.F., Hughes, G.O., Thuiller, W. & Rebelo, A.G. (2006) Migration rate limitations on climate change-induced range shifts in Cape Proteaceae. *Diversity and Distributions*, **12**, 555–562.

Midgley, G.F., Davies, I.D., Albert, C.H., Altwegg, R., Hannah, L., Hughes, G.O., Ries, L.P. & Thuiller, W. (in press) BioMove – an integrated platform simulating the dynamic response of species to environmental change (Software Report). *Ecography*, doi: 10.1111/j.1600-0587.2009.06000.x.

Mladenoff, D.J. & Baker, W.L. (1999) Development of forest and landscape modeling approaches. *Spatial modeling of forest landscape change: approaches and applications*, (ed. by D.J. Mladenoff and W.L. Baker), pp. 1–13. Cambridge University Press, Cambridge.

Ohmann, J.L. & Gregory, M.J. (2002) Predictive mapping of forest composition and structure with direct gradient analysis and nearest neighbor imputation in coastal Oregon, U.S.A. *Canadian Journal of Forest Research*, **32**, 725–741.

Ostendorf, B., Hilbert, D.W. & Hopkins, M.S. (2001) The effect of climate change on tropical rainforest vegetation patterns. *Ecological Modelling*, **145**, 211–224.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics*, **37**, 637–669.

Pearson, R.G., Dawson, T.P. & Liu, C. (2004) Modelling species distribution in Britain: a hierarchical integration of climate and land cover. *Ecography*, **27**, 285–298.

Pearson, R.G., Thuiller, W., Araújo, M.B., Martinez-Meyer, E., Brotons, L., McClean, C., Miles, L., Segurado, P., Dawson, T.P. & Lees, D.C. (2006) Model-based uncertainty in species range prediction. *Journal of Biogeography*, **33**, 1704–1711.

Peterson, A.T. (2003) Predicting the geography of species' invasions via ecological niche modeling. *Quarterly Review of Biology*, **78**, 419–433.

Phillips, S.J. & Dudík, M. (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*, **31**, 161–175.

Pitelka, L.F., Gardiner, R.H., Ash, J. et al. (1997) Plant migration and climate change. *American Scientist*, **85**, 464–473.

Possingham, H.P., Lindenmayer, D.B. & McCarthy, M.A. (2001) Population viability analysis. *Encyclopedia of biodiversity*, **4**, 831–843.

Pulliam, H.R., Dunning, J.B. & Liu, J. (1992) Population dynamics in complex landscapes: a case study. *Ecological Applications*, **2**, 165–177.

Randin, C.F., Dirnbock, T., Dullinger, S., Zimmermann, N.E., Zappa, M. & Guisan, A. (2006) Are niche-based species distribution models transferable in space? *Journal of Biogeography*, **33**, 1689–1703.

Regan, H.M., Crookston, J.B., Swab, R., Franklin, J. & Lawson, D.M. (2010) Habitat fragmentation and altered fire regime create trade-offs for an obligate seeding shrub. *Ecology*, **91**, 267–276.

Richardson, D.M. & Thuiller, W. (2007) Home away from home – objective mapping of high-risk source areas for plant introductions. *Diversity and Distributions*, **13**, 299–312.

Richardson, D.M. & Whittaker, R.J. (2010) Conservation biogeography – foundations, concepts and challenges. *Diversity and Distributions*, **16**, 313–320.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57–60.

Scheller, R.M., Mladenoff, D.J., Thomas, R.C. & Sickley, T.A. (2005) Simulating the effects of fire reintroduction versus continued fire absence on forest composition and landscape structure in the Boundary Waters Canoe Area, northern Minnesota, USA. *Ecosystems*, **8**, 396–411.

Scheller, R.M., Van Tuyl, S., Clark, K., Hayden, N.G., Hom, J. & Mladenoff, D.J. (2008) Simulation of forest change in the New Jersey Pine Barrens under current and pre-colonial conditions. *Forest Ecology and Management*, **255**, 1489–1500.

