Constrained range expansion and climate change assessments

(Peer-reviewed letter)

Modeling the future distribution of keystone species has proved to be an important approach to assessing the potential ecological consequences of climate change (Loehle and LeBlanc 1996; Hansen *et al.* 2001). Predictions of range shifts are typically based on empirical models derived from simple correlative relationships between climatic characteristics of occupied and unoccupied sites (Pearson and Dawson 2003; Scheffer *et al.* 2005). Using such models to predict species response to climate change assumes that climate exerts a major, if not the dominant, control on where species occur across a region (Scheffer *et al.* 2005). Although this assumption is often accompanied by the recognition that other factors (eg interspecific interactions, dispersal barriers, population adaptation) can affect future distributions (Loehle and LeBlanc 1996), it is rare to see an examination of how predicted species responses may change if factors other than climate are important in shaping future distributions.

We claim that models ignoring actual colonization rate – the ability of a species to move across the landscape – may substantially underestimate the impact of climate change (eg McLachlan *et al.* 2005). Statistical climate envelope models typically delineate three types of habitats: lost (suitable habitats that are expected to become unsuitable), retained (habitats that would remain suitable) and gained (unsuitable habitats that become suitable). This latter component could be underestimated if colonization potential is constrained by non-climatic factors. Under this approach, predicting future distributions is based on the premise that the species of interest would reach a distributional equilibrium with the new climate regime and would fully occupy the suitable habitat (Hansen *et al.* 2001; Scheffer *et al.* 2005). We believe that this premise is not supported generally, and that under some circumstances new potential habitat may remain uncolonized.

We exemplify this claim using a recently published model by Kueppers *et al.* (2005), which predicted future habitat for two Californian oak species under climate change scenarios. They predicted that approximately 39% of the future suitable habitat area for blue oak (*Quercus douglasii*) and valley oak (*Quercus lobata*) would involve expansion into previously unsuitable habitat. We maintain that their models may substantially overestimate the future expansion of these two oak species ("gained habitats"), perhaps by an order of magnitude. In their succinct description of the pressure on Californian oaks, Kueppers *et al.* (2005) understate a major phenomenon of concern, namely the general lack of regeneration of these oaks across most of their range, even in suitable habitats (Standiford *et al.* 1997). We have recently found that oak habitats that were cultivated and then abandoned were not revegetated 60 years later, even in the close proximity of oak forests. Such phenomena were found in seven of eight sites we visited across California (Table 1 in Carmel and Flather 2004). The low rate of oak regeneration we observed is corroborated by the findings of other California oak studies (Callaway and Davis 1993; Brooks and Merenlender 2001), and is in strong contrast to results from the Mediterranean basin, where the colonization potential is higher by a factor of three to twelve (Carmel and Flather 2004; Figure 1). Given the low colonization potential within the current distribution of California oak woodland, we believe that oaks are likely to encounter similar constraints when expanding to areas outside their current distribution. While predictions of future disappearance of oaks in some regions due to climate change (Kueppers *et al.* 2005) may be valid, predictions of oak colonization into new regions of Californian Mediterranean climates is perhaps unrealistic. Kueppers *et al.* (2005) acknowledge that "climate-driven range shifts will be constrained by non-climate factors that affect recruitment and establishment…", but this brief account does not illustrate the severity of the oak regeneration problem in California, and the potential disparity between the predicted and realized range expansion that could be observed for both species. Current estimates of oak regeneration rates suggest negligible expansion of these species into suitable new habitat under climate change. It is likely that future distribution of these oaks would consist only of the habitats predicted to remain suitable following climate change. Using data derived from Kueppers *et al.* (2005) we calculated that future habitat for blue and valley oak would be 36% and 33% of their current distributional extent, rather than 59% and 54%, respectively, as predicted by

