**BIODIVERSITY RESEARCH**

# Impacts of past habitat loss and future climate change on the range dynamics of South African Proteaceae

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## ABSTRACT

**Aim** To assess how habitat loss and climate change interact in affecting the range dynamics of species and to quantify how predicted range dynamics depend on demographic properties of species and the severity of environmental change.

**Location** South African Cape Floristic Region.

**Methods** We use data-driven demographic models to assess the impacts of past habitat loss and future climate change on range size, range filing and abundances of eight species of woody plants (Proteaceae). The species-specific models employ a hybrid approach that simulates population dynamics and long-distance dispersal on top of expected spatio-temporal dynamics of suitable habitat.

**Results** Climate change was mainly predicted to reduce range size and range filling (because of a combination of strong habitat shifts with low migration ability). In contrast, habitat loss mostly decreased mean local abundance. For most species and response measures, the combination of habitat loss and climate change had the most severe effect. Yet, this combined effect was mostly smaller than expected from adding or multiplying effects of the individual environmental drivers. This seems to be because climate change shifts suitable habitats to regions less affected by habitat loss. Interspecific variation in range size responses depended mostly on the severity of environmental change, whereas responses in range filling and local abundance depended mostly on demographic properties of species. While most surviving populations concentrated in areas that remain climatically suitable, refugia for multiple species were overestimated by simply overlying habitat models and ignoring demography.

**Main conclusions** Demographic models of range dynamics can simultaneously predict the response of range size, abundance and range filling to multiple drivers of environmental change. Demographic knowledge is particularly needed to predict abundance responses and to identify areas that can serve as biodiversity refugia under climate change. These findings highlight the need for data-driven, demographic assessments in conservation biogeography.

## INTRODUCTION

Habitat loss and climate change are major drivers of biodiversity loss (Sala *et al.*, 2005; Pereira *et al.*, 2010). While habitat loss has already caused severe habitat transformations and species extinctions in the past (e.g. Tabarelli *et al.*, 1999; Latimer *et al.*, 2004; Helm *et al.*, 2006), climate change is expected to exacerbate biodiversity loss in the future (e.g. Bakkenes *et al.*, 2002; Thomas *et al.*, 2004; Thuiller *et al.*, 2005). Moreover, climate change and habitat loss are likely to mutually reinforce their adverse impacts on the persistence of species and populations (Warren *et al.*, 2001; Dirnböck *et al.*, 2003; Higgins *et al.*, 2003a; Travis, 2003; Opdam & Wascher, 2004; Pyke, 2004; Franco *et al.*, 2006; Pompe *et al.*, 2008; Yates *et al.*, 2010a). Firstly, this is because habitat loss reduces population sizes, which generally increases the susceptibility of populations to environmental change (Pearson & Dawson, 2003; Brook *et al.*, 2008). Secondly, habitat loss typically lowers habitat connectivity, thereby reducing migration rates and the ability of species to survive under future climate change (Higgins *et al.*, 2003a; Opdam & Wascher, 2004). So far, however, there is little quantitative understanding of how habitat loss and climate change interact in their effect on the large-scale dynamics of species.

Clearly, the future dynamics of species ranges will not only depend on the severity of environmental change but also on species traits (Morin *et al.*, 2008). For example, the ability for long-distance dispersal determines migration rates of species under environmental change (Higgins *et al.*, 2003b; Travis, 2003; Midgley *et al.*, 2006; Brooker *et al.*, 2007; Nathan *et al.*, 2008, 2011). Moreover, species suffering from reduced reproduction in small populations, (so-called Allee effects, Allee *et al.*, 1949) are expected to be more susceptible to global change because of higher local extinction (Stephens & Sutherland, 1999; Courchamp *et al.*, 2008) and lower migration rates (Kot *et al.*, 1996; Keitt *et al.*, 2001). Consequentially, Allee effects can play a pivotal role for range dynamics (Keitt *et al.*, 2001; Cabral & Schurr, 2010). The importance of other demographic traits (such as the environmental response of birth and death rates) for range dynamics and species responses to environmental change is only starting to be understood (Schurr *et al.*, 2007; Jeltsch *et al.*, 2008; Keith *et al.*, 2008; Anderson *et al.*, 2009; Pagel & Schurr, 2012).

To reliably assess the impacts of environmental change on species distributions, we thus need models that represent species traits affecting demographic processes. A step in this direction is so-called hybrid models (Thuiller *et al.*, 2008) that link correlative models for the dynamics of suitable habitat with demographic models of population dynamics within suitable habitats (Keith *et al.*, 2008; Cabral & Schurr, 2010; Midgley *et al.*, 2010). Hybrid models can describe the transitory dynamics of range size, range filling (the proportion of suitable habitat that is occupied, Svenning & Skov, 2004), local and global abundances under the non-equilibrium conditions caused by global change (e.g. Keith *et al.*, 2008;

Cabral & Schurr, 2010). The possibility to assess abundance dynamics in space and time is crucial because it yields information relevant for conservation planners (e.g. for extinction risk categorizations - IUCN, 2001). However, uncertainty about demographic processes and the parameters relevant for range dynamics is a major obstacle to the widespread application of such hybrid models (Cabral & Schurr, 2010). To overcome this problem, Cabral & Schurr (2010) developed a framework that statistically estimates hybrid models from data on large-scale abundance distributions and enables selection between alternative models for population dynamics. This serves to identify traits and processes that govern the range dynamics of a target species. Moreover, it enables the development of data-driven forecasts of range dynamics under impending environmental change.

While process-based demographic models are thus likely to improve forecasts for specific species, it seems impossible to parameterize these models for all species potentially threatened by environmental change (Myers *et al.*, 2000). Therefore, we have to find ways of generalizing predictions from a few well-studied species to the many other species for which species-level assessments are impossible (Yates *et al.*, 2010b). In particular, it is important to understand how much of a species' response to environmental change can be explained by the strength of habitat loss and habitat shift, and how much can be explained by species traits.

