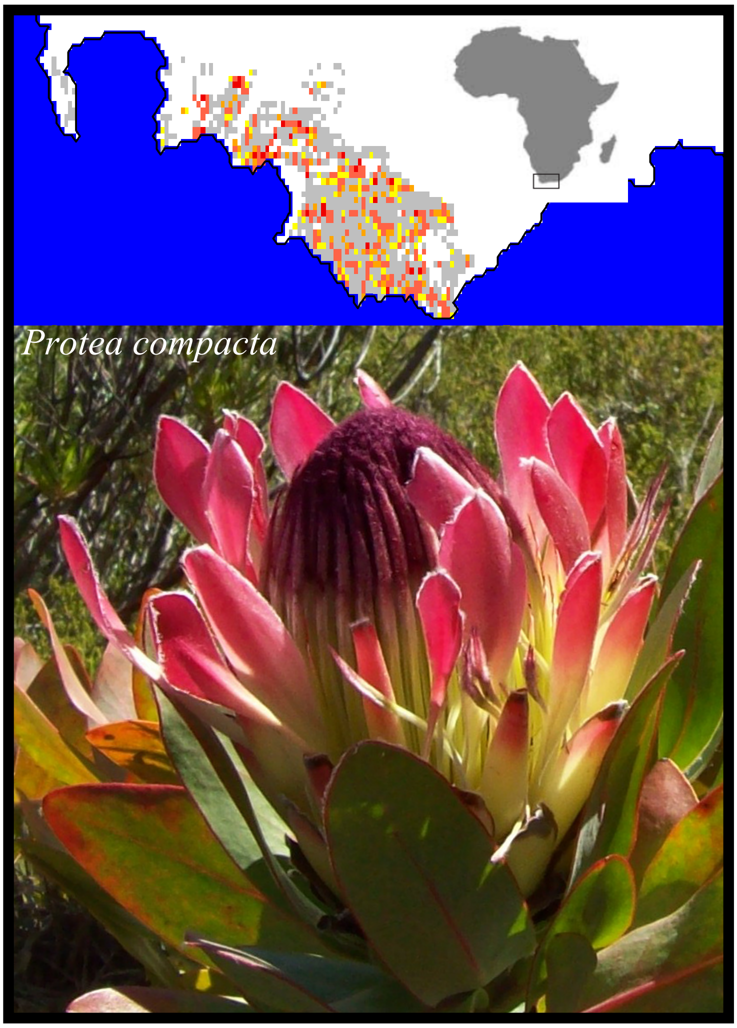
Demographic processes determining the range dynamics of plant species, and their consequences for biodiversity maintenance in the face of environmental change

Juliano Sarmento Cabral



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von
Juliano Sarmento Cabral
aus Campina Grande, Brasilien

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Summary

How demographic processes shape the range dynamics of woody plants is still poorly investigated because of the scarcity of process-based species distribution models. Moreover, models that consider demographic processes are more suitable than pure correlative species distribution models for assessments of species response to deviations from the species-habitat equilibrium due, for example, to exploitation or to environmental change. However, the few recent works with process-based models for species distribution are not tractable to be fitted to data. Therefore, the present thesis aims to introduce a process-based model for species range dynamics that can be fitted to abundance data. For this purpose, the well-studied Proteaceae species of the South African Cape Floristic Region (CFR) offer a great data set to fit process-based models. These plant species are subject to wildflower harvesting and serious environmental threats, like habitat loss and climate change. Hence, the thesis shows also the usefulness of the presented process-based models to investigate species response to wildflower harvesting, habitat loss and climate change.

The general introduction of this thesis presents shortly the available models for species distribution modelling. Subsequently, it presents the usefulness and feasibility of process-based modelling. Finally, it introduces the study system in detail, as well as the objectives and layout of this thesis.

In Chapter 1, I present the process-based model for range dynamics and a statistical framework to fit it to abundance distribution data. The model has a spatially-explicit demographic submodel (describing dispersal, reproduction, mortality, and local extinction) and an observation submodel (describing imperfect detection of individuals). The demographic submodel links species-specific habitat models describing the suitable habitat and process-based demographic models that consider local dynamics and anemochoric seed dispersal between populations. After testing the fitting framework with simulated data, I applied it to eight Proteaceae species with different demographic properties. Moreover, I assess the role of two other demographic mechanisms that are largely neglected in species distribution models: positive (Allee effects) and negative density-dependence. Results indicate that Allee effects and overcompensatory dynamics (including chaotic behaviour in local populations) seem indeed to be important for several species. There was quantitative agreement between independent data and most parameter estimates, successfully describing how abundance distributions arise from the movement and interaction of individuals. Hence, the presented approach seemed to suit the demand of investigating non-equilibrium scenarios involving wildflower harvesting (Chapter 2) and environmental change (Chapter 3).

In Chapter 2, I address an economically important activity for the CFR, but whose effects on dynamics of plant species have been poorly investigated – wildflower harvesting. The chapter includes a sensitivity analysis over multiple spatial scales and demographic properties. These properties are dispersal ability, strength of Allee effects, maximum reproductive rate, adult mortality, local extinction probability and carrying capacity. Subsequently, harvesting effects are also investigated on real case study species. Plant response to harvesting showed abrupt threshold behavior. Moreover, species with short-distance seed dispersal, strong Allee effects, low maximum reproductive rate, high mortality and high local extinction are most vulnerable to harvesting. Increasing spatial scale generally benefits species response, but the thresholds become sharper. Spatial scale also interacts with Allee effects and local extinction probability on plant response. The three case study species supported very low to moderate sustainable harvesting rates. Summarizing, demographic knowledge about the study system and careful identification of the spatial scale of interest should better guide harvesting assessments and conservation targets of exploited species. Nevertheless, results of the sensitivity analysis can be used to qualitatively assess harvesting impacts for poorly studied species.

In Chapter 3, the consequences of past habitat loss, future climate change and their interaction on plant response are investigated. To this end, I use not only the process-based model, but also the species-specific estimates of the best model describing local dynamics and its parameters obtained in Chapter 1. Both habitat loss and climate change had strong negative impacts on species dynamics. Climate change affected mainly range size and range filling due to habitat reductions and shifts combined with low colonization. Habitat loss affected mostly local abundances. The scenario with both habitat loss and climate change was the worst for most species. However, this impact was better than expected by simple summing of separate effects of habitat loss and climate change. This is explained by shifting ranges to areas less affected by humans. Range size response was predicted well by the strength of environmental change, while range filling and local abundance responses were better explained by demographic properties. Therefore, risk assessments under environmental change should consider demographic properties. Most of the surviving populations were restricted to refugia, which can serve as key conservation focus.

The findings obtained for the study system as well as the advantages, limitations and potentials of the process-based model presented here are further discussed in the General Discussion. In summary, the results indicate that 1) process-based demographic models for range dynamics can be fitted to data; 2) demographic processes improve species distribution models; 3) different species are subject to different processes and respond differently to environmental change and exploitation; 4) density regulation type and Allee effects should be considered when investigating range dynamics of species; 5) the consequences of wildflower harvesting, habitat loss and climate change could be disastrous for some species, but impacts vary depending on demographic properties; 6) wildflower harvesting impacts varies over spatial scale; 7) The effects of habitat loss and climate change are not always additive.

General Introduction

0.1 Motivation – Process-based species distribution models

One of the current greatest challenges for ecologists is to understand and mitigate the effects of the impending global changes on biodiversity. What is going to happen with the species? Are they able to migrate? Where are they going mostly probably to occur? This type of questions has gained prominent place in ecological research in recent years and ecological forecasts have been claimed to be almost mandatory (Clark *et al.* 2001b). Such forecasts call for the need for species distribution models to provide better predictions (Thuiller *et al.* 2008; Keith *et al.* 2008). Therefore, the main motivation of the thesis was to improve the understanding of the role of demographic processes on species distribution and how these processes influence species response to a changing world. For this end, I develop process-based models for range dynamics or species distribution that can be fitted to data. In this section I will briefly introduce the models that deal with species distribution, followed by the potential benefits of implementing process-based models for species range dynamics. Finally, I present the study system, which was used for the development and application of these models.

0.1.1 Species distribution models

Species distributions have a long history of interest among researchers (Darwin 1859; MacArthur 1972; Gaston 2003). With recent technical advances in computational statistics and the high availability of species presence data, it has become possible to apply niche theory when investigating species distributions (Thuiller *et al.* 2004; Guisan & Thuiller 2005). Species distribution models (SDM) were introduced as a simple method to predict species occurrence probabilities. These models infer a species' environmental requirements by correlating distribution or abundance data with environmental variables in order to describe the species' potential distribution. Several methods have recently been developed, revised or suggested (Guisan & Zimmermann 2000; Guisan & Thuiller 2005; Araújo & New 2007; Austin 2007; Thuiller *et al.* 2008). Given the correlative nature of these approaches, some researchers prefer to use terms other than species distribution models, like bioclimatic envelopes, habitat distribution, niche-based or habitat models. The term habitat or habitat distribution model may be more appropriate than niche-based model because it emphasizes its descriptive value, reserving the term niche-based or niche models to process-based or mechanistic approaches (Kearney 2006).

There is an ongoing debate about the usefulness of these pure correlative methods (Loiselle *et al.* 2003; Pearson & Dawson 2003; Peterson 2006; Dormann 2007; Beale *et al.* 2008), especially when forecasting future occurrence (Pearson & Dawson 2003; Guisan & Thuiller 2005; Kearney 2006; Keith *et al.* 2008). Part of the debate is centred on potential technical improvements (e.g. Austin 2007; Thuiller *et al.* 2008). However, the key criticism is aimed at the correlative nature of these models, which tend to only consider data from field observations. Ecological processes that prevent or allow occurrence at a given site are neglected (see Bruno *et al.* 2003). Consequently, such habitat models often predict a species to occur where it is not found (Peterson 2006). Reasons for this mismatch are manifold: for example, the target species may not occur in a given suitable habitat due to the importance of biotic interactions, such as the presence or absence of predators, preys, pollinators, dispersers, mutualists and competitors, (Soberón & Peterson 2005; Peterson 2006). Alternatively, a suitable habitat may be not colonized simply because it is too isolated from the core habitat area or because it is too small to maintain a population (Soberón & Peterson 2005; Peterson 2006).

The static character of the correlations makes these habitat models less suitable for forecasting where the species will occur under climate change if the species can not migrate fast, like plants. This happens since such methods assume species-habitat equilibrium and ignore ecological processes (Araújo & Pearson 2005; Vellend *et al.* 2006; Dormann 2007). While the forecasts from habitat models can provide an initial assessment of the potential consequences of environmental change on species suitable habitat (Pearson & Dawson 2003), it must be interpreted with caution (Dormann 2007). Any risk assessment based on habitat models under climate change should consider, for example, scenarios with and without migration ability (e.g. Midgley *et al.* 2006; see also Guisan & Thuiller 2005). Nevertheless, conservation planning must be careful when applying habitat modelling approaches due to the fact that models that overestimate false-positive occurrences may mislead conservation efforts (Loiselle *et al.* 2003). The take-home message from these debates on the application of SDM is that the incorporation of ecological processes, notably local population dynamics and dispersal, has the potential to improve the predictions of habitat models towards more niche-based and realistic species distribution models (Peterson 2006; Thuiller *et al.* 2008). Finally, the dynamic nature of such process-based models allows for simulation under transient or non-equilibrium conditions (Thuiller *et al.* 2008; Keith *et al.* 2008; Morin *et al.* 2008).

0.1.2 Mechanistic or process-based models

The inclusion of ecological processes into SDMs requires the implementation of spatially-explicit process-based or mechanistic models (Morin *et al.* 2008). Most existing process-based models of species distribution are based on cellular automata or grid-based models. The grid is composed of cells that have properties like the amount of suitable area and the number of individuals. These properties can be modified by processes like local population dynamics, dispersal or habitat loss. A vast literature on spatially-explicit models that deal with species and, at least in some extent, with their distribution can be found in studies focusing on metapopulation dynamics (see Hanski 1997) and theoretical assessments on distribution or range dynamics (see Gaston 2003).

Direct advantages of using mechanistic approaches include not only the possibility to address the relative importance of particular processes, but also to use variables that bear more biological meaning. These variables translate the role of species traits into processes. For example, the variable ‘adult mortality probability’ translates traits determining persistence ability to the process of mortality. This makes the parameters more interpretable than the mere statistical parameters of correlative models. Because mechanistic approaches simulate processes in a dynamic context, equilibrium assumptions can be relaxed (Keith *et al.* 2008) and the consequences of these assumptions can be investigated (Zurell *et al.* 2009). This important feature enables the application of process-based models to non-equilibrium scenarios, such as climate change and habitat loss. The results under non-equilibrium scenarios are then an emergent property from the processes simulated and not an inference based on the species-habitat equilibrium assumption as would be the case for a static correlative model. Finally, the inclusion of processes makes information available that is extremely valuable for conservation purposes. This information includes the properties of the grid cells directly simulated by the implemented processes. For example, if local dynamics are implemented, it is possible to assess local abundance and local extinction risk attributable to demographic stochasticity. Such properties of the grid cells, like local abundances, are important for species conservation and cannot be directly assessed by correlative models.