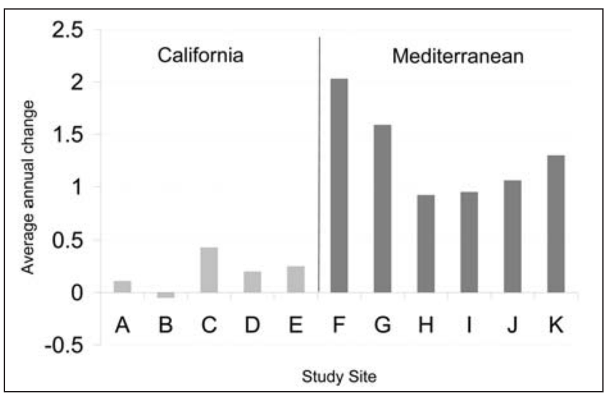

Figure 1. *Average annual change in oak tree cover from California and Mediterranean studies. See Carmel and Flather (2004) for complete references. (a) Hopland; (b) San Diego County; (c) Gaviota State Park, ungrazed; (d) Gaviota State Park, grazed; (e) Hastings Nature Reserve; (f) Mt Pilion, Greece; (g) Adulam, Israel; (h) Bar Giora, Israel; (i) Montpelier, France; (j) Mt Carmel, Israel; (k) Mt Meron, Israel.*

Kueppers *et al.* (2005).

One important implication of such predictions is that they may be overly optimistic and contribute to an unjustified complacency among decision makers about the impact of climate change on species distributions. Looking at Figure 2 in Kueppers *et al.* (2005), for example, it is easy to get an impression of "win some, lose some" while, in fact, a much harsher situation may be more realistic.

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The authors reply

Carmel and Flather emphasize an important point, namely that statistical climate envelope models (CEMs) probably overestimate species' future range sizes following anthropogenic climate change, due to the absence of ecological and landscape history constraints to colonization in these models.

CEMs should not be thought of as forecasting species' actual ranges, since they rely on uncertain predictions about future climate change that typically do not account for locally important climate forcing factors. We obtained substantially different results when regional and global climate model outputs were used (Kueppers *et al.* 2005). In addition, some climate variables can be predicted with more confidence than others. Therefore, climate change pressure is also more certain for some species than others. Perhaps most importantly, CEMs provide "snapshots" of future suitable habitat, while we know that both the climate system and ecological communities experience transient, often non-linear change over time that may either facilitate or inhibit species persistence and migration. These limitations are why reports relying on CEMs typically state results as shifts in "potential ranges". Implicit in this language is that the realized range will be more constrained. In fact, most CEMs overpredict current range sizes, presumably because they do not account for species interactions, land use pressures, and local topography/microclimates.

Clearly, for blue oak and other species with limited colonization potential, rapid climate change will present a serious challenge. To determine whether such species will be able to expand into new areas, evidence of low regeneration rates in their current habitats may be less informative than knowing under which conditions they do regenerate, and whether these conditions will be more or less prevalent in the future. Carmel and Flather show that areas previously cleared and used for agriculture may not support recolonization by oaks, while nearby woodland can fill in over time. In absolute terms, low regeneration rates in current habitat may not be a problem for species persistence with climate change, as long as recruitment replaces mortality. For blue oaks, there is some evidence that seedling/sapling:adult ratios are not sufficient in many areas to replace senescing trees, jeopardizing oak persistence with or without climate change (Zavaleta *et al.* unpublished). How-ever, high regeneration rates would not guarantee expansion into new habitat or persistence under changing climate, particularly if new, climatically suitable areas are remote or have been intensively modified by human activities, or if climate change results in new competition with more successful species. Given these uncertainties, we agree with Pearson and Dawson (2003) that CEMs, when used with high-resolution climate change scenarios, are valuable for providing first-order estimates of the potential impacts of climate change for many species for which we have scant ecological data. They are particularly useful if they prompt hypotheses that can be tested with further analyses, observations, and experiments to address the diverse ecological and landscape challenges species face when shifting their ranges with climate change.

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