In this study, we use hybrid models estimated from species distribution data (Cabral & Schurr, 2010) to investigate how past habitat loss and future climate change affect the large-scale dynamics of eight species of woody plants (Proteaceae endemic to the South African Cape Floristic Region, CFR). The CFR is a global biodiversity hotspot (Myers *et al.*, 2000), which in the past lost about 30% of its natural habitats because of agriculture, urbanization and the invasion of alien species (Rouget *et al.*, 2003). Additionally, future climate change is predicted to reduce and shift the habitat of many Proteaceae (Midgley *et al.*, 2002, 2003, 2006; Thomas *et al.*, 2004; Bomhard *et al.*, 2005; Keith *et al.*, 2008). We thus aim (1) to assess effects of habitat loss, climate change and their interaction on future range size, abundance and range filling, (2) to quantify the relative importance of demographic properties and the strength of environmental change for predicting range dynamics, and (3) to compare the ability of hybrid models and correlative habitat models to identify biodiversity refugia in which viable populations can persist in the future.

## METHODS

### Study system

We studied eight Proteaceae species that are endemic to the CFR's Fynbos biome (Table 1). Recurrent wildfires drive the population dynamics of these species by triggering seed dispersal, recruitment, individual mortality and local population extinction (Bond & van Wilgen, 1996; Schurr *et al.*, 2007). The study species do not build persistent soil seed banks but

Table 1 Properties of the studied CFR Proteaceae species. Species were grouped as related pairs (Rebelo, 2001) of non-sprouter (n) and sprouter (s). The models for local population dynamics and the parameter values were obtained from Cabral & Schurr (2010). Parameters are adult mortality ($M$), local extinction probability ($E$), maximum reproductive rate ($R_{max}$), carrying capacity ($K$, in ind. $km^{-2}$) and Allee critical point ($C$, in ind. $km^{-2}$). $M$ was 1 for non-sprouters. Dispersal ability was given as the percentage of seeds that are dispersed over 1 km and was calculated by mechanistic models (from Schurr et al., 2007). Note that although L. xanthoconus had zero dispersal ability over 1 km, this species was still predicted to reach neighbouring cells because seeds dispersed from cell centre.

| Species (persistence ability) | Red data list* | Model[†] | Parameter | | | | | Dispersal ability (%) |
| | | | $M$ | $E$ | $R_{max}$ | $K$ | $C$ | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Protea compacta (n) | EN | B-H | (1) | 0.1 | 1.5 | 8700 | – | 0.067 |
| P. scorzonerifolia (s) | EN | B-H + A | 0.2 | 0.1 | 9 | 52,300 | −17400 | 0.0034 |
| P. stokoei (n) | EN | R | (1) | 0.15 | 1.5 | 8300 | – | 0.203 |
| P. speciosa (s) | VU | B-H | 0.001 | 0.005 | 1 | 13,100 | – | 0.0039 |
| Leucadendron modestum (n) | EN | R + A | (1) | 0.1 | 9 | 348,700 | −17,400 | 0.00002 |
| L. lanigerum lanigerum (s) | EN | B-H + A | 0.675 | 0.005 | 4 | 90,2400 | 10,500 | 0.00002 |
| L. xanthoconus (n) | VU | R + A | (1) | 0.0025 | 14.5 | 279,000 | −130,800 | 0 |
| L. salignum (s) | LC | B-H + A | 0.4 | 0.0005 | 7.5 | 87,200 | 1700 | 0.00025 |

*EN, endangered; VU, vulnerable; LC, least concern (Rebelo, 2008).
[†]Local population dynamics models: B-H, Beverton-Holt; R, Ricker; B-H + A, Beverton-Holt with Allee effects; R + A, Ricker with Allee effects (see Appendix S1).

are serotinous, which means that they store their seeds in cones in the canopy (Rebelo, 2001). Cone opening, seed release, dispersal and subsequent recruitment happen shortly after a fire and wind is the predominant vector of long-distance seed dispersal (Bond, 1988; Cowling, 1992; Le Maitre & Midgley, 1992; Bond & van Wilgen, 1996; Rebelo, 2001; Schurr et al., 2005, 2007).

Cape Floristic Region Proteaceae show two alternative persistence strategies: adults of sprouter species can survive fire, whereas non-sprouter species (also called reseeders) only survive fire as seeds (Bond & van Wilgen, 1996; Bond & Midgley, 2001, 2003). Hence, sprouters are iteroparous with overlapping generations, whereas non-sprouters are semelparous with non-overlapping generations (Bond & van Wilgen, 1996; Bond & Midgley, 2001, 2003). We considered four pairs of related sprouter and non-sprouter species (Rebelo, 2001; Reeves, 2001; Table 1). Because inter-fire recruitment and inter-fire adult mortality are negligible, the population dynamics of the study species proceeds in discrete time steps whose length is determined by fire return intervals (Bond et al., 1995). Besides the 'regular' fires that result in successful regeneration of Proteaceae populations, fires with shorter return intervals can cause catastrophic local extinction of immature populations. Such 'irregular' fires are typically small because of slow post-fire accumulation of flammable biomass. The susceptibility to catastrophic extinction is higher for non-sprouters and increases with the age of first reproduction (Schurr et al., 2007; Rebelo, 2008; Cabral & Schurr, 2010). These relatively simple assumptions describe fire mortality and extinction for the large majority of cases. Yet, under certain circumstances, variability in fire intensity and season as well as fire refugia in complex terrain may complicate fire effects.

The geographical distributions of the study species seem to be shaped by metapopulation-like dynamics with local extinctions and (re-)colonization of habitat patches (Schurr et al., 2007; Cabral & Schurr, 2010; Cabral et al., 2011). Moreover, Allee effects may reduce the fecundity of serotinous Proteaceae (Lamont et al., 1993) and were found to shape range dynamics of five of our study species (Cabral & Schurr, 2010). Under future climate change, the habitat of all but one study species is predicted to contract and to undergo moderate to strong shifts (Midgley et al., 2003). The exception is Protea stokoei, whose habitat is predicted to slightly expand.

## Model description and simulation design

To assess how habitat loss and climate change impact range size, range filling and local abundance of the study species, we used spatially explicit hybrid models that describe how range dynamics of Proteaceae arise from the dynamics of local populations connected by long-distance seed dispersal (Cabral & Schurr, 2010). These hybrid models integrate species-specific habitat models (Midgley et al., 2003) and species-specific mechanistic predictions of long-distance seed dispersal by wind (Schurr et al., 2005, 2007). To determine unknown parameters describing local population dynamics of the study species, Cabral & Schurr (2010) fitted the demographic model to extensive data on range-wide variation in local abundances (from the Protea Atlas Database, Rebelo, 2001).