One main limitation of mechanistic approaches is they can be difficult to parameterize. Therefore, a statistical framework is necessary in order to fit process-based models to data.

This can be problematic if the models' simulations are very computer-intensive. This computational demand can make the investigation of the whole species potential range (or global distribution) or numerous processes computationally unfeasible. It is therefore essential to develop an approach that is plastic enough to allow the implementation of several processes, but simple enough to be manageable and still contribute to the understanding of the study system. Some processes may play an important role for a particular study species or system, but others may just be irrelevant. For range dynamics, processes influencing species' demography, such as colonization ability and local extinction are of especial interest (Schurr *et al.* 2007). Therefore, approaches that attempt to simulate range dynamics considering demographic processes have a great potential to improve understanding on species ranges (Keith *et al.* 2008). Other demographic processes may also play a role on range dynamics, like Allee effects and overcompensation. For example, Allee effects may influence range dynamics by making colonization more difficult and local extinction more likely under low densities (e.g. Kot *et al.* 1996). Moreover, the demography of plant species is direct affected by human activities that trigger non-equilibrium scenarios, like wildflower harvesting, habitat loss and climate change. However, what demographic processes and at which extent the relevant processes indeed play a role on range dynamics, either in equilibrium or not, has not been largely investigated (e.g. Keith *et al.* 2008; Morin *et al.* 2008).

One way researchers can investigate the importance of different processes is to implement competing models. When fitting these competing models to the same data, modellers are able to select between them (Akaike 1974) and important information is gained about the most relevant processes. Although process-based models of species distribution are starting to emerge in the literature (Keith *et al.* 2008; Morin *et al.* 2008), no method to date attempts to statistically fit such models to data. Models that are sufficiently simple to minimise the number of parameters are therefore warranted since they can be more easily fitted to available data than more complex models. Another limitation that must be considered when developing process-based models is the general lack of high quality data, which is required for model fitting (Thuiller *et al.* 2008). Given the large amount of data required to statistically parameterize ecological processes, the development of process-based models for species distribution must be based on well-studied study systems.

0.1.3 The study system: the Cape Floristic Region and its Proteaceae in changing world

My studies were focused on Proteaceae species of the South African Cape Floristic Region. This well-studied system was chosen on the basis of the high quality data available and the unique properties of the study region and species as well as advanced information about impending environmental change, as indicated below.

0.1.3.1 Study region

The Cape Floristic Region (CFR) has an area of ca. 90000 km^2, located at south-west South Africa. The CFR is topographically diverse and includes coast lines, flat low-lands and mountainous areas that reach above 2000 m of altitude (Linder 2003). There are two main soil types: clays of intermediate nutrient richness and nutrient-poor sands (Goldbaltt & Manning 2002). The Mediterranean-type of climate characterizes the western part of the study region, with cool and wet winters and with hot and dry summers (Deacon *et al.* 1992). In the East, the annual temperature range is smaller and the rainfall regime is characterized by two precipitation peaks, one in spring and the other in fall (Deacon *et al.* 1992). Mean annual precipitation varies from 200 mm/yr to 2000 mm/yr (Goldbaltt & Manning 2002).

The CFR is listed as one of the world's 25 biodiversity hotspots (Myers *et al.* 2000), with a highly diverse flora composed of ca. 9030 vascular species, 69% of which are endemic (Goldblatt & Manning 2002). This high species richness competes with that of tropical areas and the percentage of endemism rivals that of oceanic islands (Linder 2003). However, the CFR has undergone and still suffers from anthropogenic threats, including agriculture, urbanization, alien species invasions (Rouget *et al.* 2003; Latimer *et al.* 2004), wildflower harvesting (Turpie *et al.* 2003) and climate change (see Fig. 1; Midgley *et al.* 2002; Thomas *et al.* 2004). For example, Rouget *et al.* (2003) addressed past and future habitat transformation in the CFR due to urbanization, alien species and mainly due to agricultural transformation. About 30% of the CFR already underwent habitat loss, especially in the endemic-rich Cape Flats (Rouget *et al.* 2003).

The flora of the CFR can be divided into three main vegetation types or biomes: renosterveld, strandveld and fynbos. The latter biome occupies most of the CFR (Fig. 1) and holds most of its diversity. Fynbos is a Mediterranean-type fire-prone sclerophyllous shrubland dominated by Ericaceae, Restionaceae and Proteaceae. The current thesis concentrates on the distribution and range dynamics of two genera of Proteaceae, *Protea* and *Leucadendron*.

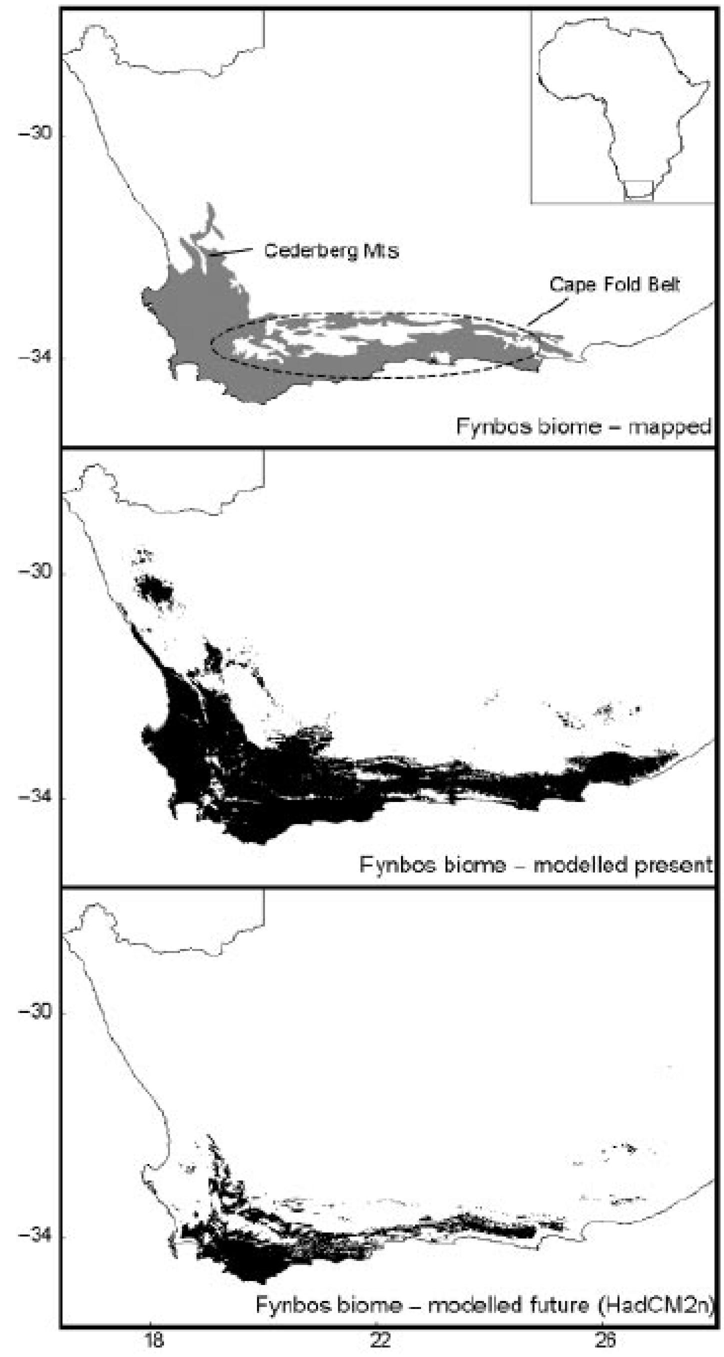

Figure 1. Fynbos biome. Source: Midgley *et al.* (2002). The top panel shows the current extension of the biome, the centre panel shows the biome according to habitat models and the bottom panel shows the forecast for future distribution of the biome. Note the biome contraction in the bottom panel.

0.1.3.2 Study species

With ca. 330 species in the CFR, Proteaceae dominate most of the fynbos vegetation, being the largest woody plants (Rebelo 2001). Accordingly, the family Proteaceae plays an important role for this ecosystem's functioning (Stock & Allsopp 1992) and community composition (Cowling & Gxaba 1990). The large and attractive inflorescences of many family members pursue a high ornamental value, and are also of substantial economical and horticultural importance. For example, *Protea cynaroides* was selected to be South Africa's National Flower. The flower industry of the region relies on cultivated and on wild populations of several Proteaceae species, being an important economical activity for the region, with a multi-million dollar revenue per year (Turpie *et al.* 2003).

For this study, I selected ten Proteaceae species: four *Leucadendron* and six *Protea* species. The life history and demography of the study species are closely linked to the recurrent fires typical of the fynbos biome. All study species are serotinous, storing their seeds in woody cones and forming a ‘canopy seed bank’ that can last for a prolonged period of time or until fire. The storage period of seeds ranges from one year in weakly serotinous species to about 7 years in strongly serotinous species (Bond & van Wilgen 1996; Rebelo 2001). The closed cones protect the seeds during a fire and release them once the water supply ceases, for example, when the branch or the individual has been burnt (Rebelo 2001). Released seeds are then dispersed into the post-fire landscape. All study species are wind dispersed (Bond 1988; Le Maitre & Midgley 1992; Rebelo 2001). Their wind-dispersal can be divided into two phases: a primary air-borne dispersal followed by a secondary tumble dispersal over the ground (Bond 1988; Schurr *et al.* 2005, 2007). Secondary seed dispersal by wind can move Proteaceae seeds over long distances (Bond 1988), up to several kilometres (Schurr *et al.* 2005, 2007). Schurr *et al.* 2005 developed a process-based model to describe this secondary dispersal and validated the model with seeds of seven CFR Proteaceae species.

After being dispersed, seeds germinate as soon as the conditions are favourable (Bond 1985). Hence, serotinous Proteaceae do not seem to form persistent soil seed banks (Le Maitre & Midgley 1992; Bond & van Wilgen 1996). Seed dispersal and successful establishment of serotinous Proteaceae normally occur during the first year after a fire and can be considered as temporally discrete events (Rebelo 2001; Schurr 2005). Although serotinous CFR Proteaceae show density-dependent establishment (Bond *et al.* 1984, 1995), seedling mortality seems to be negligible after the seedlings survive their first summer drought (Le Maitre & Midgley 1992; Bond & van Wilgen 1996). Accordingly, adult mortality during inter-fire intervals is low (Bond *et al.* 1995). The density and spatial structure of Proteaceae stands is thus largely influenced during seed dispersal and the short period between dispersal and establishment (Bond *et al.* 1984).

The adult plants of four study species can survive fire by re-sprouting whereas the six remaining study species survive fire only as seeds. These two life-history strategies are called sprouters and nonsprouters, respectively (Bond & Midgley 2001). The adults of nonsprouters are killed by fire, whereas the adults of sprouters have an underground rootstock or a thick bark that enables fire survival (Bond & van Wilgen 1996; Bond & Midgley 2001, 2003). Further differences between sprouters and nonsprouters are that sprouters are long-lived and iteroparous with overlapping generations, whereas nonsprouters are short-lived and effectively semelparous with non-overlapping generations (Bond & van Wilgen 1996; Bond & Midgley 2003). Moreover, because populations of nonsprouters are formed by even-aged cohorts, whose age is the time since last fire, stands can go locally extinct if a fire happens before the stand reaches sexual maturity (Le Maitre & Midgley 1992; Rebelo 2001). Among the study species, the age at which half of the individuals of a population produce their first flowers ranges from 2 to 8 years after fire (Rebelo 2008).

The CFR and the fynbos Proteaceae have been studied exceptionally well. Besides studies on the life history and demography of Proteaceae (summarized above for serotinous species), many studies have been carried out on their spatial distribution, potential range, dispersal ability, local abundance and phylogeny. For example, species-level molecular phylogenies include *Protea*, *Aulax* and *Leucadendron* (Reeves 2001; Gail Reeves *unpublished data*). Sauquet *et al.* (2009) constructed a 'family tree' with aged clades for all Proteaceae worldwide and indicated a recent hyperdiversification in the CFR Proteaceae.

