

# Migration rate limitations on climate change-induced range shifts in Cape Proteaceae

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#### ABSTRACT

Modelling of climate change-induced species range shifts has generally addressed migration limitations inadequately, often assuming 'null' migration or instantaneous 'full' migration extremes. We describe methods for incorporating simple migration rate assumptions into multispecies modelling, using the Proteaceae of the Cape Floristic Region. Even with optimistic migration assumptions, range loss projections more closely approximate null migration than full migration assumptions. Full migration results were positively skewed by few species with large range increases, an overestimate eliminated by dispersal-limited migration rate assumptions. Windand ant/rodent-dispersed species responded differently to climate change. Initially larger ranges of wind-dispersed species were more strongly reduced by climate change, despite far greater assumed dispersal distances - we suggest that these welldispersed species populate more marginal areas of potential range, causing lower resilience to climatic changes at range margins. Overall, range loss rate slowed with advancing climate change, possibly because species ranges contracted into core areas most resilient to climate change. Thus, a consideration of simple dynamics of range change (rather than single step, present-future comparisons of range) provide new insights relevant for conservation strategies, in particular, and for guiding monitoring efforts to detect and gauge the impacts of climate change on natural populations.

#### Keywords

Bioclimatic models, conservation, dispersal, extinction, fynbos, GAM, global change.

## INTRODUCTION

Evidence from palaeoecological studies (Prentice *et al.*, 2000; Davis & Shaw, 2001) and multiple signs of species geographical range shifts in apparent response to regional warming (Parmesan & Yohe, 2003; Root *et al.*, 2003) suggest that migration will be a major autogenic adaptive response of wild species to ongoing and future climate change. However, rapid changes in local conditions threaten to outpace migration abilities in non-vagile species (Pounds *et al.*, 1999), with negative implications for species persistence. Dispersal abilities and migration rates are emerging as among the most significant uncertainties in projecting climate change impacts on populations and communities (Pitelka, 1997; Neilson *et al.*, 2005), and on projections of potential changes in biodiversity (Peterson *et al.*, 2002; Thomas *et al.*, 2004; Thuiller *et al.*, 2005).

Niche-based modelling (see Guisan & Thuiller, 2005; for a review) has been widely applied as a tool to project species range shifts under changing climate regimes (Huntley *et al.*, 1995; Midgley *et al.*, 2003; Thuiller, 2003), and despite its many assumptions and shortcomings (Hampe, 2004), has been widely

used to assess risks of species range loss and extinction. Next to the uncertainties relating to niche-based modelling (Thuiller *et al.*, 2004a; Thuiller, 2004) and GCM (global climate model) projections of climate (Weaver & Zwiers, 2000), uncertainties due to migration rate result in a wide range in the projections of impacts on species ranges (Higgins *et al.*, 2003a). Niche-based modelling efforts, with few exceptions (Carey, 1996; Schwartz *et al.*, 2001; Iverson *et al.*, 2004), have not yet attempted to narrow uncertainties due to migration and commonly project species range shifts under two extreme assumptions — 'null' (zero) and 'full' (unlimited and instantaneous) migration.

Migration of plant species is a complex process determined by fecundity, dispersal ability, and population establishment and growth rate (Higgins *et al.*, 2003b). Dispersal is commonly seen as the major limiting step in this process, but the populationlevel processes that make up the migration process are also important (Malanson & Cairns, 1997; Higgins *et al.*, 2003b). Modelling of dispersal limitations has explored the role of habitat fragmentation and suitability on stand level diversity (Malanson & Armstrong, 1996), and some protocols for simulating migration processes in range shift modelling have been developed (Collingham *et al.*, 1996; Collingham & Huntley, 2000; Schwartz *et al.*, 2001), but they require species-specific parameterization, and thus are not yet suitable for multiple species modelling efforts.

Here we describe a method that makes simple assumptions of migration rate that can be incorporated into typical niche modelling approaches to project species' range shifts due to global change. The method can be used to explore the role of migration assumptions beyond the simple assumptions of null and full migration commonly made previously. We use the method to assess whether dispersal-limited estimates yield range shift results more similar to null or full migration assumptions, and compare the responses of Cape Proteaceae species with two different dispersal vectors: namely, animals (short-distance dispersal by ants or rodents) and wind (potentially long-distance dispersal).