The model is grid-based with each grid cell having a size of $1' \times 1'$ (ca. 1.55 km × 1.85 km) and holding one population. To describe the spatiotemporal dynamics of suitable habitat, we used predictions of species-specific generalized additive models that used five bioclimatic and three edaphic

variables to explain spatial variation in the presence and absence of each species (details in Midgley *et al.*, 2003 and in Schurr *et al.*, 2007). Based on the distribution of suitable grid cells, the demographic model describes local reproduction, long-distance seed dispersal, recruitment, individual mortality and local extinction. Model parameters are maximum reproductive rate, carrying capacity, per-fire mortality of adults ($M$), probability of local extinction and Allee critical point (for species subject to Allee effects). Fire was not modelled explicitly, but the local extinction probability describes the effects of catastrophic fires. Most study species co-occur so that interspecific differences in demographic parameters are likely to arise from trait differences rather than environmental variability. A general description of the demographic model is given below (for details see Cabral & Schurr, 2010). In the model, local population dynamics proceed in discrete time steps following

$$\mathbf{N}(t+1) = S(\mathbf{N}(t)) + G(\mathbf{N}(t)) \qquad (1)$$

where the vectors $\mathbf{N}(t+1)$ and $\mathbf{N}(t)$ describe local abundances in all cells at time $t +$ and $t$, $S$ is a function describing adult survival and $G$ is a function describing dispersal and recruitment. For sprouters, the survival function $S$ is a binomial random variate with denominator $N_i(t)$ and success probability $1-M$, where $N_i(t)$ is the local abundance in cell $i$. For non-sprouters, $M = 1$ and $S(\mathbf{N}(t)) = 0$. The function $G$ describes the number of recruits with a Poisson distribution whose mean equals the expected number of offspring that is dispersed to each cell. For cell $i$, this expected number is

$$\sum_j D_{i,j} N_j(t) R(N_j(t)) \qquad (2)$$

where $D_{i,j}$ describes the per-offspring dispersal probability from cell $j$ to cell $i$ and the function $R$ describes the per-capita reproduction. With per time-step probability local extinction ($E$), local populations undergo catastrophic extinction, which sets local abundance to 0. These catastrophic extinctions occur independently for individual grid cells.

Species-specific two-dimensional dispersal kernels described the per-seed probability of dispersal from a source cell to each of the neighbouring cells in a 5 × 5 cell neighbourhood (typical extent of regular fires, Schurr *et al.*, 2007). These species-specific dispersal kernels were produced by validated mechanistic models for primary (airborne) and secondary (tumble) seed dispersal by wind that were parameterized with extensive measurements of dispersal environments and species-specific dispersal traits (Schurr *et al.*, 2005, 2007).

By combining these mechanistic dispersal kernels with habitat models (Midgley *et al.*, 2003) and alternative models for local population dynamics (for functions see Appendix S1 of the supporting information), Cabral & Schurr (2010) identified for each species the local population model and demographic parameter values that best explain range-wide abundance distribution (Table 1).

Simulations were initialized by setting the initial local abundances of all suitable cells to carrying capacity $K$. The initial habitat model represented occurrence probabilities for climatic conditions in 2000 (Midgley *et al.*, 2002, 2003). We ran the simulations for 1000 time steps to reach a quasi-stationary state. Subsequently, the environmental forcing factors entered the simulation following environmental change scenarios in a sequential fashion (see Fig. 1). The first time step under environmental change scenarios was assumed to be 1960. In this time step, we split the simulation and subjected the same abundance distribution to two scenarios: one with and the other without habitat loss. In 2010, each of the two parallel simulations was split again, and one simulation from each split was subject to climate change. This resulted in four scenarios: no environmental change (Control), habitat loss only (HL), climate change only (CC), or habitat loss and climate change (HL + CC) (Fig. 1). For each species, we ran 100 sets of these grouped simulations until 2050.
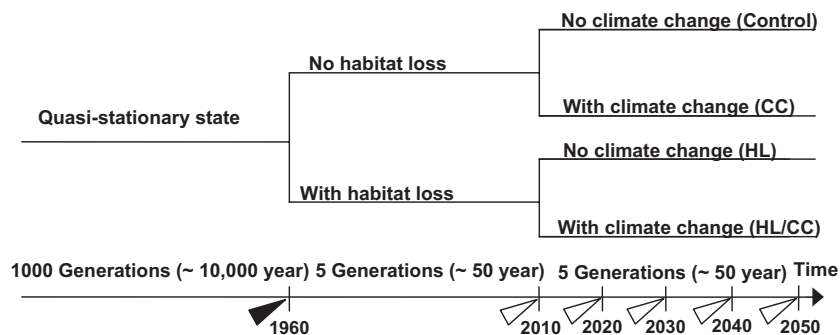


**Figure 1** Time schedule for the simulation of habitat transformation and climate change scenarios. Each simulation was first run for 1000 time steps, so that a species' range dynamics could reach quasi-equilibrium with its habitat. Thereafter, the simulation was split into two parallel simulations, of which one simulation underwent habitat loss (HL) in 1960. Subsequently, each of the two parallel simulations was again split into two simulations, of which one was exposed to climate change (CC) for five generations (~ 50 years), from 2010 to 2050. The onset of HL happened once (closed arrowhead), whereas gradual CC events occurred in five consecutive time steps (open arrowheads).

Past habitat loss was implemented as a sudden single event of habitat transformation in 1960 (Fig. 1). We described the spatial distribution of past habitat loss with data describing the proportion of each grid cell that was transformed by agriculture, urbanization and alien plant invasions (for details and maps, see Rouget *et al.*, 2003). In total, 30% of the CFR has been transformed (Rouget *et al.*, 2003). In the model, habitat transformation affected population dynamics by lowering the carrying capacity according to

$$K_{\text{eff},i} = H_i K, \qquad (3)$$

where $K_{\text{eff},i}$ is the effective carrying capacity in cell $i$ after habitat transformation, $H_i$ is the proportion of this cell that is untransformed and $K$ is the maximum carrying capacity of a cell without transformation (assumed to be constant). Note that the species experienced different habitat loss.

We described climate change using the species-specific habitat models to predict the distribution of suitable grid cells for climate forecasts of the HadCM2 global circulation model under the IS92a climate scenario (Houghton *et al.*, 1996; Bomhard *et al.*, 2005; Keith *et al.*, 2008). These habitat forecasts were produced for ten-year time slices from 2010 to 2050 and were sequentially applied to the climate change simulations in consecutive time steps, mimicking gradual climate change (Fig. 1).