In particular, the Protea Atlas Project (Rebelo 2001) recorded spatial distributions and local abundance estimates of all Southern African Proteaceae species. This extensive effort resulted in the Protea Atlas Database, one of the largest and highest quality datasets in the world for studying biodiversity (Gelfand *et al.* 2005). Therefore, the Protea Atlas Database has turned the endemic CFR Proteaceae species into an ideal model system for biogeographical investigations. For example, Laurie and Silander (2002) used range-based null models and the Protea Atlas Database to indicate that biogeographical patterns of species richness must take into account edge effects, determined by the spatial continental configuration. Gelfand *et al.* (2003, 2005) and Latimer *et al.* (2006) also used the Protea Atlas Database to present a novel approach of estimating correlative species distribution models in a hierarchical Bayesian framework. Pearson *et al.* (2006) assessed model-based uncertainty by applying different range distribution methods to CFR Proteaceae and found significant differences between predictions. Midgley *et al.* (2002, 2003, 2006) used the Protea Atlas Database to develop statistical bioclimatic envelopes that describe current and future (year 2050) potential habitats of CFR Proteaceae. The authors concluded that more than one third of the CFR Proteaceae (~110 species) will experience complete shift of their habitat and that ca. 20 species will have no suitable habitat by 2050 (Migley *et al.* 2002). Thomas *et al.* (2004)

used the results presented by Midgley *et al.* (2002) in a global assessment of extinction risk due to climate change. Hannah *et al.* (2002) also used examples from Midgley *et al.* (2002) in order to generate guidelines for conservation planning under climate change. Williams *et al.* (2005) presented a method that uses these predictions to identify 'migration corridors': networks of conservation areas designed to facilitate the migration of Proteaceae under climate change. However, better estimates of the migration ability of species are still needed (Williams *et al.* 2005). The impact of future climate change on the red list status of 227 CFR Proteaceae was also investigated (Bomhard *et al.* 2005).

Schurr *et al.* (2007) used mechanistic models of seed dispersal by wind (Tackenberg 2003; Schurr *et al.* 2005) to investigate processes shaping the range dynamics of 37 CFR Proteaceae. Schurr *et al.* (2007) were able to assess the effect of the investigated processes on ‘range filling’, which is the ratio between the realized range and the total amount of potential suitable range (Svenning & Skov 2004). Local extinction and colonization ability were indicated as key processes determining the range dynamics of CFR Proteaceae (Schurr *et al.* 2007): a species' range filling increases with its colonization ability and is higher for species with low local extinction probability. However, Schurr *et al.* (2007) found that the spatially-implicit metapopulation Levins’ model cannot explain interspecific variation in range filling.

Furthermore, Keith *et al.* (2008) assessed potential species response to climate change using the current and future habitat models coupled with spatially-explicit demographic processes and different life history and fire regime scenarios (a so-called hybrid model, Thuiller *et al.* 2008). Keith *et al.* (2008) observed complex interactions between life history, disturbance regime and distribution patterns and indicated a general negative effect of climate change on abundances, especially for species with widespread habitat contraction. Nevertheless, Keith *et al.* (2008) assessed range dynamics in a scenario-based study design, being unable to parameterize the model for specific study species and hence could not generate species-specific forecasts. Finally, although there is an indication that some Proteaceae may have chaotic local dynamics (Bond *et al.* 1995) and that they are subject to Allee effects (Lamont *et al.* 1993), the importance of chaotic behaviour and Allee effects to range dynamics has not been assessed in previous studies on range dynamics of CFR Proteaceae.

0.2 Objective of the Thesis

The present thesis has the objective to investigate the role of demographic processes on plant species distribution, or range dynamics, and how these processes influence species response to wildflower harvesting and environmental change. For this end, I introduce a novel spatially-explicit process-based model for species range dynamics that can be fitted to data and the applications of this model to non-equilibrium scenarios. The method developed is a hybrid approach because it 1) considers habitat models in order to describe the potential habitat, and 2) simulates demographic processes in and between these habitats to predict the dynamics of species ranges. The present work aims not only to describe species range dynamics through demographic processes, but also to go a step further and to fit the models to abundance data, which has not been achieved by previous studies. The possibility of fitting the model to data allows parameterization, range prediction and range forecasts to be species-specific. Moreover, the present study aims to introduce a fitting approach that enables model selection, which allows for detection of processes that might play a role in range dynamics of a study species.

Process-based models of range dynamics are also suitable for investigating species responses to deviations from habitat-species equilibrium because they can directly simulate transient dynamics. Hence, the present thesis intends to demonstrate the usefulness of such a process-based approach for the non-equilibrium scenarios of wildflower harvesting, climate change and habitat loss. For this purpose, I based the model structure and the investigations on the CFR and its Proteaceae. Finally, by investigating the role of demographic properties under non-equilibrium scenarios, the present work aims to add to the theoretical understanding of species range dynamics and, when appropriate, to discuss the meaning of the results for species conservation.

0.3 Thesis outline

Given the cumulative format of the present thesis, the Chapters 1, 2 and 3 can be read independently. Because these chapters were prepared as separate articles for publication, they contain overlapping information, especially regarding the introduction and methods sections, and they are written in first person of plural because they are co-authored. In the first chapter[1], I introduce the process-based model for range dynamics and the fitting framework used to fit this model to abundance distribution data. The method includes not only demographic models, but also an observation model to account for imperfect detection in order to fit the model to observation data. I first tested the fitting procedure on virtual data, using a 'virtual ecologist' approach (Zurell *et al.* 2009; Zurell *et al.* submitted), and then I applied the method to real data of eight selected CFR Proteaceae species that vary in life history.

The following Chapters 2[2] and 3[3] apply the demographic models for range dynamics presented in Chapter 1 to non-equilibrium scenarios. In Chapter 2, I assess the effects of wildflower harvesting on species dynamics through a sensitivity analysis over demographic properties at multiple spatial scales. The assessment was complemented by simulating wildflower harvesting for three CFR Proteaceae species that are economically important. Demographic parameters of one of the study species were already estimated in Chapter 1. For the other two studied species, these parameters were obtained with the same approach. In Chapter 3, I investigated the effects of climate change and habitat loss on the species dynamics of the eight species studied in Chapter 1. Subsequently, I finalize the thesis with a brief general discussion of the findings for CFR Proteaceae, and the limitations and advantages of the presented approach. The general discussion gives also an outlook on future directions for research and summarizes the general conclusions of the thesis.

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[1] In press as **Cabral JS**, Schurr FM. Estimating demographic models for the range dynamics of plant species. *Global Ecology and Biogeography*.

[2] To be submitted to *Conservation Biology* as **Cabral JS**, Bond WJ, Midgley GF, Rebelo AD, Thuiller W, Schurr FM. Effects of wildflower harvesting on plant dynamics at different spatial scales: lessons from the Proteaceae of the Cape Floristic Region.

[3] In preparation as **Cabral JS**, Jeltsch F, Higgins SI, Midgley GF, Phillips SI, Rebelo AG, Rouget M, Thuiller W, Schurr FM. Impacts of past habitat loss and future climate change on the range dynamics of South African Proteaceae. To be submitted to *Global Change Biology*.

Chapter 1 – Estimating demographic models for the range dynamics of plant species [1]

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[1] A version of the chapter is in press as **Cabral JS,** Schurr FM. Estimating demographic models for the range dynamics of plant species. *Global Ecology and Biogeography*.

1.1 Abstract

To better understand how demographic processes shape the range dynamics of woody plants (Proteaceae), we introduce a likelihood framework for fitting process-based models of range dynamics to spatial abundance data. The study species occur in the fire-prone Fynbos biome (Cape Floristic Region, South Africa). Our process-based models have a spatially-explicit demographic submodel (describing dispersal, reproduction, mortality, and local extinction) as well as an observation submodel (describing imperfect detection of individuals), and are constrained by species-specific predictions of habitat distribution models and process-based models for seed dispersal by wind. Free model parameters were varied to find parameter sets with highest likelihood. After testing this approach with simulated data, we applied it to eight Proteaceae species that differ in breeding system (hermaphroditism vs. dioecy) and adult fire survival. We assess the importance of Allee effects and negative density-dependence for range dynamics, by using AIC to select between alternative models fitted for the same species. The best model for all dioecious study species included Allee effects, whereas this was true for only one of four hermaphroditic species. As expected, sprouters (in which adults survive fire) were estimated to have lower rates of reproduction and catastrophic population extinction than related nonsprouters. Overcompensatory population dynamics seem important for three of four nonsprouters. We also found good quantitative agreement between independent data and most estimates of reproduction, carrying capacity and extinction probability. This study shows that process-based models can quantitatively describe how large-scale abundance distributions arise from the movement and interaction of individuals. It stresses links between life history, demography and range dynamics of Proteaceae: dioecious species seem more susceptible to Allee effects which reduce migration ability and increase local extinction risk, and sprouters seem to have high persistence of established populations, but their low reproduction limits habitat colonization and migration.

1.2 Introduction

The processes driving the range dynamics of species have long been in the focus of biogeography, ecology and evolutionary biology (e.g. Darwin 1859; Reid 1899; MacArthur 1972). Awareness of global change has reinforced this interest: an understanding of range dynamics is necessary to assess and mitigate the ecological impacts of climate change, land use change, and biological invasions (Fischlin *et al.* 2007; Thuiller *et al.* 2008).

The need to quantify species ranges inspired the development of various phenomenological species distribution models (Guisan & Thuiller 2005). While these phenomenological models differ in methodological details, their common basis is the statistical estimation of spatial correlations between the environment and the occurrence or abundance of species. Phenomenological models are now used widely both to test fundamental hypotheses and to forecast environmental change effects on biodiversity (Wiens & Graham 2005). Recently, however, there is increasing awareness of problems with the phenomenological approach. These problems are in part methodological: predictions of alternative phenomenological models can vary substantially (e.g. Pearson *et al.* 2006), the usefulness of summarizing such alternative predictions is debated (Araújo & New 2007), and most phenomenological models ignore errors in the observation of species distributions and abundances (Latimer *et al.*, 2006). Even more important than these methodological problems are the fundamental limitations of phenomenological models: their static nature precludes predictions for species in disequilibrium with the environment (e.g. Thuiller *et al.* 2008), and they are poorly linked to ecological theory because they do not represent ecological processes (e.g. Araújo & Guisan 2006).

The ecological processes that may influence range dynamics are many (Thuiller *et al.* 2008). Eventually, however, all of these processes affect range dynamics through their effect on the reproduction, mortality and/or dispersal of individuals (Holt & Keitt 2005): the balance of reproduction and mortality defines local population dynamics, whereas dispersal determines how strongly these local dynamics are interlinked. Hence, basic demography seems useful for understanding range dynamics. Theoretical ecology has long examined the links between demography and large-scale dynamics. For instance, metapopulation theory explored effects of dispersal and local extinction on habitat occupancy (Levins 1969). Other studies examined how the density-dependence of population growth shapes range dynamics. This led to the realization that Allee effects (a decrease of population growth rate in declining populations) increase the extinction probability of small populations, can substantially reduce migration rates (Kot *et al.* 1996) and limit species ranges (Stephens & Sutherland 1999; Keitt *et al.* 2001). Additionally, the strength of negative density-dependence (arising from competition) can have important consequences for large-scale dynamics (Münkemüller & Johst 2007).

Studies using demographic models to predict range dynamics are only beginning to emerge (Thuiller *et al.* 2008). These studies mostly use a "hybrid" approach in which a demographic model simulates the range dynamics of a species under habitat dynamics predicted by a phenomenological model (Keith *et al.* 2008). Strengths of demographic models are that they can, in principle, incorporate all demographic processes discussed above and be parameterized from independent field data. In practice, however, there are substantial problems of model formulation and parameterization (Higgins *et al.* 2003): a priori it is often not clear whether demographic phenomena such as Allee effects are relevant for the range dynamics of a given species, and for most species we lack the data necessary to parameterize demographic models. Interestingly, the statistical framework used to fit phenomenological models provides well-established solutions to these questions of model selection and parameter estimation (Burnham & Anderson 1998; Bolker 2008). Embedding demographic models of range dynamics into a statistical framework thus seems a promising way forward for quantitative biogeography.

Here we present a novel approach that fits process-based hybrid models of range dynamics to spatially-explicit abundance data while accounting for errors in data collection (Fig. 1). We first apply this approach to an artificial dataset in which 'reality' is known (Austin *et al.* 2006), and show that model parameters can be estimated by fitting the dynamic model to abundance distributions observed in a single time slice. After confirming the usefulness of the method for artificial data, we apply it to data on the spatial distribution of abundances in serotinous South African Proteaceae, a group of woody plants whose range dynamics seem to be shaped by interspecific differences in colonization and local extinction (Schurr *et al.* 2007). In analysing the Proteaceae data, we (1) consider alternative models for local population dynamics to assess the role of Allee effects and negative density-dependence for range dynamics, (2) apply these models to species with different life-history traits, to test whether life history systematically affects the processes driving range dynamics, and (3) compare the obtained parameter estimates to independent data. Based on this analysis, we then discuss to what extent the statistical fitting of demographic models can advance our ability to understand and predict range dynamics.