## METHODS

## Data sources

We consider range responses of 336 Proteaceae species endemic or nearly endemic to the Cape Floristic Region (CFR) of South Africa. Species distribution data were taken from the Protea Atlas Project (PAP) database, comprising field-determined species presence and absence at more than 60,000 georeferenced sites, totalling more than 250,000 species records (see http:// www.nbi.ac.za/protea). Modelling was conducted using a grid of  $1 \times 1$  minute cells (1.85 × 1.55 km, area approximately 2.87 km<sup>2</sup> at this latitude). Climate data were interpolated for the oneminute grid (Schulze, 1997). Future projections were based on (Schulze & Perks, 1999), according to the 2050 projections for the region from the General Circulation Model HadCM2 (see http://cera-www.dkrz.de/IPCC\_DDC/IS92a/Hadley-Centre/ Readme.hadcm2), using IS92a emissions assumptions for CO<sub>2</sub> equivalent greenhouse gas concentrations, and excluding sulphate cooling feedback. We included in species models three soil variables: fertility, sand, and clay content, as defined and mapped by Schulze (1997). This is a minimum set that may influence plant performance both through nutrient availability and through soil texture effects on soil water. Information on nomenclature and on species' dispersal vectors was taken from Rebelo (2001).

For this exercise we ignored the impacts of habitat transformation and changing land use on range, as we aim to illustrate a general principle rather than make specific projections for landuse planning or conservation purposes. We acknowledge that land transformation compounds the effects of climate change, and is likely to exacerbate range losses due to climate change (Travis, 2003).

## **Bioclimatic and dispersal time-slice modelling**

Models relating species distributions to five bioclimatic variables critical for plant growth (Midgley *et al.*, 2003) were fitted using a generalized additive modelling (GAM) approach (Yee & Mitchell, 1991) on a random sample of the initial data (70%). The model for each species was evaluated on the remaining 30% of the

initial data set using the values obtained for the area under the curve (AUC) of a receiver operating characteristic (ROC) plot of sensitivity against (1-specificity) (Swets, 1988). Sensitivity is defined as the proportion of presences correctly predicted, whereas specificity is the proportion of absences correctly predicted. We transformed the modelled probability of occurrence back to presence/absence using a threshold maximizing the percentage of presence and absence correctly predicted (Pearce & Ferrier, 2000; Guisan & Thuiller, 2005).

From ROC curve analysis, only one species had an AUC less than 0.8 (i.e. fair model, the exception being *Leucadendron salignum*, the most widely distributed Proteaceae in the CFR, with an AUC of 0.76). The median AUC value for all species was 0.98, indicating excellent fit, and therefore no species was excluded from the modelling.

Current and expected future distributions were modelled for individual Proteaceae species on the one-minute grid at 10-year time intervals -2000, 2010, 2020, 2030, 2040, and 2050, which we term decadal 'time slices'. We projected the niche-based models using climate data interpolated for each variable between 2000 and 2050 (i.e. we assumed a linear change in each climatic variable between 2000 and 2050). Our assumption of linear changes in climate variables is a pragmatic solution to modelling more complex temporal shifts in climate regime, and we adopted it to illustrate the method and to attempt to reduce complexity in interpretation of results introduced by possible extreme events. However, in a more complex application, modelling of more complex temporal shifts would make an interesting comparison, and would allow extreme event impacts to be assessed against the linear change assumption, possibly identifying changed projections for particularly event-sensitive species, for example.

Range shifts after 2000 were calculated under three migration assumptions: null migration, full migration, and dispersallimited range shift. Under null migration, only the range overlap between current range and future range was considered viable for each species. Under full migration, the entire future range for each time slice was considered viable.

For dispersal-limited range shifts, two methods were applied. In one method, an estimate of migration rate per decadal time slice was estimated according to the dispersal agent. Dispersal was assumed to be a maximum of one grid cell per time slice for ant- and rodent-dispersed species - this is likely to be an overestimate, given the pattern of transport and hoarding of seeds by these species over only a few metres from seed sources (Johnston & Bonde, 1989; Midgley et al., 2002), and a maximum of three cells per time slice for wind-dispersed species, at the high end of the range determined by empirical measurements for seed dispersed by secondary 'tumbling' seed dispersal (Bond, 1988; Schurr et al., 2005). The latter corresponds to at least 4 km in 10 years (i.e. per fire event), or an average of 400 m in 1 year, which may be considered long-distance dispersal (Cain et al., 2000), and compares with high rates as inferred from the fossil record (Clark et al., 1998). We did not model rare exceptional long-distance dispersal events, as the size of fires ultimately sets the limit for potential seed dispersal distance (viable seeds would either not germinate or establish in unburnt vegetation).