To measure the overall severity of environmental change experienced by a species in a given scenario, we calculated a Habitat Shift Index (HSI):

$$\text{HSI} = (H_{\text{control}} - O_{2050})/H_{\text{control}} \qquad (4)$$

where $O_{2050}$ is the total amount of overlapping area between the suitable habitat in 2050 and the control scenario and $H_{\text{control}}$ is the suitable habitat of the control scenario. HSI can vary from 0 (all initial habitat is retained) to 1 (complete habitat shift). $O_{2050}$ and $H_{\text{control}}$ are calculated as the sum of $H_i$ over all cells belonging to the respective category. We also calculated a Habitat Loss Index (HLI) in a similar fashion, where $O_{2050}$ is substituted by the amount of lost habitat. However, as both indexes were highly correlated (Spearman's rho = 0.94), we excluded HLI from further analyses.

For each scenario, we finally overlaid the predicted ranges of all species to identify areas where the greatest number of study species is predicted to survive. This served to assess whether biodiversity refugia predicted by hybrid models differ from refugia predicted solely by habitat models.

### Analyses of simulation results

For all scenarios, we recorded from 2010 to 2050 the range size (number of grid cells), range filling (number of occupied cells divided by the number of suitable cells), mean local and global abundances. As global abundance was strongly correlated with range size (Spearman's rho = 0.876), we omitted it from further analyses. For the climate change scenarios, we additionally assessed to what extent the study species

colonized habitat that became newly available because of climate change. To this end, we also recorded range size and local abundances in this newly available habitat. To investigate the relative effects of climate change, habitat loss and their interaction, we performed two-way ANOVAs with range size, range filling and mean local abundance as response variables. We conducted ANOVAs with non-transformed and with log-transformed response variables to evaluate additive and multiplicative interactions between the two environmental change drivers, respectively. Note that these analyses focussed on effect sizes rather than statistical significance. This is because any significance level could be achieved by simply increasing the number of simulation replicates (Murray & Conner, 2009). All statistical analyses were conducted using R 2.6.2 (R Development Core Team, 2008).

To assess the importance of demographic properties and the strength of environmental change for relative changes in range size, range filling and local abundance (compared with the control scenario), we calculated the proportion of variance explained by different linear models that varied in their explanatory variables. These explanatory variables were either (1) the HSI index, (2) demographic properties (dispersal ability, maximum reproductive rate, carrying capacity, adult mortality rate, local extinction probability and Allee critical point) or (3) both HSI and demographic properties. For the latter model, we quantified the importance of each explanatory variable as its partial $R^2$. Note that we were interested only in the proportion of variance explained ($R^2$), not in whether model inputs significantly affect the model output (which we know is the case).

## RESULTS

Both climate change and habitat loss generally reduced the predicted abundance and occupied range of the study species. While habitat loss was predicted to affect mostly local abundances, climate change mainly altered range filling and range size (Fig. 2). The differential impacts of these two drivers of environmental change are exemplified for *Protea compacta*: habitat loss markedly decreased local abundance without changing range size, whereas climate change drastically reduced range size (Fig. 3). The effects of combined habitat loss and climate change were generally less severe than expected from both adding and multiplying the individual effects of climate change and past habitat loss (Fig. 2, Appendix S2). Under the combination of habitat loss and climate change, range size and range filling behaved similarly to the 'climate change only' scenario, whereas local abundances responses were more complex, but generally more similar to the 'habitat loss only' scenario (Figs 2 & 3, Appendix S2). Habitat loss and climate change do not seem to mutually reinforce their effects because habitat loss is higher in areas that were predicted to be never occupied or colonized (Fig. 4) and in areas becoming climatically unsuitable (for areas once occupied: interspecific median of 37% and interspecific range of 20–73% of cell area) than in areas
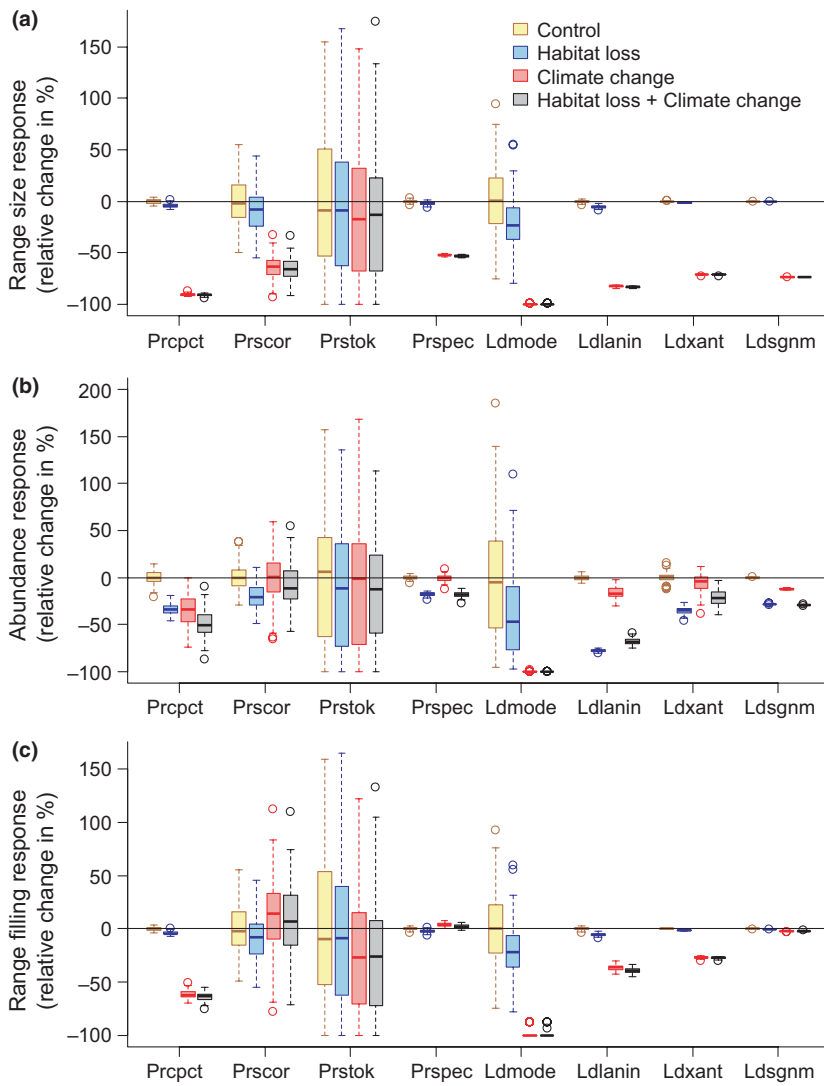
**Figure 2** Effects of past habitat loss and future climate change on range size (a), local abundance (b) and range filling (c) in 2050. Effects are measured as changes relative to the respective predictions for the control scenario without environmental change. Box plots show variation between 100 simulation replicates. Whiskers represent 1.5 interquartile ranges, whereas circles are outliers. Species acronyms are Ldlanin: *Leucadendron lanigerum lanigerum*, Ldmode: *L. modestum*; Ldsgnm: *L. salignum*, Ldxant: *L. xanthoconus*, Prcpct: *Protea compacta*, Prscor: *P. scorzonerifolia*, Prspec: *P. speciosa*, Prstok: *P. stokoei* (Rebelo, 2001).
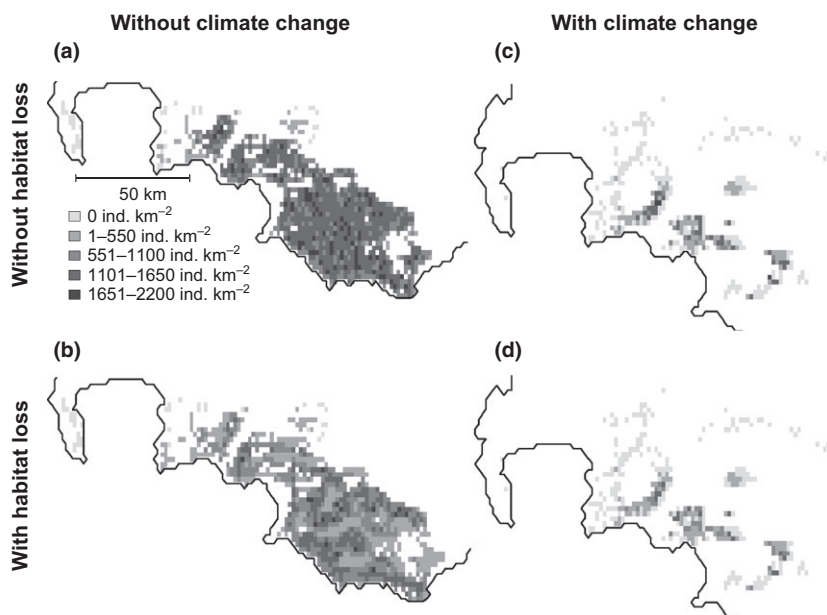