1.3 Methods

The approach used to fit process-based models of range dynamics involves three steps (Fig. 1): (1) based on a description of suitable habitat, a spatially-explicit **demographic model** simulates local population dynamics, dispersal and the resulting range dynamics; (2) an **observation model** transforms the simulated number of individuals in each habitat patch into a statistical distribution for the number of individuals observed in this patch (thereby accounting for the fact that not all individuals are observed); (3) these distributions of observed abundances in each cell are used to calculate the likelihood of spatially-distributed abundance data given a set of parameters for the demographic and observation model. Parameters of both models are then varied to maximize the likelihood of the abundance data given the models.

1.3.1 Demographic model

Local population dynamics and dispersal between populations were simulated with spatially-explicit lattice models in C++. Each grid cell holds one population and local dynamics proceed in discrete time steps according to

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

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

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

where $D_{i,j}$ is the per-individual probability of dispersal from cell j to cell i, and R is a function describing per-capita reproduction.

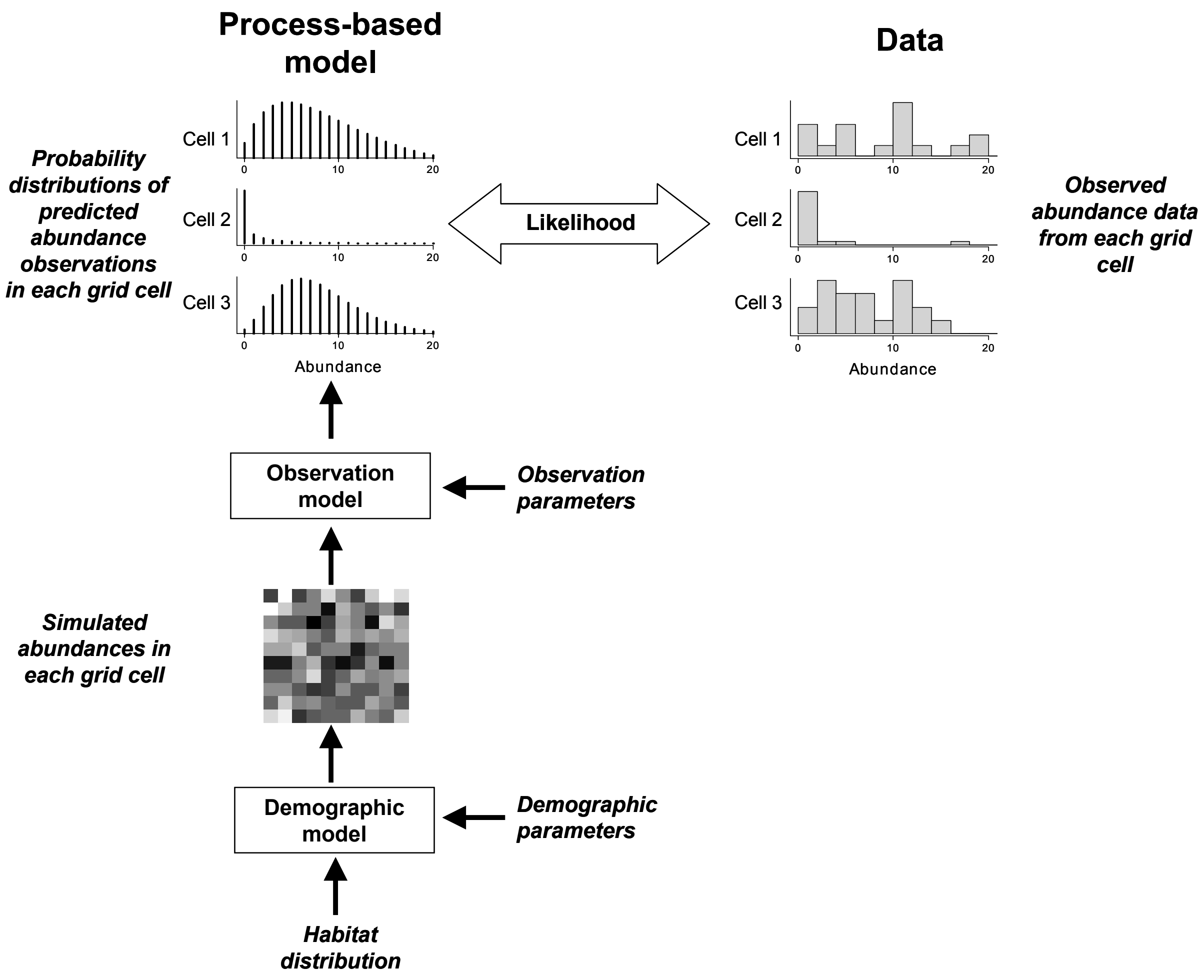

Figure 1. Schematic representation of the likelihood framework used to fit process-based models of range dynamics to data on the spatial distribution of abundances. The process-based models consist of a demographic and an observation component.

With per-time-step probability E, local populations experience catastrophic extinction which sets local abundance $N_i(t)$=0 before Eq. 2 is evaluated. For populations not affected by catastrophic extinction, we model per-capita reproduction, R, with one of four alternative submodels: the Beverton-Holt model (Beverton & Holt 1957), the Ricker model (Ricker 1954) and variants of these models that describe Allee effects. Table 1 shows how these submodels relate R to reproduction parameter, R_{mod}, carrying capacity, K, and (where applicable) Allee critical threshold C. To simplify the equations in Table 1, the reproduction parameter R_{mod} is a theoretical quantity (the maximum reproductive rate at densities ≥0 ind cell^{-1}). However, for parameter interpretation, it makes sense to calculate the biologically relevant quantity R_{max} (the maximum reproductive rate at densities ≥1 ind cell^{-1}). In most cases, R_{max} and R_{mod} are very similar, but they differ if R drops steeply between 0 and 1 ind cell^{-1}. Figure 2 illustrates the difference between the equations presented in Table 1 on the pre-capita reproduction rate over population density. Note also that the two Ricker variants are only applicable to species with non-overlapping generations (M=1). We chose the Beverton-Holt and Ricker models because they are simple and differ in the strength of density-dependence (Caswell 2001): reproduction is overcompensatory in the two Ricker variants and the Beverton-Holt model with Allee effects, but compensatory in the Beverton-Holt model without Allee effects. For M=1, population growth shows the same density-dependence as reproduction, whereas for M<1, population growth is undercompensatory. Overcompensatory population growth can destabilize local population dynamics and increase local extinction risk (e.g. Münkemüller & Johst 2007). By fitting alternative models that differ in the reproduction function R, we can thus assess the importance of both Allee effects and negative density dependence for range dynamics.

Table 1. Comparison of four alternative submodels used to describe the density-dependence of per-capita reproduction, $R(N_i(t))$, as a function of reproduction parameter, R_{mod}, carrying capacity, K, and Allee critical threshold C. See footnotes for how K and C are related to the Beverton-Holt parameters K_p, k and c. Note that R_{mod} (the maximum of the equations in Table 1) can deviate from R_{max} (the maximum reproductive rate at biologically relevant densities >=1 ind cell^{-1}).

Model	Formula	Applied to
Beverton-Holt*	$R(N_i(t)) = \frac{R_{\mathrm{mod}}}{1+\frac{R_{\mathrm{mod}}N_i(t)}{K_p}}$	overlapping and non-overlapping generations (sprouters and nonsprouters)
Beverton-Holt + Allee#	$R(N_i(t)) = \frac{R_{\mathrm{mod}}}{1+k(N_i(t)-c)^2}$	overlapping and non-overlapping generations (sprouters and nonsprouters)
Ricker	$R(N_i(t)) = R_{\mathrm{mod}}^{1-\frac{N_i(t)}{K}}$	non-overlapping generations (nonsprouters)
Ricker + Allee	$R(N_i(t)) = R_{\mathrm{mod}}^{\frac{4(K-N_i(t))(N_i(t)-C)}{(K-C)^2}}$	non-overlapping generations (nonsprouters)

*The Beverton-Holt model has carrying capacity $K = \frac{(R_{\mathrm{mod}} - M)K_p}{R_{\mathrm{mod}}M}$, where M is the mortality probability.

The Beverton-Holt + Allee model has carrying capacity $K = c + \sqrt{\frac{(R_{\mathrm{mod}} - M)}{Mk}}$ and Allee critical threshold $C = c - \sqrt{\frac{(R_{\mathrm{mod}} - M)}{Mk}}$.

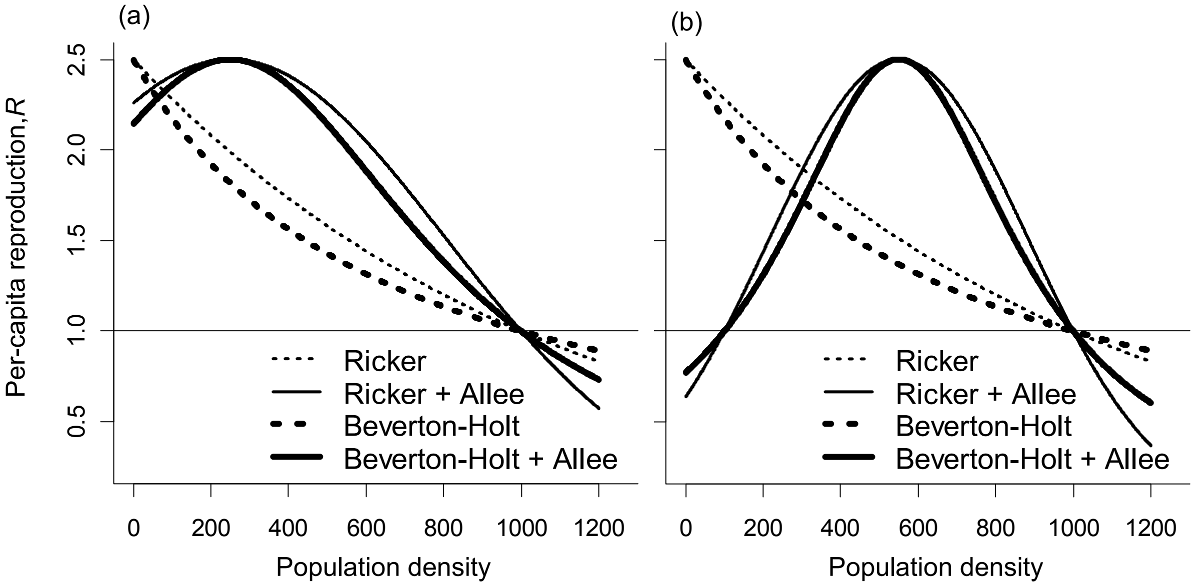

Figure 2. Comparison of the four alternative submodels used to describe per-capita reproduction in local populations (see Table 1). All submodels reach a reproductive rate of 1 (horizontal line) at carrying capacity (*K*), and the Allee submodels also reach this rate at the Allee critical point (*C*). In (a) the Allee submodels describe weak Allee effects (*C*=-500), whereas in (b) they describe strong Allee effects (*C*=100). To facilitate comparison, all submodels have the same *K* (=1000 individuals) and reproductive parameter (R_{mod}=2.5, which for the depicted functions is virtually identical to maximum reproductive rate, R_{max}).

At initialization, each suitable grid cell has a 50% chance of being occupied and each occupied cell is assigned an initial abundance drawn from a uniform random distribution varying between 1 and carrying capacity *K* (see Appendix 1.A). Subsequently, the model is run until it reaches a quasi-stationary state (Appendix 1.A). In the quasi-stationary state, local abundances in each cell are recorded for a fixed period or until global extinction. By averaging these abundances over the recording period and over replicate simulations we obtain the expected abundance in each cell ($\overline{N_i}$) given a set of demographic parameters.

1.3.2 Observation model

A simple model relates the expected abundances to abundances observed in the field. This observation model assumes that the number of individuals observed during a single visit to grid cell *i*, $A_{i,o}$, follows a negative binomial distribution with mean $f\rho\overline{N_i}$ and size parameter *s*, where *f* is the proportion of the grid cell area covered during one visit, and ρ is the per-individual observation probability. The parameter *s* (which we term the 'regularity index') describes the degree to which individuals are regularly distributed within the grid cell (lower values of *s* represent stronger clumping).