**Figure 1** Modelled range (a) for an ant/rodent-dispersed species at time slice (t), as represented on the spatial grid by light grey-coloured cells. In (b) the range at time slice (t) is overlaid with the projected range at time slice (t + 1) represented by outlined cells. In (c) the cells marked 'x' are considered climatically unsuitable at time (t + 1) under all three dispersal assumptions, and thus are no longer part of the species range. The updated range (c) at time slice (t + 1) is therefore given by the dark grey-coloured cells under the null migration assumption, by the union of the dark grey and intermediate grey cells under the dispersal limited assumption, and by the union of dark-grey, intermediate, and light grey cells under the full migration assumption.

Dispersal events were assumed to occur on average every decade, assuming decadal fires that provide the only dispersal opportunities to these fire-adapted species — this fire return time is probably above average for the CFR, but greater than the minimum required for seed set in Proteaceae (Bond *et al.*, 1995).

**Table 1** Impacts of climate change on the range size (in terms of<br/>numbers of pixels of  $1' \times 1'$  size), range increase and extinctions<br/>(complete elimination of potential range) of Cape Proteaceae<br/>(climate scenario based on Schulze & Perks (1999) according to the<br/>2050 projections for the Cape Floristic Region from the General<br/>Circulation Model HadCM2). Numbers in brackets are standard<br/>errors of the means reported

	2000 (current modelled)	2050 full migration	2050 null migration	2050 dispersal- limited
Range size (no. of pixels)				
All species $(n = 336)$	1898 (108)	1349 (165)	466 (54)	802 (104)
Wind-dispersed $(n = 202)$	2364 (179)	982 (111)	478 (48)	724 (73)
Ant/rodent-dispersed $(n = 134)$	1590 (131)	1592 (264)	458 (84)	878 (166)
Range increasers (no. of species)				
Wind-dispersed		19	_	10
Ant/rodent-dispersed		62	_	38
Extinctions (no. of species)				
Wind-dispersed		2	11	5
Ant/rodent-dispersed		9	27	18

Figure 1 illustrates how the migration expansion limits for ant/ rodent- and wind-dispersed species were applied iteratively to the modelled time-slice ranges. It was further assumed that bioclimatically unsuitable areas would not persist as viable range between time slices. The result was time-slice models for each species for each of the years 2000, 2010, 2020, 2030, 2040, and 2050 according to all three assumptions.

In a second method, we used a greatly simplified approach to the one described above, by assuming 'one-step' dispersal between 2000 and 2050. In other words, over 50 years we assumed a maximum dispersal distance of five cells (one cell per decade) for animal-dispersed species and 15 cells (three cells per decade) for wind-dispersed species over that time period, and used these dispersal distances to link the 2000 and 2050 range maps for each species, as described in Fig. 1.

## RESULTS

Species range changes at 2050 varied widely, with the greatest variability shown under the full migration assumption. With full migration, 255 species overall showed range decreases, and 81 showed increases, compared with 47 species that showed a range increase given dispersal-limited range shifts, and, by definition, no species with null migration assumptions (Table 1). Overall mean species range sizes were reduced by climate change in 2050 by 29% with full migration, by 75% with null migration, and by an intermediate figure of 58% assuming dispersal-limited range shift (Table 1).