**Figure 3** Range-wide abundance distribution of *Protea compacta* in 2050 as predicted for (a) the control scenario without climate change and without habitat loss, (b) habitat loss only, (c) climate change only, and (d) climate change and habitat loss. Different shades of grey indicate local abundance averaged over 100 replicate simulations. Note that the light grey area with 0 individual/ha illustrates the unoccupied but suitable habitat. Most of the range in (c) and (d) corresponds to areas predicted to be climatically suitable from the present through 2050.
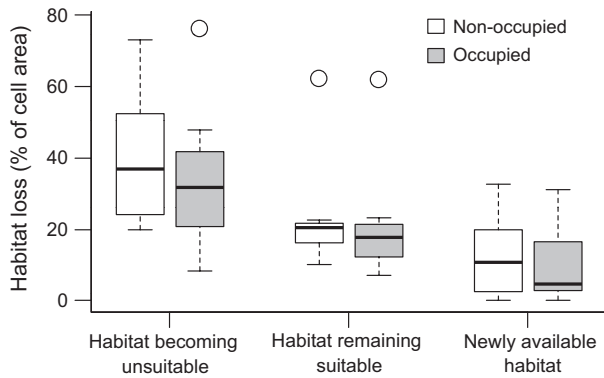
**Figure 4** Past habitat loss in parts of species ranges predicted to be differentially impacted by climate change up to 2050. The box plot distinguishes areas becoming climatically unsuitable, remaining suitable or becoming newly suitable in which the study species are predicted to be present or absent. For each category, the boxes indicate interspecific variation in habitat loss among the eight study species, whiskers represent 1.5 times the interquartile range and circles denote outliers.

remaining suitable (for occupied area: median, 18% and range, 7–62%) as well as in areas expected to become newly available (for colonized area: median, 4% and range, 0–31%, see Fig. 4).

Beyond these general trends, the study species showed marked differences in their response to environmental change (Fig. 2). Six species were predicted to have 100% survival probability in all scenarios, but smaller survival probabilities were found for the narrowly distributed *P. stokoei* (97% for all scenarios, including the control) and for

*Leucadendron modestum* (7% under scenarios with climate change against 100% for scenarios without climate change). *Leucadendron modestum* was predicted to have very low ability to migrate under climate change: in the few surviving simulations, it was restricted to a single population in 2050 (Fig. 5). In contrast, the range size, range filling and local abundance of *P. stokoei* showed no clear response to environmental change (Fig. 2). The range filling of two species (*P. scorzonerifolia* and *P. speciosa*) even increased under climate change (Fig. 2). However, this was attributed to a decrease in habitat area rather than an increase in range size.