1.3.3 Parameter estimation

We estimated demographic and observation parameters by searching the parameter set $\boldsymbol{\beta}$ for which a vector of observed abundances **A** has the lowest negative log-likelihood, calculated as

$$-\ln L(\mathbf{A}|\boldsymbol{\beta}) = -\sum_{i=1}^{Ncells} \sum_{o=1}^{Nobs(i)} \ln L(A_{i,o}|\boldsymbol{\beta}) \tag{3}$$

where *Ncells* is the total number of cells, *Nobs*(*i*) is the number of observations in cell *i*, and $L(A_{i,o}|\boldsymbol{\beta})$ is the likelihood of observing $A_{i,o}$ individuals at visit *o* to cell *i*. If the observed abundance is a count, this likelihood is the probability density of the negative binomial distribution described above (see section **Observation model**). If the observed abundance is not a count but has been estimated to fall in category $O_{i,o}$ with lower limit A_{low} and upper limit A_{upp}, the likelihood is

$$L(O_{i,o}|\boldsymbol{\beta}) = CDF\left(A_{upp}, \mu = f\rho\overline{N_i}, s = s\right) - CDF\left(A_{low}, \mu = f\rho\overline{N_i}, s = s\right), \tag{4}$$

where $CDF(x,\mu,s)$ is the cumulative density function of a negative binomial.

For a given set of demographic parameters (reproduction parameter, R_{mod}; probability of mortality, *M*; carrying capacity, *K*; Allee critical point, *C*; local extinction probability, *E*) and the resulting expected abundances $\overline{\mathbf{N}}$, we estimated the observation parameters (observation probability, ρ; regularity index, *s*) by minimising the negative log-likelihood -ln *L* with the Nelder-Mead simplex algorithm in R 2.4.1, (R Developement Core Team 2006). To estimate the demographic parameters, we followed the general strategy for direct parameter search (Bolker 2008): we varied demographic parameters in a multidimensional grid spanning the realistic range of values, and iteratively zoomed at least 2 times into the sub-region of the grid with lowest negative log-likelihoods. The zooming procedure was stopped when the refined parameter grid did not produce lower negative log-likelihoods than the previous grid. Due to the computational intensity of the models, we could not obtain full maximum-likelihood parameter estimates. However, we ensured that the final grid of demographic parameter values was fine enough to cover ecologically important variation.

1.3.4 Test with artificial data

We applied the fitting procedure to artificial abundance data simulated by combining the demographic model with Beverton-Holt dynamics (Table 1) and the observation model. For this test, we simulated dynamics of two hypothetical species: one was iteroparous with overlapping generations, whereas the other was semelparous with non-overlapping generations. These two hypothetical species differed in demographic and observation parameters and in dispersal ability. The medians of parameter estimates for five different landscapes showed good agreement with the 'true' values (see Appendix 1.A for description of simulations and results).

1.3.5 Study system: Cape Proteaceae

After successful validation with artificial data, we applied the models to eight endemic Proteaceae species of the South African Cape Floristic Region (CFR). Four study species belong to the dioecious genus *Leucadendron*, and four belong to the hermaphroditic genus *Protea* (Tables 2 and 3). The population dynamics of the study species are driven by recurrent fires (Bond & van Wilgen 1996). They form four pairs of related sprouters and nonsprouters (Rebelo 2001; Reeves 2001): sprouters can survive fire as adults, are iteroparous and have overlapping generations, whereas nonsprouters survive fire only as seeds and are semelparous with non-overlapping generations (Bond & van Wilgen 1996; Bond & Midgley 2001, 2003; Schurr *et al.* 2007). All species are serotinous: they form canopy seed banks but no soil seed bank (Rebelo 2001). Fire triggers seed release from the canopy so that seed dispersal and recruitment occur after fires (Bond 1988; Le Maitre & Midgley 1992; Bond & van Wilgen 1996; Rebelo 2001; Schurr *et al.* 2005, 2007). Serotinous Proteaceae differ in the density-dependence of reproductive rates *R*, with compensation strength varying from compensation to overcompensation (Bond *et al.* 1995). Because inter-fire recruitment and inter-fire mortality of recruits are rare, population dynamics proceed in discrete time steps whose length is determined by fire return intervals (Bond *et al.* 1995). The single-aged populations of nonsprouters regularly experience catastrophic extinction if fire occurs before sexual maturity, whereas sprouters have substantially lower extinction probability (Bond & van Wilgen 1996). Fires that generate catastrophic extinctions tend to be small because post-fire re-growth of flammable biomass is slow. Hence, we assumed that catastrophic extinction independently affects individual grid cells.

1.3.6 Model fitting

We fitted process-based models to data on the spatial distribution of abundances throughout the global geographical ranges of our study species (Protea Atlas Database - Rebelo 2001). This database arguably is 'the largest and highest quality of its kind in the world for studying biodiversity' (Gelfand *et al.* 2005). It records abundance in circles of 500m diameter in the following categories: 0 individuals, 1-10 individuals, 11-100 individuals (‘frequent’), 101-10000 individuals (‘common’) and >10000 individuals (‘abundant’). We aggregated these abundance estimates in grid cells of 1’x1’ (ca. 1.55 km x 1.85 km, so that f=0.0684). Individual grid cells received between 0 and 163 visits. For individual species, the number of abundance estimates >0 ranges between 55 and 16137.

In the model fits, we used species-level estimates of habitat distribution and dispersal kernels. Spatial habitat distributions were obtained from species-specific generalized additive models that use five bioclimatic and three edaphic variables (details in Midgley *et al.* 2003 and in Schurr *et al.* 2007). Species-specific dispersal kernels were obtained from mechanistic models for seed dispersal by wind, which is the predominant dispersal vector in the post-fire environments where serotinous Proteaceae release their seeds (Bond 1988; Schurr *et al.* 2005). We used kernels produced by Schurr *et al.* (2007), who parameterised mechanistic models for primary and secondary wind dispersal (Tackenberg 2003; Schurr *et al.* 2005) with species-level measurements of eight dispersal traits. For each study species, Schurr *et al.* (2007) simulated 10000 seed dispersal events in each of 10000 empirically determined environments. The proportion of dispersal events from cell i to cell j yields an estimate of the per-seed dispersal probability $D_{i,j}$. Since seed dispersal of the study species is largely limited by fire extent (Bond 1988; Schurr *et al.* 2005), we restricted dispersal to the 5x5 cell neighbourhood of each cell, a typical size of large fynbos fires (Horne 1981; Schurr *et al.* 2007).

To estimate the free model parameters, we ran 25 replicate simulations of the demographic model for each parameter combination, model version, and species. Once a simulation reached quasi-stationarity (see Appendix 1.A), we recorded abundances for 500 timesteps or until global extinction, and used them to calculate long-term mean abundances per cell, $\overline{N_i}$.

1.3.7 Model selection

We compared alternative models fitted for the same species by Akaike`s An Information Criterion (AIC) calculated from the number of estimated parameters and the optimal likelihood obtained for each model (Burnham & Anderson 1998). In this comparison, we also included a null model assuming constant abundance throughout the grid. This null model has two parameters (observation probability, ρ; regularity index, s).

1.3.8 Independent information on model structure and parameters

Extensive demographic studies for serotinous Proteaceae provide the opportunity to quantitatively compare the parameter estimates of our model to independent data. The probability of local extinction, E, was measured by the Protea Atlas Project as the proportion of populations that disappeared from an area after a fire (Rebelo 2008). The adult mortality, M, of the sprouter *L. salignum* has been quantified as the proportion of adults that did not resprout after fire (M. Gaertner & F. Schurr unpublished data). The reproductive rate R can be calculated as the ratio between the number of recruits approximately two years after a fire and the number of adults before the fire (Bond *et al.* 1984). Estimates of carrying capacity can be obtained from relationships between reproductive rate R and population density (Higgins *et al.* 2008) as the density at which $R=M$. Finally, the Protea Atlas Project recorded the proportion of clumped populations, which is expected to correlate negatively with regularity index s.

In addition to these quantitative expectations, previous research also leads to qualitative expectations. Because dioecious species are more likely to suffer from pollination failure (Bond 1994), they should be more prone to Allee effects. Moreover, nonsprouters are expected to have higher rates of reproduction and local extinction than related sprouters (Bond & van Wilgen 1996; Bond & Midgley 2001).

1.4 Results

The process-based models introduced here predict both the spatial distribution of 'true' abundances (resulting from demographic submodels) and the spatial distribution of observed abundances (resulting from demographic and observation submodels, Fig. 3). Fig. 3 illustrates the superior performance of these process-based models: phenomenological habitat models for Proteaceae predict large areas as suitable in which the study species have not been observed (lightest grey areas in Fig. 3 a and b). In contrast, the process-based models correctly predict that observed abundances in these areas are low or zero (Fig. 3 c and d). Hence, the abundance observations predicted by the fitted process-based models show good agreement with abundance observations from the Protea Atlas Database (Fig. 3).

1.4.1 Model comparison

For all eight study species, the considered process-based models explained the observed abundance data substantially better than null models of constant abundance (AIC of all null models is at least 35 above that of the worst process- based model, Table 2). For five species a single process-based model is clearly better than all others (AIC difference to the second-best model >16), whereas for the remaining three species, AIC differs relatively little between alternative process-based models (AIC difference to the second-best model between 2 and 5, Table 2). Alternative models produce largely similar parameter estimates, but for simplicity we restrict the following analyses to the best model for each species. The best model included Allee effects for all dioecious *Leucadendron* species, but only for one hermaphroditic *Protea* (Table 2). The estimated Allee critical points C (Table 3) indicate the strength of these Allee effects: for three species we estimated weak Allee effects ($C<0$), meaning that population growth rate R does not drop below 1 as population size approaches 0. For two sprouters (*L. lanigerum lanigerum* and *L. salignum*), however, the best model describes strong Allee effects ($C>0$) so that very small populations are predicted to decline without immigration. According to the best models, reproduction is overcompensatory in six study species, and population growth is overcompensatory in three of the four nonsprouters (Table 2; note that all models for sprouters describe undercompensatory population growth).

Table 2. Comparison of alternative models for the abundance distribution of the study species. The species are grouped as related pairs of nonsprouters (NS) and sprouters (S) (Rebelo 2001). Mon indicates hermaphroditic and Di dioecious reproductive systems. The table gives Akaike's An Information Criterion (AIC) for four process-based models and a null model (number of parameters in brackets). For each species, the best model (with lowest AIC) is highlighted in bold. Note that variants of the Ricker model were only fitted for nonsprouters.

		Model (number of parameters)				
Species	Life history	Null (2)	Ricker (5)	Ricker +Allee (6)	Beverton-Holt (NS: 5, S: 6)	Beverton-Holt +Allee (NS: 6, S: 7)
Protea compacta	NS, Mon	6381.5	6083.0	6082.2	**6079.7**	6084.0
P. scorzonerifolia	S, Mon	2261.1	-	-	2219.7	**2203.0**
P. stokoei	NS, Mon	702.0	**638.1**	641.0	640.1	641.8
P. speciosa	S, Mon	7789.9	-	-	**7749.0**	7754.0
Leucadendron modestum	NS, Di	4615.7	4529.9	**4360.7**	4523.4	4416.9
L. lanigerum lanigerum	S, Di	4917.5	-	-	4774.7	**4459.0**
L. xanthoconus	NS, Di	31026.9	30883.7	**30818.1**	30889.6	30837.5
L. salignum	S, Di	82330.8	-	-	82271.9	**81956.1**

1.4.2 Parameter estimates vs. independent information

The parameter estimates of the best models (Table 3) generally agree with independent information. In particular, we found the expected differences in demographic parameters between related sprouters and nonsprouters. As expected, nonsprouters were estimated to have higher probabilities of catastrophic population extinction E than related sprouters (Table 3). For most species, the estimated extinction probabilities show very good quantitative agreement with independent data on extinction rates (Rebelo 2008; Fig. 4a). The exceptions to this are the nonsprouter *L. xanthoconus* for which we estimated E to be only 0.25% whereas Protea Atlas data suggest E=10% (n=478 populations), and the sprouter *P. scorzonerifolia* which has a high estimate of E=10% (Protea Atlas data: 0%, n=58 populations; Rebelo 2008).

To examine the estimated reproduction functions, we evaluated maximum reproductive rates at densities ≥1 ind cell^{-1} (R_{max}, Table 3) and reproductive rates at a minimal density of 1 individual per cell (R_1, Fig. 4b). In agreement with qualitative observations that nonsprouters have higher fecundity and establishment rates (Bond & van Wilgen 1996; Bond & Midgley 2001; Higgins *et al.* 2008), both reproductive rates were generally higher for nonsprouters (Table 3, Fig. 4b). The only exception to this is the sprouter *P. scorzonerifolia* which was estimated to have a high R_{max} of 9.0 (but nevertheless a low R_1 of 0.8). We also found that nonsprouting *Leucadendron* species have higher reproductive rates than nonsprouting *Protea* (Table 3), which is consistent with independent data on the reproduction of nonsprouters from both genera (Schurr 2005). For nonsprouters we are furthermore able to compare estimated reproductive rates to quantitative data: at realistic densities between 1 and 1.5 K, the range of estimated reproductive rates (0.002 - 14.5) matches data from Bond *et al.* (1984) who found R to range from values smaller 0.1 to 18 in 115 populations of 14 nonsprouter species.