Range shift results differed between ant/rodent- and winddispersed species. Overall, wind-dispersed species had 49% larger



Figure 2 Time course of range changes for wind-dispersed (a) and ant/rodent-dispersed (b) Proteaceae species, given different dispersal assumptions; 'full migration' (big dots) assumes no limitation to migration, 'null migration' (small dots) assumes zero migration potential, and 'dispersal limited' (circles) uses the methods described here to simulate either decadal dispersal events, or 'one step' dispersal between 2000 and 2050 (open symbols offset from 2050). Rate of change (triangles, secondary axis) is the mean rate of range change between decadal time slices for the 'dispersal limited' assumption. Error bars represent standard errors.

modelled ranges under current climate conditions than did ant/ rodent-dispersed species. Under full migration assumptions, 62 of the 134 ant/rodent-dispersed species showed mean range increases by 2050 of 13 times their current range size (Table 1). This average increase was strongly skewed by five species that increased range by more than 20 times, two species by more than 40 times, and one species by almost 450 times, with the remainder showing relatively small range increases. Only 19 of 202 wind-dispersed species showed increases in range, averaging 17.5 times their current range (but dominated by three species with range increases of 66, 83 and 147 times current range size, data not shown). These numbers dropped with dispersal-limited range shifts to 38 and 10 species, respectively, for the two dispersal types, with range size increases averaging only 1.5 and 1.3 times (data for range increases only not shown).

The mean range size of ant/rodent-dispersed species (see Table 1) did not change by 2050 with full migration assumptions, but decreased by almost 71% with null migration assumptions, and by 45% with dispersal-limited range shift. For winddispersed species, ranges decreased by 58%, 80%, and 69% under full, null, and dispersal-limited range shift assumptions. Dispersal assumptions also had significant impacts on projections of species extinction, as reflected by the projection of complete range loss by 2050 (Table 1). Two and nine extinctions in wind- and animal-dispersed groups, respectively, increased to five and 18 under dispersal-limited assumptions and to 11 and 27 species, respectively, under null migration assumptions.

The dynamics of range change over time reveals interesting differences between animal- and wind-dispersed species, and the important moderating role of migration assumptions in range change projections (Fig. 2). Dispersal-limited range shifts are, obviously, intermediate between null and full migration projections for wind-dispersed species (e.g. Fig. 3), but on average are somewhat closer to null dispersal projections for ant/rodentdispersed species as illustrated in Fig. 2a,b. Wind-dispersed species (Fig. 2a) show a rapid initial absolute decrease in range size, but in relative terms, range size loss peaks at roughly 20% between 2020 and 2030 and declines slightly afterward. For ant/rodentdispersed species, the initial absolute range reduction is also high, but mean range size surprisingly increases with full migration assumptions after 2030 and returns to original mean range size. This is due to the few species that show very large modelled increases in range size, as discussed above. Under assumptions of no migration, the rate of range loss began to drop after 2020, and range size had almost stabilized by 2050, albeit at about 25% of the original mean range size. With migration-limited range change assumptions, this stabilization of range loss was projected to occur even more rapidly, and at about 50% of original mean range size.



Figure 3 Resulting modelled geographical ranges for *Leucospermum rodolentum*, an ant-dispersed protea, using null migration (top), dispersallimited (middle), and full migration assumptions (bottom).

Using the simplified 'one-step' dispersal method, the resulting ranges of species at 2050 were higher by approximately 10% than those obtained using the 'time-slice' method (Fig. 2a,b).

#### DISCUSSION

Projections of climate change impacts on species persistence, and hence community richness, biodiversity, and ecosystem function are weakly constrained due to large uncertainties, important among these are assumptions relating to the expected migration rates of species (Pitelka, 1997; Higgins et al., 2003a). Uncertainties due to migration rates raise concerns for conservation planning, especially given that signs of range shifts are emerging in nature (Parmesan & Yohe, 2003; Root et al., 2003). These uncertainties lead to a wide range in projections of species extinction risk (Thuiller et al., 2005), with important implications for conservation planning that is increasingly seeking spatially explicit guidance on adapting to climate change impacts (Araújo et al., 2004; Rodrigues et al., 2004) or finding ways of adjusting estimates of extinction risk to species (Bomhard et al., 2005). We find here that relatively simple migration rate estimates can credibly moderate range projections based on unrealistic full migration assumptions, and provide a narrower range of uncertainty for range shift projections, and related projections of species' risk of extinction. We also find that full dispersal assumptions may grossly underestimate range losses and overestimate range gains relative to the more conservative null dispersal and dispersal-limited range shift projections, and should essentially be abandoned in any realistic planning or projection exercise for plant species.

