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Moving Beyond Static Species Distribution Models in Support of Conservation Biogeography

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ABSTRACT

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

Methods Three approaches were considered: a) incorporating models of species migration in order to understand the ability of a species to occupy suitable habitat in new locations; b) linking models of landscape disturbance and succession to models of habitat suitability; and, c) 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-modeling 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 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 have been 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.

Introduction

Species distribution modeling (SDM) has exploded in recent years in the literature and in practice (Franklin in press). SDM extrapolates species location data in space based on correlations of species occurrence with environmental variables thought to influence habitat suitability. The modeling framework can be a statistical (in the broadest possible sense) or rule-based model, and a spatially explicit prediction of species' distribution based on an SDM results in a predictive map (Franklin 1995). The modeling 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, modeling methods, model parameterization and selection, assessment of model performance, and evaluation of spatial predictions (Elith and Leathwick 2009; Franklin in press). Nonetheless, these are static, correlative models that rely on the assumptions that species location data used for modeling 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 and Zimmermann 2000; Guisan and Thuiller 2005).

Advances in conservation biogeography (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 (D. M. Richardson, pers comm., 2009). Species distribution modeling has been deployed in support of each of these worthy practices (Franklin in press). 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, 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 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 and Thuiller 2007; van Wilgen et al. 2009). Because of the limitations of this correlative approach, the results have sometimes been controversial (Thuiller *et al.* 2004; Akçakaya *et al.* 2006; Carmel and Flather 2006; Kueppers *et al.* 2006; Botkin *et al.* 2007), and have even been satirized (Lozier et al. 2009).

Many authors have urged that in order to meet the needs of conservation biogeography we need to move beyond static SDM predictions to incorporate key dynamic processes determining species distributions (Guisan and Thuiller 2005; Araújo and Guisan 2006; Thuiller et al. 2008). I added my voice to this recommendation in the tenth and final chapter of my recently completed book on species distribution modeling (Franklin in press). 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 slag), 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 been demonstrated to be feasible and informative.

Guisan and Thuiller (2005) suggested a modeling 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, these authors also noted that modelers 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. 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 (Figure 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. 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; Parmesan 2006). In order 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 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 is occupied. 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 dynamics ecological communities, it is only a start. Akcakaya 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 mechanistic 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 number of studies have done just that. 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).

Studies of potential impacts of invasive species also need to account for dispersal ability or species migration rates, and some of the fundamental spatial modeling work on this problem has been done in the context of invasive species or pathogen spread (Higgins and 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) modeling 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 can be based on the values of neighboring 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 modeling the fate of its population in each grid cell as a function of changing climate suitability and dispersal from neighboring cells using a CA model, DISPERSE. CA modeling 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 accounted for dispersal limitations and migration rates by imposing spatial constraints on the transition of a grid cell to a new community type based on proximity to forest types in the Australian Wet Tropics. New distributions of suitable habitat under climate change scenarios were modeled using an SDM. Imposing spatial constraints lead to as much as a 27% difference in vegetation transitions as compared to ignoring them (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 modeled as a function of that species abundance in neighboring cells, forest density, and distance; an inverse power function was used to describe the distance decay of seed dispersal (Iverson *et al.* 2004b; Iverson *et al.* 2004a). In their study, the proportion of new suitable habitat that was actually likely to be colonized was low, generally less than 15% 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).

A CA model called MigClim has been developed to simulate plant migration in the presence of climate change and habitat fragmentation (Engler and Guisan 2009). Sharing qualities with both Carey's DISPERSE model 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 taking into account barriers to dispersal and gaps in the distribution of suitable habitat.

Another grid-based plant spread simulator 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, related to population modeling approaches. In this study, colonization by trees above present treeline was predicted to occur more slowly than would be expected based on climate alone (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 modeling of plant community dynamics requires spatially explicit information on the initial distribution of key species or functional types comprising the community (He and Mladenoff 1999; Mladenoff and Baker 1999). Often this information is derived from SDMs (Franklin 2002; Franklin et al. 2005), although these baseline maps can also be derived from dense forest inventory data (where they exist) 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; Syphard et al. 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; Akçakaya *et al.* 2005).

Modeling 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 modeling 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 modeling framework for assessing threats to species persistence, estimating extinction risk and ranking potential management options (Akçakaya and Burgman 1995; Possingham *et al.* 2001; Beissinger and 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 modeling, 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 and Possingham 1996; Akçakaya and 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; Goodchild 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 modeling (reviewed by Akçakaya and Regan 2002), and several of these have been coupled with models of habitat suitability (SDMs) and landscape dynamics in order to predict the impacts of environmental change on species persistence. For example, a patch occupancy or incidence function model predicts the presence of 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 modeling 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; Akçakaya *et al.* 2005) when habitat suitability is linked to community dynamics driven by natural disturbance (Regan et al. in press). A PVA framework, using SDMs to characterize present and future habitat conditions, can be used to address the interactions among potential habitat shifts due to 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. 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 due to 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. submitted); they concluded that dramatic habitat losses due to climate change (Figure 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 unable to reach newly suitable habitat 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. in press).