In general, the study species were predicted to persist mostly in the portion of their current habitat that remains suitable (Fig. 3). Interspecific differences in responses to climate change were partially due to differences in the ability to colonize newly available habitat. When considering related species and both scenarios with climate change, non-sprouter *Protea* species had higher range size (mean = 6 km$^2$) and higher range filling (mean = 4%) at the newly available habitat compared with their sprouting relatives (range size: mean = 0.9 km$^2$; range filling: mean = 1.3%). All *Protea* species were present in very low densities at the newly available habitat (mean = 98 ind. km$^{-2}$). For non-sprouter *Leucadendron* species, range size (mean = 38 km$^2$) and range filling (mean = 13.3%) in the newly available habitat were lower compared with their sprouting counterparts (228 km$^2$ mean range size; 45% mean range filling). Moreover, *Leucadendron* largely varied their predicted abundances at the newly available habitat (210 000 ind. km$^{-2}$, 140 ind. km$^{-2}$, 1 ind. km$^{-2}$, 315 ind. km$^{-2}$ mean abundances for *L. xanthoconus*, *L. lanigerum lanigerum*, *L. modestum*, *L. salignum*, respectively).
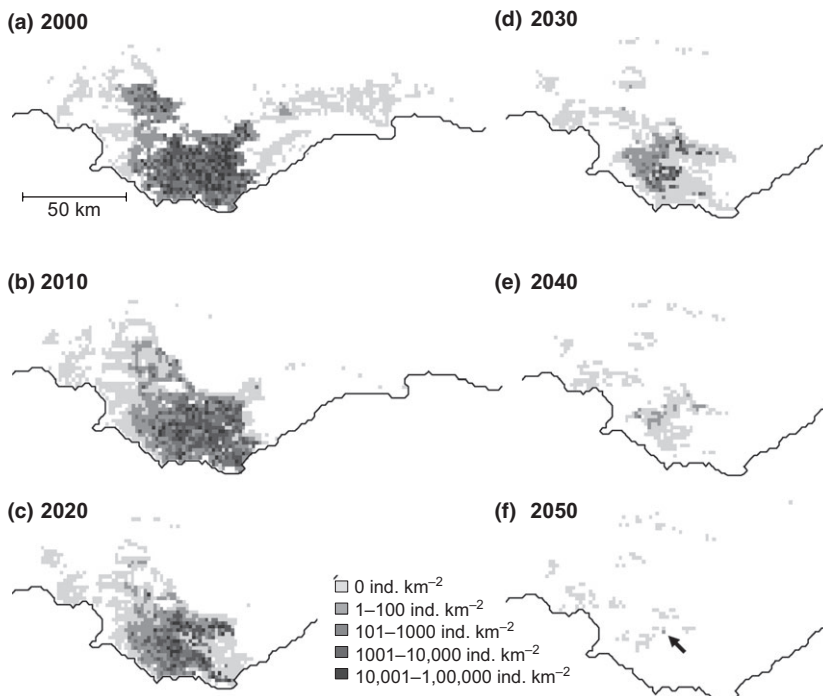


**Figure 5** Predicted range dynamics of *Leucadendron modestum* under climate change and habitat loss. The map in (a) shows abundance distributions in 2000 for the control scenario, without climate change and without habitat loss. Maps in (b)–(f) show abundance distributions in 2010–2050 under climate change and habitat loss. Different shades of grey represent the local abundance averaged over 100 replicate simulations. Note that the light grey area with 0 individual illustrates the unoccupied but suitable habitat. Up to 2050, climate change is predicted to completely shift the habitat of *L. modestum*. The arrow in (f) indicates the only cell that occasionally held a population surviving up to 2050 (in 7% of replicate simulations).

**Table 2** Proportion of variance in range size, local abundance and range filling responses explained ($R^2$) by demographic properties, strength of environmental change (HSI) and their combination. Responses were measured across species as relative changes from environmental change scenarios compared with the control scenario.

| Species responses | Demographic properties | HSI | Both |
|---|---|---|---|
| Range size | 0.25 | 0.86 | 0.89 |
| Local abundance | 0.62 | 0.2 | 0.62 |
| Range filling | 0.57 | 0.3 | 0.66 |

Across species and scenarios, demographic properties and the severity of environmental change (HSI index) together explained 89%, 62% and 66% of the variance in relative changes in range size, local abundance and range filling, respectively (Table 2). Variance in range size changes was mostly explained by HSI (Table 2, partial $R^2 = 0.64$ in the full model with demographic properties). In contrast, relative changes in range filling and local abundance varied more with demographic properties than with HSI (Table 2). Variance in abundance changes was best explained by adult mortality rate (partial $R^2 = 0.18$), dispersal ability (partial $R^2 = 0.15$) and maximum reproductive rate (partial $R^2 = 0.12$). Variance in range filling changes was best explained by mortality (partial $R^2 = 0.19$), followed by HSI (partial $R^2 = 0.09$) and dispersal ability (partial $R^2 = 0.06$).

The importance of simulating demography was also confirmed for future biodiversity refugia. Under climatic conditions of the year 2000, the areas of highest diversity showed six co-occurring species (considering eight study species). For these climatic conditions, the refugia predicted by our process-based approach were only slightly different from those identified by correlative habitat models. This difference was characterized by scattered small areas containing generally only one species less in the demographic predictions than in the habitat model predictions (Fig. 6a,c). However, under climate change (year 2050), the demographic model predicted considerably large contiguous areas with up to three less co-occurring species than predicted solely by habitat models (Figs. 6b,d). This species loss would affect ca. 13% of all cells predicted by the habitat models to be suitable for any of our study species.

## DISCUSSION

The presented model represents recent efforts of making species distribution modelling more mechanistic (Schurr *et al.*, 2012). From the dynamic simulation of local populations, it is possible to assess direct effects of environmental change, like abundance decreases because of changes in habitat configuration under climate change and in habitat availability under habitat loss. Abundance predictions are an advance to environmental change risk assessments and cannot be achieved by standard correlative distribution models. The advantage is enhanced by models parameterized for target species, whereas most previous hybrid studies assess risks based solely on sensitivity analyses. Moreover, besides demonstrating the necessity of simulating demography, data-driven models can serve to better identify refugia expected to sustain viable populations.

**Habitat model predictions**

**Difference between habitat and demographic model predictions**
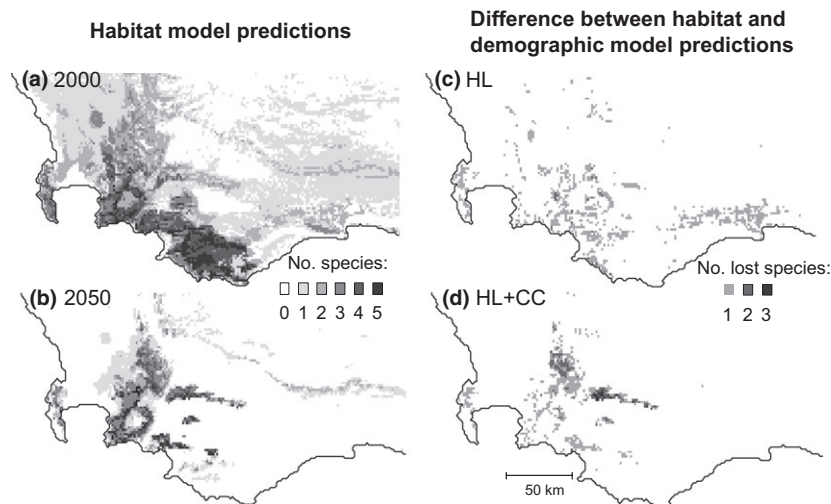


**Figure 6** Predicted range overlap among the eight studied Proteaceae species in a section of the CFR. The maps show predictions derived from overlaying only correlative habitat models (a–b) and the difference in species number between habitat and demographic model predictions (c–d). We further distinguished maps without climate change considering climatic conditions of the year 2000 (a and c) and with climate change considering predicted climatic conditions for year 2050 (b and d). Note the relatively more profound difference between model predictions under climate change. Demographic predictions without habitat loss were very similar and, thus, are not shown.