The problem of migration has been addressed by complex approaches (Collingham *et al.*, 1996; Malcolm *et al.*, 2002; Clark *et al.*, 2003; Higgins *et al.*, 2003b). These approaches are useful in their context, and have allowed, for example, exploration of the role of landscape fragmentation in exacerbating climate change

(Collingham & Huntley, 2000; Higgins *et al.*, 2003b). However, protocols to incorporate these findings into simple bioclimatic modelling approaches have not yet emerged. As we show, it is a relatively easy matter to incorporate some straightforward migration rules into these approaches, but these rely in our case study on some important simplifications.

Most importantly, the 'time-slice' approach depends on the interpolation of species ranges in a series of time slices - in the case of the flammable CFR ecosystems, the assumption of 10 year intervals between dispersal events greatly reduces the complexity of iterative range shift calculations. In the case of plants dispersing annually, it may be feasible to assume average migration distances for 10-year periods and apply the method we have used. One of the key points here is the spatial grid scale being modelled — pixel sizes of roughly  $1.5 \times 1.8$  km as used by us may demand integrating and applying dispersal rules over time intervals longer than one or two years when using this straightforward approach. Taking this concept further, it is tempting to apply the simplifying assumption of 'one-step' dispersal by estimating the maximum dispersal distance over the time period in question and applying this as we have described - however, we show here that this method may overestimate the resulting modelled range, and also obscures the potentially useful dynamics of modelled range change revealed by the 'timeslice' approach. It is likely that the optimal frequency of timeslices is determined by an interaction between spatial scale and dispersal distance — and it would be useful to explore this in refining the method.

The more complex approaches developed up to now to incorporate migration in species range projections are not currently well suited to the multiple species analyses being conducted in many systems worldwide (Midgley & Thuiller, 2005). This is because they require careful parameterization of species-specific parameters that may have significant impacts on projection results, and therefore add to uncertainty if used inappropriately,

rather than reduce it in the way that we have done using simple assumptions with traceable effects. Nonetheless, it remains desirable and necessary to develop more realistic methods of modelling species range shifts to cater for the increasing needs of conservation planners for advice on spatially explicit strategies for ensuring species persistence (Midgley & Thuiller, 2005). For example, the approach we describe could also easily incorporate land-use impacts on migration through moderating the availability of cells as migration routes, where land use acts as a filter for dispersal events (e.g. Williams et al., 2005). But most importantly, a major factor missing from this approach is the persistence of populations, either as consistent or as occasional sources of propagules in parts of the geographical range that are modelled to become unsuitable for the species. Persistence of established individuals or seed banks under unsuitable conditions or in response to disturbance may be a significant means of avoiding local extinction especially for long-lived species (e.g. Bond & Midgley (2001), but is currently not considered in range shift modelling of the type described here. This shortcoming is especially important for conservation strategies, as it may provide additional time for adaptation strategies to keep pace with climate change impacts, and add to the resilience of populations and their potential dispersal in a changing climate.

The dynamics of range change over time in the Proteaceae modelled reveals an interesting phenomenon in that the rate of range reduction is not constant with time, and its time course differs between ant/rodent- and wind-dispersed species. Winddispersed species appear to be far more susceptible to range reduction than ant/rodent-dispersed species, especially beyond 2020, and this occurs despite the threefold higher migration rate accorded them. It is possible that ant/rodent-dispersed species find themselves restricted closer to a core geographical range where climate is most suitable for their persistence, whereas wind-dispersed species explore more marginal areas of their potential geographical range due to their greater vagility (Thuiller et al., 2004b). This interpretation is supported by a review of a range of European and North American species showing that dispersal plays an important role, in addition to physiological characteristics, in controlling species geographical ranges (Woodward & Kelly, 2003).

A related pattern that also emerges is the apparent reduction in range loss rate with advancing climate change. This suggests either that future climate change impacts may restrict species to core ranges, as controlled physiologically, but that these may be quite resilient to longer term climate change, or that rare species are lost progressively and resilient generalist species remain. We are not aware of other studies that have explored the time course of range shifts in response to climate change at this level of time resolution — but the finding certainly provides some hope that conservation strategies could capitalize on those parts of the species range defined as 'core' to facilitate a higher level of resilience to climate change in target areas. This insight could also guide field-based monitoring efforts to gauge the relative impact of climate change on natural populations at key points in their ranges, and provide a well-focused early warning system for conservation planners.

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