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). 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 modeling is almost always a means to an end, and rarely an end in itself. The limitations of this static, empirical modeling approach are well-documented. 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:

- 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 applying a single estimate of migration rate, using a dispersal kernel to account for dispersal distance from occupied map cells, developing a rule-based CA model that imposes constraints to species movement based on dispersal ability, barriers, and other factors, and developing a grid-based population model to investigate species migration as a function of abundance, dispersal ability, fecundity, longevity and mortality (if demographic data area available to support this).
- At the other end of the modeling 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 (Figure 1). These dynamic factors not only affect the geographical distribution of suitable habitat, they also can affect vital rates. However, good knowledge of species habitat requirements and life history is required, and so this approach may not be feasible in all cases.

Species distribution modeling is a powerful tool for conservation biogeography (Franklin in press). The limitations of static species distribution modeling have been repeatedly enumerated in the literature, and there have been many calls to move beyond SDM in order to address

dynamic processes affecting species' distributions in the face of environmental change. However, the examples discussed here show that as a research community we are already moving in that direction, coupling correlative models of habitat suitability with spatially explicit models of community and population dynamics. 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 begin addressed and data available.

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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 due to 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 due to land use change (e.g., urbanization), as well as distant from current habitat.

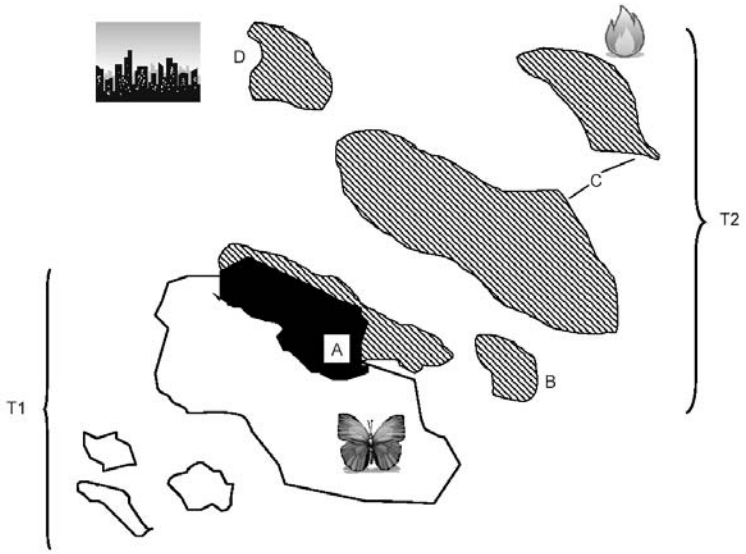
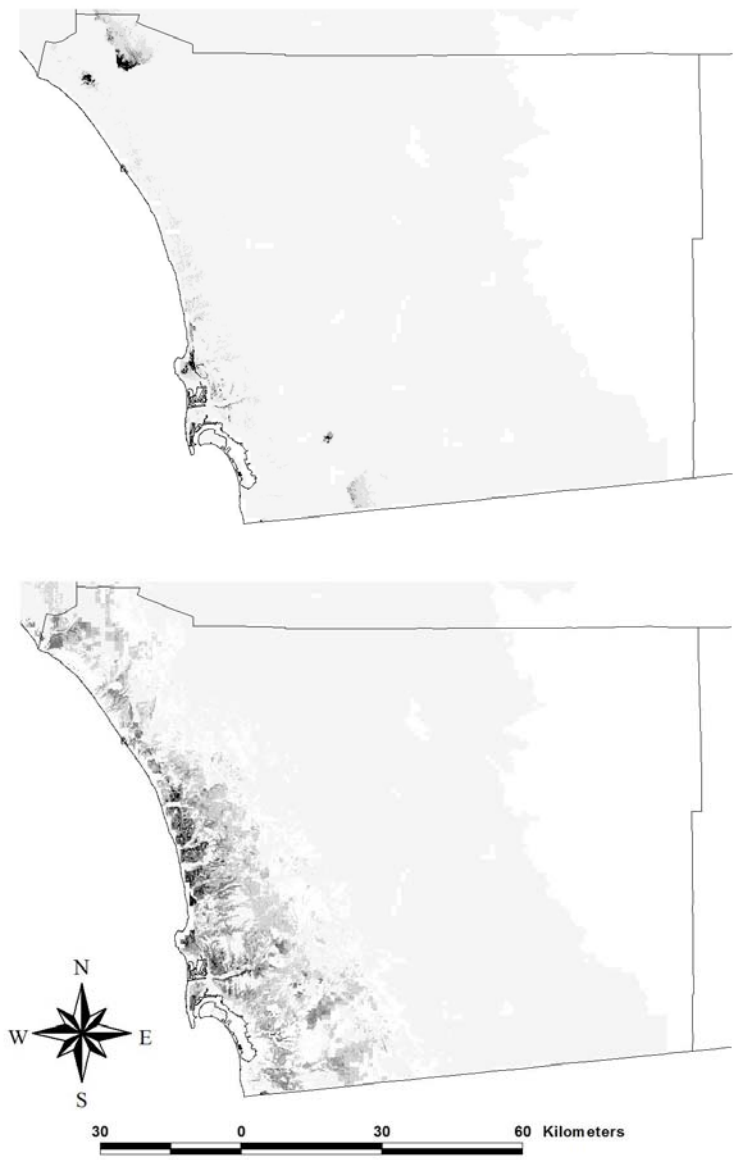
Figure 2. Example of shift in distribution of climatically suitable habitat shown for *Ceanothus verrucosus*, a narrowly endemic shrub found in the Southwest Ecoregion of the California Floristic Province (Lawson *et al.* submitted), modeled using Maxent (Phillips and Dudík 2008). Darker tones indicates 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 modeled 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.