Schumaker, N.H. (1998) *A user's guide to the PATCH model.* US Environmental Protection Agency, Environmental Research Laboratory, Corvalis, OR.

Scott, J.M., Heglund, P.J., Morrison, M.L., Haufler, J.B., Raphael, M.G., Wall, W.A. & Samson, F.B. (2002) *Predicting species occurrences: issues of accuracy and scale*, Island Press, Covelo, CA.

Segurado, P. & Araújo, M.B. (2004) An evaluation of methods for modelling species distributions. *Journal of Biogeography*, **31**, 1555–1568.

Syphard, A.D., Franklin, J. & Keeley, J.E. (2006) Simulating the effects of frequent fire on southern California coastal shrublands. *Ecological Applications*, **16**, 1744–1756.

Syphard, A.D., Clarke, K.C. & Franklin, J. (2007) Simulating fire frequency and urban growth in southern California coastal shrublands, USA. *Landscape Ecology*, **22**, 431–445.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.

Thuiller, W., Araújo, M.B., Pearson, R.G., Whittaker, R.J., Brotons, L. & Lavorel, S. (2004a) Biodiversity conservation - Uncertainty in predictions of extinction risk. *Nature*, **430**, doi:10.1038/nature02716.

Thuiller, W., Brotons, L., Araújo, M.B. & Lavorel, S. (2004b) Effects of restricting environmental range of data to project current and future species distributions. *Ecography*, **27**, 165–172.

Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T. & Prentice, I.C. (2005) Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences USA*, **102**, 8245–8250.

Thuiller, W., Lavorel, S., Sykes, M.T. & Araújo, M.B. (2006) Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe. *Diversity and Distributions*, **12**, 49–60.

Thuiller, W., Albert, C., Araújo, M.B., Berry, P.M., Cabeza, M., Guisan, A., Hickler, T., Midgley, G.F., Paterson, J., Schurr, F.M., Sykes, M.T. & Zimmermann, N.E. (2008) Predicting global change impacts on plant species' distributions: future challenges. *Perspectives in Plant Ecology Evolution and Systematics*, **9**, 137–152.

Travis, J.M.J. (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **270**, 467–473.

Whittaker, R.J., Araújo, M.B., Jepson, P., Ladle, R.J., Watson, J.E.M. & Willis, K.J. (2005) Conservation biogeography: assessment and prospect. *Diversity and Distributions*, **11**, 3–23.

van Wilgen, N.J., Roura-Pascual, N. & Richardson, D.M. (2009) A quantitative climate-match score for risk-assessment screening of reptile and amphibian introductions. *Environmental Management*, **44**, 590–607.

Williams, J.W. & Jackson, S.T. (2007) Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment*, **5**, 475–482.

Williams, N.S.G., Hahs, A.K. & Morgan, J.W. (2008) A dispersal-constrained habitat suitability model for predicting invasion of alpine vegetation. *Ecological Applications*, **18**, 347–359.

Wilson, R.J., Davies, Z.G. & Thomas, C.D. (2009) Modelling the effect of habitat fragmentation on range expansion in a butterfly. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 1421–1427.

Wintle, B.A., Elith, J. & Potts, J.M. (2005) Fauna habitat modelling and mapping: a review and case study in the Lower Hunter Central Coast region of NSW. *Austral Ecology*, **30**, 719–738.

Xu, C.G., Gertner, G.Z. & Scheller, R.M. (2007) Potential effects of interaction between CO_2 and temperature on forest landscape response to global warming. *Global Change Biology*, **13**, 1469–1483.

Zurrell, D., Jeltsch, F., Dormann, C.F. & Schroder, B. (2009) Static species distribution models in dynamically changing systems: how good can predictions really be? *Ecography*, **32**, 733–744.

BIOSKETCH

Janet Franklin is a Professor in the Schools of Geographical Sciences and Urban Planning, and Life Sciences, at Arizona State University. She is interested in the diversity and disturbance dynamics of terrestrial plant communities and in species distribution modelling and uses the tools of landscape and spatial ecology and GIScience. She is the author of *Mapping Species Distributions* (2009).

Editor: David Richardson