Table 3. Parameter estimates and resulting reproductive rates of the best process-based model (see Table 2) for each study species. The species are grouped as related pairs of nonsprouters (NS) and sprouters (S) (Rebelo 2001). Her indicates hermaphroditic and Di dioecious reproductive systems. Parameters are *M*, probability of adult mortality; *E*, local extinction probability; *K*, carrying capacity; R_{mod}, reproduction parameter; *C*, Allee critical point; ρ, observation probability; *s*, regularity index. The reproductive rates are R_1, reproduction at density 1 ind cell^{-1}, and R_{max}, the maximum reproduction for densities ≥1 ind cell^{-1}.

Species	Life history	Parameter estimates							Reproductive rates	
		*M**	*E*	*K* (ind ha^{-1})	R_{mod}	*C* (ind ha^{-1})	ρ	s	R_1	R_{max}
Protea compacta	NS, Her	-	0.1	87	1.5	-	0.999	0.018	1.5	1.5
P. scorzonerifolia	S, Her	0.2	0.1	523	9.0	-174	0.012	0.007	0.8	9.0
P. stokoei	NS, Her	-	0.15	83	1.5	-	0.089	0.005	1.5	1.5
P. speciosa	S, Her	0.001	0.005	131	2.0	-	0.002	0.016	1.0	1.0
Leucadendron modestum	NS, Di	-	0.1	3487	9.0	-174	0.333	0.028	1.5	9.0
L. lanigerum lanigerum	S, Di	0.675	0.005	9024	4.0	105	0.001	0.057	0.6	4.0
L. xanthoconus	NS, Di	-	0.0025	2790	14.5	-1308	0.016	0.068	10.2	14.5
L. salignum	S, Di	0.4	0.0005	872	7.5	17	0.021	0.091	0.4	7.5

*For nonsprouters, *M* was not estimated but assumed to be 1.

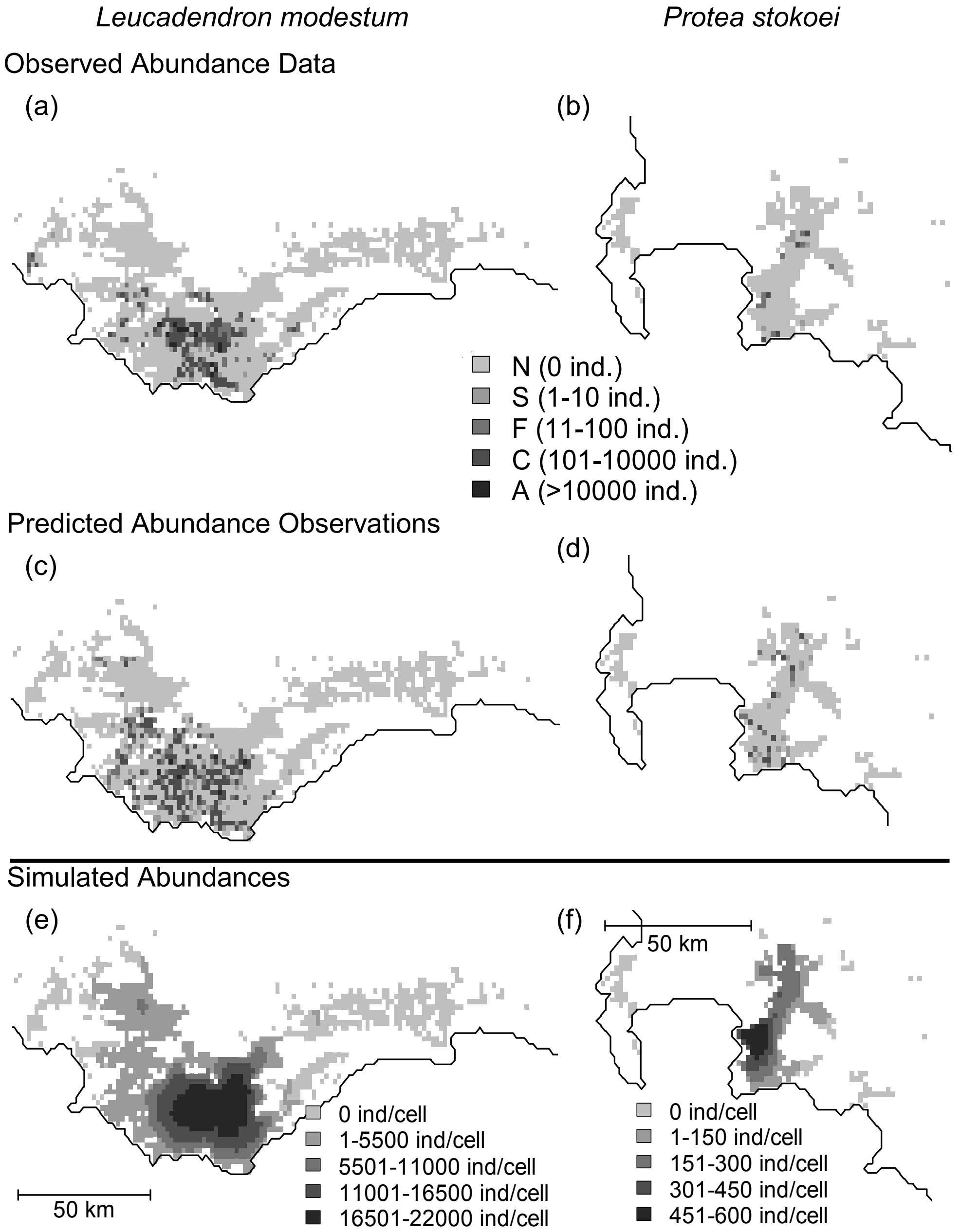

Figure 3. Observed and predicted abundance distributions for *Leucadendron modestum* (a, c, e) and *Protea stokoei* (b, d, f), two Proteaceae endemic to the Cape Floristic Region (CFR). (a) and (b) largest observed abundance class (in circles of 500 m diameter) for each cell according to the Protea Atlas Database (Rebelo 2001). (c) and (d) corresponding predictions of the best process-based model (based on 500 replicate runs of the demographic model and one realization of the observation model). (e) and (f) mean abundance per cell as predicted by the demographic component of the best process-based model. Note that the colouring of (a) - (d) follows a logarithmic scale whereas (e) and (f) have linear scales. Non-white areas are predicted to be suitable by phenomenological habitat models. Note that these habitat models predict large areas as suitable in which the study species have not been observed (category N in a and b), whereas the process-based models fit recorded distributions more closely (c and d).

Independent estimates of carrying capacity *K* can be obtained from data reported in Higgins *et al.* (2008) for two of our study species. These data suggest that *L. salignum* and *L. xanthoconus* have a *K* of 654 and 2255 ind ha^{-1}, respectively, whereas our estimates are 872 and 2790 ind ha^{-1}, respectively (Table 3). For *L. salignum* we also have independent data on adult mortality *M*: in five populations, per-fire mortality ranged from 6-19% (M. Gaertner & F. Schurr unpublished data), indicating that our estimate of M=0.4 may be too high. Interestingly, however, the taxon for which we obtained the highest estimate of *M* (*L. lanigerum lanigerum*) has a nonsprouting sister taxon (*L. lanigerum laevigatum*), and was recorded to show high adult mortality (Rebelo 2008).

Our final comparison concerns parameter estimates of the observation model. While we have no independent data on observation probability ρ, there is independent information related to regularity index *s* (which decreases with the clumping of populations). As expected, the percentage of clumped populations observed in Protea Atlas surveys is negatively correlated with our estimates of *s* (Fig. 4c).

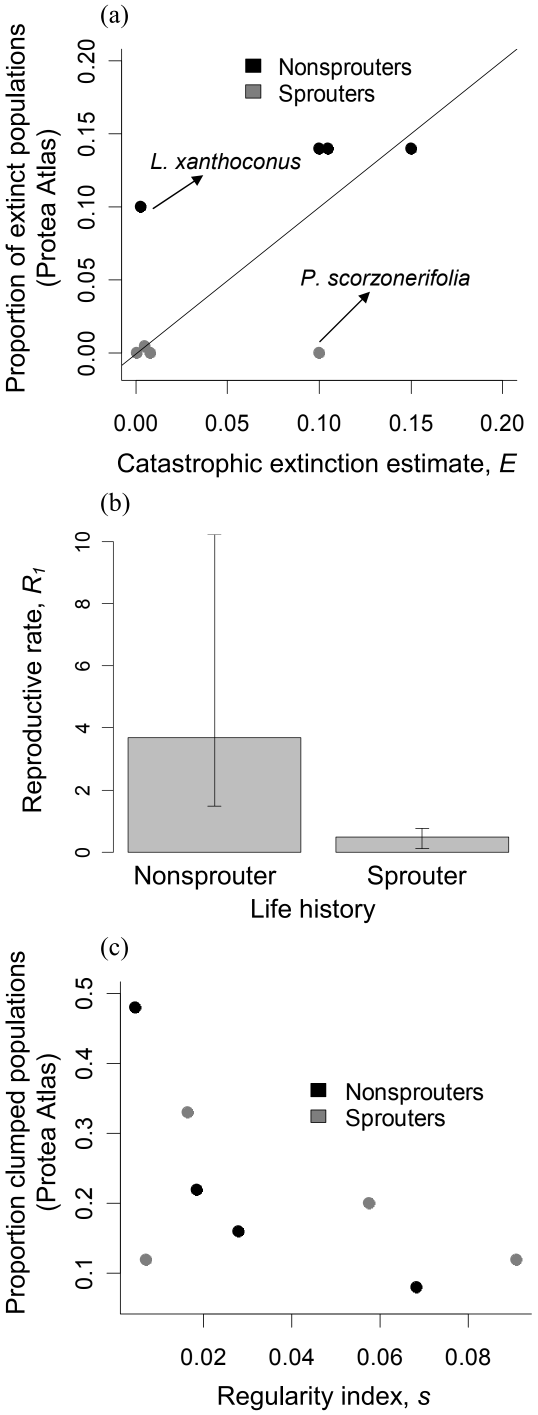

Figure 4. Comparison between parameter estimates and independent information. (a) Catastrophic extinction estimate (*E*) against the recorded proportion of populations that went extinct after fire (Rebelo 2008). The line indicates 1:1 identity, and species strongly deviating from this line are indicated by arrows. (b) Estimated per-capita reproduction at 1 individual per cell (R_1) for nonsprouters and sprouters. The whiskers show the range of estimates in each group (see Table 3). (c) Estimated regularity index (*s*) against the recorded proportion of clumped populations (Rebelo 2008).

1.5 Discussion

This study presents an approach for fitting process-based models of range dynamics to data on the spatial distribution of abundances (Fig. 1). The combination of process-based and statistical approaches to range modelling has a number of advantages: the statistical framework provides a way to estimate unknown parameters (Table 3) and to select between alternative models for range dynamics (Table 2), whereas the process-based nature of the models means that parameter estimates can be compared to independent data (Fig. 4), and that spatial autocorrelation in distributions (Dormann *et al.* 2007; Beale *et al.* 2008) arises naturally from habitat configuration and dispersal. Most importantly, process-based demographic models help to understand how a species occupies its potential range and how this occupied range varies over time. Below we consider the performance of our approach for serotinous Proteaceae, discuss how it promotes our understanding of the range dynamics of these species, and highlight further applications and extensions.

1.5.1 Model performance

The studied Proteaceae vary widely in adult size, longevity, breeding system and dispersal ability (Rebelo 2001; Schurr *et al.* 2007). Irrespective of this variation, process-based models of range dynamics outperformed a null model of constant abundance for all study species (Table 2). In contrast to static habitat models, these dynamic models correctly predict which parts of their potential range are too isolated for serotinous Proteaceae to establish stable populations (Fig. 3).

Our analyses largely confirmed the expected differences between life history types in the structure of the best model as well as the quality and quantity of demographic parameter estimates. For instance, the best model for all dioecious study species included Allee effects, whereas this was true for only one of four hermaphroditic species (Table 2). Life-history also explains qualitative differences in parameter estimates of the best model: as expected (e.g. Bond & van Wilgen 1996; Bond & Midgley 2001), nonsprouters were estimated to have higher rates of reproduction and catastrophic population extinction than related sprouters (Table 3, Fig. 4). Furthermore, most demographic parameter estimates show good quantitative agreement with available independent information (Fig. 4): estimates of extinction probability E (except those for *L. xanthoconus* and *P. scorzonerifolia*) match remarkably well with independent estimates (Fig. 4a), estimated reproductive rates R fall within the range defined by empirical data (Bond *et al*. 1984), and estimated carrying capacities agree with data on the density-dependence of reproduction in *L. xanthoconus* and *L. salignum* (see Results).