The demographic models presented here predict that past habitat loss and future climate change will have severe effects on the range dynamics of the studied Proteaceae. It is also important to critically assess the assumptions underlying model predictions. The predictions partly depend on correlative habitat models that may either underestimate or overestimate the sensibility of our study species to climate change (Schurr et al., 2012). Climate sensibility is overestimated if species do not occupy their entire climatic niche, whereas it is underestimated if they show marked source–sink dynamics or time-delayed extinction in response to past environmental change (Schurr et al., 2012). In general, however, we expect our predictions to underestimate the negative effects of environmental change. This is the consequence of five model assumptions. Firstly, fire interval (and thus the generation time of non-sprouters) was assumed to be 10 years, although average fire intervals in the CFR tend to be higher (18.75 years, Wilson et al., 2010). Secondly, no future habitat loss was considered, although Rouget et al. (2003) predicted a loss of 30% in remaining natural habitat within the next 20 years, which would result in over 50% loss of original vegetation. Thirdly, the coarse resolution of the spatial grid (1′ x 1′) might overestimate dispersal because dispersal events outside the source cell result in dispersal over at least 1 min, even though in continuous space, the respective seed may land close to the source cell border (note, however, that this discretization bias is intrinsic to all grid-based models). Fourthly, we ignore local adaptation that can substantially increase the susceptibility of species to climate change (Atkins & Travis, 2010). Finally, our model does not explicitly represent biotic interactions, such as competition, which may limit migration (Kissling et al., 2011) or restrict populations to suboptimal conditions (Cabral & Kreft, 2012).

In comparison, two assumptions that may have led us to overestimate negative effects of environmental change seem to be of minor importance. Firstly, the neglect of niche or dispersal microevolution in response to climate change (Kuparinen et al., 2010; Travis et al., 2010) is unlikely to have big effects because the time of our predictions is short compared with the generation time of the studied Proteaceae. Secondly, mechanistic dispersal models predict that the truncation of dispersal kernels to an assumed $5 \times 5$ cell fire extent is unlikely to severely limit long-distance dispersal and migration ability of our study species (mostly poor dispersers, see Table 1; Schurr et al., 2007).

Under these generally optimistic assumptions, some species are predicted to survive despite strong habitat shrinkage and shift (Fig. 3). However, L. modestum – the only study species predicted to undergo a complete habitat shift under climate change – had only a 7% survival chance. This demonstrates that complete habitat shift enlarges extinction risks of Proteaceae with low colonization ability. Midgley et al. (2002) predicted that over one-third of all 330 Cape Proteaceae will experience complete habitat shifts by 2050 under climate scenario HadCM2n = GGa[IS92a]. Moreover, our results possibly underestimate climate change impacts because we used a relatively mild scenario compared with recent projections of drier future conditions for southern Africa (Tabor & Williams, 2010) and that climate change will likely not cease by 2050 (IPCC, 2007). Nevertheless, for the CFR, there are greater differences between different climate models than between two generations of projections (Nakićenović & Swart, 2000).

The two drivers of environmental change diverged in their impacts. The main effect of climate change was a reduction in range size and a decrease (or occasional increase) in range filling (Fig. 2). The main reason for this negative effect is that relatively small areas were predicted to remain climatically suitable, although they were predicted to host most of the future populations. In contrast, past habitat loss mainly affected local abundances, probably through direct decrease in carrying capacity. Differences between species seem to reflect the differential habitat loss experienced by them, because the species most affected by habitat loss (e.g. L. xanthoconus and L. lanigerum lanigerum) were also predicted to suffer the strongest negative effects on abundances (Fig. 2). Nevertheless, most cells undergoing habitat loss were still predicted to sustain viable populations as indicated by the small impact of habitat loss on range size. However, range reductions because of habitat loss might have occurred in other Cape Proteaceae (see Latimer et al., 2004), mostly in species inhabiting agriculturally suitable areas. Interestingly, although the scenario combining both habitat loss and climate change had generally the most negative results (as found for ecologically similar South West Australian Proteaceae, Yates et al., 2010a), this scenario was still less severe than expected from adding or multiplying the individual effects. This is because the areas remaining climatically suitable or becoming newly available and colonized under climate change tend to be more pristine than the areas becoming climatically unsuitable (Fig. 4). Those more pristine areas are concentrated in the cooler mountain ranges (Midgley et al., 2002), where anthropogenic impact has been relatively small (Midgley et al., 2003; Rouget et al., 2003). This finding supports a previous study that identified upland–lowland gradients as focal areas for systematic conservation in the CFR because of their importance as migration corridors (Cowling et al., 2003). We do not necessarily expect this to hold in other systems. Yet, our example shows the importance of jointly considering spatiotemporal heterogeneity in habitat loss, climate change and the migration ability of species.

Species responses to environmental change varied with both the strength of change and demographic properties. Similar effects of species traits and environmental change have for instance been observed for British butterflies (Warren et al., 2001). Range size responses can be reliably assessed from the severity of environmental change as measured by the HSI index (Table 2). Yet, conservation planners are interested in how range filling and local abundances respond to environmental change. Both of these responses were better explained by demographic properties than by HSI (Table 2).

Such demographic influence is evident by the predicted low migration ability. This limited colonization of areas becoming suitable directly influenced range filling and local abundances, with interspecific and intergeneric differences. Whereas *Protea* species confirmed the expectation that long-lived sprouters have lower colonization ability than short-lived non-sprouters (Schurr *et al.*, 2007; Higgins *et al.*, 2008), the *Leucadendron* species showed the opposite. This unexpected result seems to arise from equal or higher dispersal ability (Table 1) and larger initial ranges and populations than their non-sprouting congeners. The lower abundances in the colonized habitat predicted for sprouters seem to result from lower reproductive rates. These trait-related interspecific variations also support that mortality, reproduction and dispersal were the most important demographic processes (see partial $R^2$ results). In summary, high reproductive rates and dispersal ability seem to enhance range filling, whereas low mortality rates promotes higher abundances in colonized habitats.