Despite the generally good match between demographic parameter estimates and independent data, some estimates deviate from a priori expectations. With few exceptions (Fig. 4a), these deviations occur for species and parameters for which few independent data are available. This holds for *P. scorzonerifolia*, which - albeit being a sprouter - had high maximum reproductive rates (Table 3). However, *P. scorzonerifolia* is a dwarf shrub with a maximum height (<10 cm) far below that of all other study species (50-245cm; Rebelo 2001). Reproductive rates of dwarf Proteaceae have not been quantified yet, but might differ substantially from those of larger species. Further data are also needed on adult mortality in sprouters. While limited data suggest that we overestimated mortality of *L. salignum*, our mortality estimates are not generally implausible: the sprouter with the highest mortality estimate (*L. lanigerum lanigerum*) has a nonsprouting sister subspecies in which adults do not survive fires (Rebelo 2001) and was frequently reported to suffer high adult mortality (Rebelo 2008). These examples show how the process-based approach summarizes demographic knowledge, identifies knowledge gaps, and formulates hypotheses to be tested in field studies.

The observation component of our models is more difficult to evaluate than the demographic component. Support for this component comes from the agreement between estimated regularity indices and independent data on population clumping (Fig. 4c). In contrast, there is no independent information on observation probability ρ. The large interspecific variability in estimates of this parameter (Table 3) raises the question whether ρ can be estimated independent from demographic parameters (notably from carrying capacity K). However, two pieces of information suggest that such independent estimation is indeed possible: i) estimates of K agree with available independent data, and ii) for simulated data, the approach produced estimates close to the true values of ρ and K (Table S1).

1.5.2 Life history, demography and range dynamics of Proteaceae

The combination of process-based models for population dynamics and long-distance seed dispersal by wind explains the global abundance distribution of our study species for parameter values that are largely consistent with independent information. To our knowledge, this is the first example demonstrating that process-based models can quantitatively describe how biogeographical distributions arise from the movement and interaction of individuals (Nathan *et al*. 2008; Thuiller *et al*. 2008). The good performance of our metapopulation-type models is remarkable since Schurr *et al*. (2007) found the metapopulation model of Levins

(1969) to be a poor description of interspecific variation in range filling of 37 species of serotinous Proteaceae. In contrast to the spatially-implicit Levins model, the models fitted here explicitly represent spatial habitat heterogeneity and local population dynamics; and in contrast to Schurr *et al*. (2007) our study accounted for species-level variation in demography. Hence, interspecific variation, spatial heterogeneity and local population dynamics seem important for the range dynamics of our study species. In this section we focus on how local dynamics mediate the effect of life history on range dynamics. In particular, we consider the role of Allee effects (which determine density-dependence in small populations) and compensation strength (which determines density-dependence around carrying capacity).

Allee effects seem more important for dioecious than for hermaphroditic study species (Table 2), probably because the former are more prone to pollination failure (Bond 1994). This has profound consequences for both local and range dynamics: Allee effects increase the extinction probability of local populations and metapopulations (e.g. Stephens & Sutherland 1999), reduce rates of patch colonization and can generate abrupt range limits (Keitt *et al.* 2001). Because Allee effects strongly reduce migration rates of populations (Kot *et al*. 1996; Taylor & Hastings 2005), they may also seriously limit the ability of species to shift their ranges under climate change (Thuiller *et al*. 2008).

According to our analysis, compensation strength differs between sprouters and nonsprouters. For three of four nonsprouters the best model describes overcompensatory population dynamics, whereas for sprouters density-independent adult mortality causes undercompensatory population dynamics (even if reproduction is overcompensatory). This difference is important because overcompensation can destabilize local dynamics (e.g. Caswell 2001) thereby increasing the probability that local populations go extinct due to internal dynamics rather than external catastrophes (Münkemüller & Johst 2007). This increase in local extinction might reduce the large-scale persistence of nonsprouters if dispersal and habitat connectivity synchronize local dynamics (Münkemüller & Johst 2007). While a full analysis of how compensation strength, Allee effects, dispersal, and habitat configuration interact to determine range dynamics is beyond the scope of this paper, our results show that these complex interactions deserve greater attention from theoretical ecologists.

In general, our study suggests that life history can help to predict the risk serotinous Proteaceae face from climate and land use change. It strengthens previous results suggesting that sprouters have high persistence of established populations but low rates of reproduction and habitat colonization, and may thus be seriously threatened by rapid habitat shifts (Schurr *et al.* 2007; Higgins *et al.* 2008). Our study additionally emphasizes the importance of breeding systems: dioecious species seem more likely to suffer from Allee effects which limit their migration ability and increase their risk of local extinction.

1.5.3 Applications and extensions

Our general framework for fitting process-based models of range dynamics can be applied to a wide range of systems. For instance, if dispersal rates are poorly known, they can be estimated in the same way as parameters of local population dynamics. Moreover, the simple models of population dynamics used in this study can be replaced by more complex models describing size-structured populations, interspecific interactions, soil seed banks and/or spatially-correlated extinction. While the use of such complex models will increase ecological realism, it will also complicate parameter estimation and increase variance in model predictions (e.g. Thuiller *et al.* 2008). In this trade-off, model selection in a likelihood framework will help to identify models of optimal complexity (Burnham & Anderson 1998).

Another possible extension is the relaxation of equilibrium assumptions: in order to compare predicted long-term mean abundances to a single timeslice of abundance observations, we assumed that species are currently in (quasi-)equilibrium with their environment (note that this is comparable to the approach Hanski (1994) used to fit process-based models of metapopulation dynamics to a single time slice of occupancy data). While this equilibrium assumption is inherent to static phenomenological models (Guisan & Thuiller 2005), it can be relaxed in our dynamic process-based approach if time series of abundance distributions are available. This stresses the importance of large-scale and long-term monitoring schemes (e.g. Scholes *et al.* 2008).

The fitted process-based models can be used to forecast range dynamics under future environmental change in the same way as other process-based models (e.g. Keith *et al.* 2008); but the advantage of using fitted models is that they incorporate the information contained in current distributions. It is important to note that even if process-based models are fitted under equilibrium assumptions, they still produce forecasts for future non-equilibrium situations: by estimating rates of population extinction and habitat colonization, they predict how quickly ranges can shift in response to environmental change.

A final extension of our approach is to model demographic and observation parameters as a function of the environment (rather than assuming that they are constant throughout the potential range). Currently, estimating the relationship between several environmental variables and several parameters of a dynamic model still poses severe computational problems. However, increasing computer power and the development of more efficient algorithms (e.g. Clark & Gelfand 2006) may enable such estimation in the near future. This seems a worthwhile aim as it would make the process-based approach presented here completely independent of phenomenological habitat models.

1.6 Conclusions

Our study highlights interactions between life history, demography and range dynamics of Proteaceae, and shows that process-based models of range dynamics can explain large-scale abundance distributions. The fitting of these models in a likelihood framework improves descriptions of species distribution, and enables parameter estimation and model selection as a basis for predicting range dynamics under non-equilibrium conditions. The presented framework strengthens links between the largely disjunct disciplines of species distribution modelling, empirical demography and theoretical ecology. Combining knowledge from these disciplines is necessary to better understand the range dynamics of species and their response to a changing world.

1.7 Appendix 1.A - Fitting process-based models of range dynamics to abundance data

The first part of this appendix describes how we assessed whether simulations of process-based models had reached the quasi-stationary state and how we initialized these simulations. The second part describes how we evaluated the fitting of process-based models with artificial data.

Definition of the quasi-stationary state and selection of initial conditions

To determine when simulations reached the quasi-stationary state, we considered time series of range filling (the proportion of suitable cells occupied, Svenning & Skov 2004) from which we discarded the first 100 time steps. If range filling initially decreased/increased, we defined the quasi-stationary state to be reached 1000 time steps after range filling was first greater/smaller than range filling 15 time steps earlier.

To test this definition, we ran simulations with four different initial range fillings (25%, 50%, 75% and 100%) in each of three artificial landscapes (Hurst factor=0.8; Saupe 1988), using the Beverton-Holt model extended with Allee effects (see Table 1 in the Main Text). For each of these 12 simulations we calculated the long-term mean range filling in the 500 time steps after the definition was met. For a wide range of parameter values (E: 0.01 to 0.2; M: 0.1 to 1; R_{mod}: 1.5 to 15.0; C: -500000 to 25000; K=500000) these long-term means differed by a maximum of 3.5% (maximum standard deviation 0.016), indicating that the definition reliably identified convergence to a quasi-stationary state.

For some parameter values, an initial range filling of 25% led to rapid global extinction, whereas the initial range fillings between 50% and 100% resulted in long-term persistence. Simulations with an initial range filling of 50% typically were the fasted to reach the quasi-stationary state. Therefore, we chose 50% as the standard initial range filling.

Evaluation of the fitting procedure with artificial data

Artificial data

We evaluated the model fitting procedure by applying it to artificial abundance data simulated with the Beverton-Holt version of the demographic model (Table 1 in Main Text) and the observation model. We simulated the range dynamics of two hypothetical species, of which one is iteroparous and has overlapping generations, whereas the other is semelparous and has non-overlapping generations. The two hypothetical species differed in ecological and observation parameters (Table S1) and in dispersal. Dispersal occurred within the 5 x 5 cell neighbourhood of each source cell, with the iteroparous species having dispersal probabilities of 0.998 for the source cell, 0.00024 for adjacent cells and 0.000005 for the margins of the neighbourhood. The semelparous species had slightly more long-distance dispersal, with dispersal probabilities of 0.992, 0.000875 and 0.0000625, respectively.

The dynamics of both hypothetical species was simulated in five different fractal landscapes of 129 x 129 cells. Aggregated fractal distributions of suitable habitat were obtained by the midpoint displacement algorithm with Hurst factor 0.8 (Saupe 1988). For each hypothetical species, simulations were run for five different fractal landscapes in which 3-5% of the cells were suitable. In each of these five simulations, the local abundances were recorded at time step 4000 after reaching the quasi-stationary state. From these local abundances we generated five sets of artificial abundance observations with the observation model. Each grid cell was 'surveyed' i times, where i was a Poisson random number with mean 10, and each survey covered f=1/1000 of the grid cell area.

Fitting the model to the artificial data

When fitting the generating model to each of these five artificial data sets, we ran 30 replicate simulations for the corresponding landscape per parameter combination and calculated the expected abundance in each cell, $\overline{N_i}$, as the average over 2000 time steps in quasi-stationary state. The medians of the parameter estimates for five different landscapes show good agreement with the 'true' values and the variation between individual estimates is small except for mortality rate M and extinction probability E (Table S1).

Table 1.A.1. **Test of the fitting approach with artificial data**. For two hypothetical species (iteroparous and semelparous), the table gives the 'true' value of each parameter, the search interval within which the parameter was varied, the median of parameter estimates for five artificial data sets as well as the range of the five estimates (in brackets). Note that the mortality M of the semelparous species was not estimated but set to 1.

Species		Probability of adult mortality (M)	Local extinction probability (E)	Carrying capacity (K, 10^3 ind per cell)	Reproduction parameter (R_{mod})	Observation Probability (ρ)	Regularity index (s)
Iteroparous (overlapping generations)	‘True’ value	1.0×10^{-2}	1.0×10^{-5}	1000	1.5	0.90	0.50
	Search interval	$10^{-3} – 7.5 \times 10^{-1}$	$10^{-7} – 5 \times 10^{-1}$	1 – 10000	1.1 – 21.0	Nelder-Mead optimization	
	Estimate (Min, Max)	1.5×10^{-2} (9.5×10^{-3}, 1.8×10^{-1})	2.5×10^{-5} (9.0×10^{-6}, 2.0×10^{-3})	1000 (900, 1100)	1.5 (1.4, 2.1)	0.90 (0.80, 0.98)	0.49 (0.48, 0.51)
Semelparous (non-overlapping generations)	‘True’ value	1	1.0×10^{-2}	1000	3.5	0.70	0.10
	Search interval	-	$10^{-7} – 5.0 \times 10^{-1}$	1.0 – 10000	1.1 – 21.0	Nelder-Mead optimization	
	Estimate (Min, Max)	-	1.0×10^{-2} (9.5×10^{-3}, 7.0×10^{-2})	1100 (750, 1150)	3.4 (3.2, 3.7)	0.68 (0.61, 0.97)	0.09 (0.09 , 0.10)

Link to the next chapter

In the Chapter 1 I introduced a process-based model for range dynamics or species distribution. The model was a 'hybrid' approach (Thuiller et al. 2008) because it considered a habitat model in order to describe the suitable habitat and a demographic model that simulate key processes that determine range dynamics (Schurr *et al.* 2007). The model could be fitted to data, taking also into account an observation model for considering imperfect detection. The model and the fitting procedure were successfully evaluated with artificial data. This gave me the confidence to apply the approach to my study system, CFR Proteaceae. Simulation results seem to match spatial distribution of abundances and the parameter estimates were comparable to independent estimates. Once the process-based approach was developed, it turned possible to investigate factors that deviate plant metapopulations from the species-habitat equilibrium achieved by the processes implemented in chapter 1 and that can affect range dynamics.