The simple superposition of correlative habitat models may not adequately indicate future viable refugia, because those models do not exclude areas where species cannot colonize or persist because of demographic constraints (Figs 3 & 5; Hanski, 1998; Cabral & Schurr, 2010). Integration of these demographic constraints considerably reduced the number of species predicted to occur in future habitat (Fig. 6). The capacity to predict refugia is crucial because of their importance for both survival and evolutionary adaptation to environmental change (Kitching, 2000). The explicit simulation of ecological processes improves process-based identification of refugia (until now limited to environmental or geological processes – Keppel *et al.*, 2012) and distinguishes habitat- or climatic-based refugia (Ashcroft, 2010) from demographically viable refugia.

The presented predictions demonstrate that the joint assessment of persistence, range filling and abundances is a major advantage of process-based demographic models over correlative habitat models. This yields more information for conservation planners than forecasts based solely on habitat models, which provide only habitat predictions and have to assume species-habitat equilibrium to predict species responses (Guisan & Thuiller, 2005). In contrast, demographic models can relax the species-habitat equilibrium assumption and are thus suited to investigate dynamics under the non-equilibrium conditions caused by environmental change (Kearney *et al.*, 2008; Keith *et al.*, 2008; Morin *et al.*, 2008; Pagel & Schurr, 2012). However, previous demographic predictions have not considered how different environmental change drivers affect range dynamics. Furthermore, a major advantage of the demographic models used here is that they were parameterized from dispersal data and range-wide abundance distributions (Schurr *et al.*, 2007; Cabral & Schurr, 2010).

Forecast of hybrid models are affected by uncertainty in the selection of the habitat and the population submodel and by uncertainty in the parameters of these models (Cabral *et al.*, 2011; Fordham *et al.*, 2012). To assess uncertainty arising from the selection of a habitat submodel, one could thus repeat our simulations with alternative correlative habitat models (Fordham *et al.*, 2012). More fundamentally, however, all correlative habitat estimates are likely to be biased because they do not account for effects of spatial population dynamics on species distributions (Pagel & Schurr, 2012; Schurr *et al.*, 2012). To avoid this problem and to comprehensively quantify the uncertainty of range shift forecasts, the habitat and population models have to be estimated jointly, rather than independently as in hybrid models (Pagel & Schurr, 2012). Such joint estimates can be obtained with recently developed 'Dynamic Range Models' (Pagel & Schurr, 2012). Yet, the application of these fully mechanistic models to our study species, and thus adequate estimates of uncertainty, still requires major research efforts (Schurr *et al.*, 2012).

In the meantime, hybrid approaches offer important alternatives to purely correlative forecasts. This is because climate change alters the spatial arrangement of suitable habitat and thus immigration rates, which in turn affect local abundances. This effect of climate change can be taken into account even if demographic rates are assumed to be constant across suitable habitats described by habitat models, as in our model. In fact, such effects of habitat arrangement on the local abundance of our study species were found in Cabral & Schurr (2010). In addition, climate change can gradually alter demographic rates. Such gradual effects have not been considered here, but could change predictions on local abundances by increasing or decreasing reproductive performance and population viability (Fordham *et al.*, 2012).

The presented approach is flexible in that it can include time series of species-specific habitat predictions, and alternative functions for reproduction, dispersal kernels or other demographic processes. This should make it applicable to a wide range of species and systems. However, absence of appropriate habitat models and the data required to parameterize the processes may limit the application to other species. For many species, potentially endangered by environmental change, such high-quality data will not become available in the foreseeable future. Nevertheless, if data are lacking, demographic models can still be used in scenario-based studies, varying dispersal kernels and unknown demographic parameters (e.g. reproductive rate) within realistic ranges (e.g. Keith *et al.*, 2008; Cabral *et al.*, 2011; Cabral & Kreft, 2012). An important future extension of demographic analyses is the statistically sound treatment of model and parameter uncertainty (Higgins *et al.*, 2003b; Pagel & Schurr, 2012). Additionally, the demographic models provide entry points for enriching dynamical behaviour by explicitly describing fire dynamics (Zinck & Grimm, 2009; Wilson *et al.*, 2010), effects of interspecific competition (Esther *et al.*, 2008; Higgins *et al.*, 2008; Kissling *et al.*, 2011; Cabral & Kreft, 2012), reduced reproduction through commercial wildflower harvesting (Maze & Bond, 1996; Turpie *et al.*, 2003; Cabral *et al.*, 2011), climate change effects on wind-driven seed dispersal and migration (Kuparinen *et al.*, 2009;

Nathan *et al.*, 2011) or evolutionary responses to climate change (Kuparinen *et al.*, 2010).

In summary, data-driven demographic models of range dynamics provide a powerful tool for comprehensive projections of how range size, range filling and species abundance will respond to changing environments. For species with low migration ability that are likely to experience strong range shifts (like many Proteaceae, Midgley *et al.*, 2002), alternative conservation actions are likely to be needed. In particular, assisted migration is a hotly debated conservation measure for species highly threatened by climate change (McLachlan *et al.*, 2007; Hoegh-Guldberg *et al.*, 2008; Hunter Jr, 2007; Ricciardi & Simberloff, 2009; Sax *et al.*, 2009). Risk assessments of assisted migration require us to quantify the migration ability of species (Hoegh-Guldberg *et al.*, 2008). The demographic approach presented here provides a powerful method for doing this.

## ACKNOWLEDGEMENTS

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Reproduction functions.

**Appendix S2** Relative effects of environmental change.

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## BIOSKETCH

**Juliano Sarmento Cabral** is interested in process-based models for range dynamics of plant species at various spatio-temporal scales and has a large theoretical interest in niche ecology, macroecology and biogeography. Author contributions: JSC and FMS conceived the simulation experiment and manuscript drafts; WT and GFM provided habitat models; AGR provided field data of abundance distributions; MR provided spatial data on past habitat loss; JSC implemented the model, performed the simulation experiments, analysed results and led the writing; all authors contributed to manuscript writing.

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