The first application to such perturbation factors is addressed in the next chapter. In Chapter 2, I used the process-based demographic model to assess the impact of wildflower harvesting on species range size and global abundance. I investigate this effect in two different steps:

1- A sensitivity analysis, where I applied nested scales and varied the parameter values in a full-factorial design. This analysis allowed me to draw general understanding on the role of different demographic properties on the species response to wildflower harvesting. I could also assess the importance of the scale at which wildflower harvesting is observed.

2- Application to selected Proteaceae species. For this end, I used the best model and its parameter estimates obtained in chapter 1 for *P. compacta*. The fitting procedure introduced in chapter 1 was also used to obtain the best model and its parameter estimates for *P. repens* and *P. neriifolia*.

Therefore, the Chapter 1 delivered me not only the mechanistic method to assess species response to wildflower harvesting but also the species-specific estimates to generate specific results.

Chapter 2 – Effects of wildflower harvesting on plant dynamics at different spatial scales: lessons from the Proteaceae of the Cape Floristic Region [1]

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[1] To be submitted to *Conservation Biology* as **Cabral JS**, Bond WJ, Midgley GF, Rebelo AD, Thuiller W, Schurr FM. Effects of wildflower harvesting on plant dynamics at different spatial scales: lessons from the Proteaceae of the Cape Floristic Region.

2.1 Abstract

Wildflower harvesting is an economically important activity in some parts of the globe, but its ecological effects are still poorly understood. Here we assess how wildflower harvesting affects plant dynamics at multiple spatial scales. To this end, we introduce a process-based model of spatial dynamics of shrubs harvested for wildflowers (serotinous Proteaceae from the South African Cape Floristic Region - CFR). The model describes how harvesting affects demographic processes in spatially heterogeneous landscapes. We first used the model as a simulation tool to analyse which parameter affects most the species response to harvesting through a comprehensive sensitivity analysis over nested scales. In this analysis, we varied dispersal ability, strength of Allee effects, maximum reproductive rate, adult mortality, local extinction probability and carrying capacity. Afterwards, we applied the approach to three CFR Proteaceae species. We calculate critical harvesting rates at which harvesting reduces long-term persistence or abundance to 90% (P_{90}, and A_{90}, respectively). Plant response to harvesting showed abrupt threshold behavior. Species with short-distance seed dispersal, strong Allee effects, low maximum reproductive rate, high mortality and high local extinction were most vulnerable to harvesting. Increased spatial scale generally increased P_{90}, A_{90} and the thresholds' sharpness. Moreover, spatial scale interacted with Allee effects and local extinction probability in its effect on critical harvesting rates. For the CFR Proteaceae species, we obtained low P_{90}, and even lower A_{90}. In summary, good demographic knowledge and careful identification of the spatial scale of interest are necessary in order to guide harvesting assessments and monitoring that should meet conservation targets of exploited species. Nevertheless, the general sensitivity analysis presented here allows qualitative risk assessments caused by harvesting impacts for poorly studied species and improves our understanding of harvesting impacts on metapopulation dynamics.

2.2 Introduction

Harvesting of wildflowers is an economically important activity in the biodiversity hotspots of the South African Cape Floristic Region and the Southwest Australian Floristic Region (Cowling & Lamont 1985; Greyling & Davis 1989; Lamont *et al.* 2001; Turpie *et al.* 2003). In the Cape Floristic Region (CFR), wildflower harvesting concentrates on the Proteaceae family which is a dominant component of the Mediterranean-type Fynbos vegetation (Cowling 1992). Many Proteaceae produce inflorescences of high ornamental appeal and their trade generates income on the order of dozens of million dollars per year (Greyling & Davis 1989; Turpie *et al.* 2003). Flower trade in the CFR is estimated to rely on more than 50% of harvesting in wild populations (Turpie *et al.* 2003). From a total of ca. 330 species of CFR Proteaceae around a third is serotinous (~ 110 species, mainly *Protea* and *Leucadendron*), keeping their seeds in a canopy seed bank of woody cones until fire triggers seed release, dispersal and recruitment (Rebelo 2001). The woody cones of some species have also ornamental value and are harvested. Due to variations on the market demands and preferences, the number of economically important CFR Proteaceae species is very high, comprising around a third of all CFR Proteaceae and more than half of the serotinous species. Moreover, wildflower and cone harvesting removes seeds from the canopy seed bank, but how this impacts Proteaceae dynamics and how much of the natural stock can be harvested is still poorly understood (Maze and Bond 1996; Turpie *et al.* 2003).

A harvesting-induced decrease in canopy seed banks only lowers recruitment if recruitment is seed-limited. The extent to which plant recruitment is seed-limited generally increases with spatial scale (Nathan & Muller-Landau 2000). This is because at short dispersal distances recruitment is often limited by intraspecific competition whereas at long dispersal distances it is more likely to be limited by seed density which depends on the strength of seed sources. Hence, harvesting which reduces the strength of seed sources may have more pronounced effects at large spatial scales. Additionally, seed limitation may be stronger in species subject to Allee effects, a decrease in *per capita* reproduction at low density (Allee *et al.* 1949; Courchamp *et al.* 1999). Allee effects seem to shape the local and large-scale dynamics of certain Fynbos Proteaceae (Cabral & Schurr in press), which have metapopulation-like dynamics (Schurr *et al.* 2007). Theoretical studies show that Allee effects can alter the outcome of population viability analyses and assessments of harvesting impacts (Stephens & Sutherland 1999; Petersen & Levitan 2001). However, even if harvesting reduces recruitment and increases the extinction probability of local populations, this will not necessarily compromise the large-scale persistence of species. For once, metapopulation persistence may be unaffected by increases in local extinction risk as long as colonization rates are sufficiently high (Levins 1969). Secondly, immigration from neighbouring populations can counteract a reduction in reproductive rates, thereby saving local populations via rescue effect (Brown & Kodric Brown 1977). The importance of these two buffering effects depends on the probability with which seeds are dispersed between habitat patches.

The effect of wildflower harvesting on plant dynamics may thus vary with spatial scale and species' demographic properties. However, the only study that assessed the impacts of wildflower harvesting on CFR Proteaceae (Maze & Bond 1996) was restricted to small spatial scales and did not make use of dynamics population models. Models describing how local dynamics are linked by long-distance dispersal have recently been developed and have been shown to explain range-wide abundance distributions of CFR Proteaceae from species-specific demographic properties (Cabral & Schurr in press). These models can describe the demographic consequences of wildflower harvesting and can be run at different spatial scales to investigate whether larger scales show greater resilience to harvesting.

The present study aims to understand the impact of wildflower harvesting on the persistence and abundance of CFR Proteaceae at multiple spatial scales. It assesses how harvesting impacts vary with spatial scale and species' demographic properties. In contrast to existing studies of harvesting impacts on metapopulations, mostly analytical (e.g. Tuck & Possingham 1994, 2000; Supriatna & Possingham 1998; Bascompte *et al.* 2002), our study uses spatially-explicit process-based models to simulate (meta-)population responses to harvesting over large geographical areas with explicit local dynamics. Our aim is to understand how harvesting affects abundance and the (meta-)population persistence at multiple spatial scales over different demographic characteristics. To address this question, we conduct a simulation experiment through a comprehensive sensitivity analysis in which we vary demographic properties and the spatial scale at which harvesting is assessed. Subsequently, we address harvesting effects on three specific CFR Proteaceae. These analyses provide a basis for developing strategies that ensure the conservation and persistence of harvested species.

2.3 Methods

To assess the impact of harvesting, we applied a process-based approach that includes key demographic processes, which were based on the CFR Proteaceae as our study system. The assessment was performed with a sensitivity analysis. For different combinations of demographic properties, we used the process-based models to examine how harvesting affects persistence and abundance at different spatial scales. Subsequently, we investigated wildflower harvesting impacts on selected Proteaceae species for which habitat arrangement as well as parameters describing local demography and long-distance dispersal are available (Midgley *et al.* 2002, 2003; Schurr *et al.* 2005, 2007; Cabral & Schurr in press).

2.3.1 Study System

The population dynamics of CFR Proteaceae are driven by recurrent fires (Bond & van Wilgen 1996). The model structure is largely based on serotinous species, which form canopy seed banks instead of soil seed bank (Rebelo 2001). Due to irrelevance of inter-fire recruitment and inter-fire recruit mortality, we assumed discrete time steps for population dynamics. The time step length is, thus, determined by fire return intervals (Bond *et al.* 1995), which in some parts of the CFR is as long as 28 years (Polakow & Dunne 1999). Serotinous Proteaceae have two fire-persistence strategies: sprouters can survive fire as adults (adult mortality by fire < 1), are iteroparous and have overlapping generations; whereas nonsprouters survive fire only as seeds (adult mortality by fire = 1) and are semelparous with non-overlapping generations (Bond & van Wilgen, 1996; Bond & Midgley, 2001, 2003; Schurr *et al.* 2007). If a fire follows too quickly after the previous one, it can cause extirpation of nonsprouter populations that are not sexually mature yet (Bond & van Wilgen 1996). Fires generating these catastrophic extinctions have small size due to slow post-fire re-growth of flammable biomass. Competition acts only on reproduction by reducing individual seed set, not causing intense adult mortality (Bond *et al.* 1995). Similarly, Allee effects in Proteaceae act on individual fecundity but not on adult survivorship (Lamont *et al.* 1993). Harvesting of flowers does not enhance the number of viable seeds produced by the remaining flowers (Mustart & Cowling 1992).

2.3.2 Process-based model

The above mentioned demographic properties of CFR Proteaceae are captured in process-based models for range dynamics developed by Cabral and Schurr (in press). In the following, we briefly describe these models and explain how they were modified to incorporate harvesting. For a given spatial-explicit habitat arrangement (grid cell size 1’x1’; equalling ca. 1.55x1.85 km), these demographic models describe the dynamics of local populations that are connected by long-distance seed dispersal. The modelled processes are density-dependent seed production, seed dispersal, recruitment, adult mortality per fire and catastrophic local extinction per fire. The model parameters, treated as demographic properties, represent maximum per-capita reproductive rate, carrying capacity, adult mortality rate, local extinction probability, Allee critical point, and a discrete two-dimensional dispersal kernel (Table 1). The dispersal kernels give the probability of seed dispersal from a source cell to each of the neighbouring cells. Alternative model versions differ in the submodel used to describe local dynamics. The processes take place one per model time step, which is implicitly defined by mean fire interval. We assumed that catastrophic extinction per fire independently affects individual grid cells. For a more detailed description of the models see Cabral and Schurr (in press).

Each model simulation used as input a grid of suitable and unsuitable patches. Initially, all suitable cells were set to contain populations at carrying capacity. After the quasi-stationary state was reached (by letting the simulation running enough model interactions), we simulated wildflower harvesting by removing a proportion *H* of the total number of seeds produced in a cell. We term this proportion *H* the harvesting rate.

2.3.3 Sensitivity analysis

We conducted a full factorial sensitivity analysis by varying species characteristics within realistic ranges (Table 1). To describe species with different long-distance dispersal ability, we used discrete versions (5 x 5 grid cells) of a generalized exponential kernel (Clark *et al.* 1998). The kernels had mean dispersal distance of 0.1 cells, and shape parameter of 1 and 0.5, yielding a negative exponential (‘thin-tailed dispersal kernel’) and a fat-tailed kernel (‘fat-tailed dispersal kernel’), respectively. To describe local population dynamics, we used the Beverton-Holt model (Beverton & Holt 1957) with Allee effects (see Cabral & Schurr in press). For each set of species characteristics, *H* varied from 0 to 100% in steps of 4%.

For each combination of species characteristics and harvesting rate, we ran the model on 100 fractal landscapes of 129 x 129 cells with 5% of the cells being suitable. Aggregated fractal distributions of suitable habitat were generated by the midpoint displacement algorithm with fractal dimension D = 2.2 and variance in displacement of points $\sigma^2 = 30$ (Saupe 1988).

We investigated the effect of spatial scale by calculating the proportion of persisting (meta-)populations in nested subregions of different sizes. These subregions represented local (1 cell), small regional (9x9 cells), regional (33x33 cells) and global (129x129 cells) scales. Nestedness of the subregions was ensured for each landscape by first selecting a focal suitable cell at random. This focal cell was set to be the local scale. The small regional and the regional subregions were obtained by symmetrically expanding from the focal cell (Fig. 1). For each simulation, we first ran the model without harvesting for 300 time steps, which were enough model interactions to let the metapopulation reach the quasi-stationary state. Subsequently, harvesting took place throughout the metapopulation at a constant rate *H* for 500 time steps.

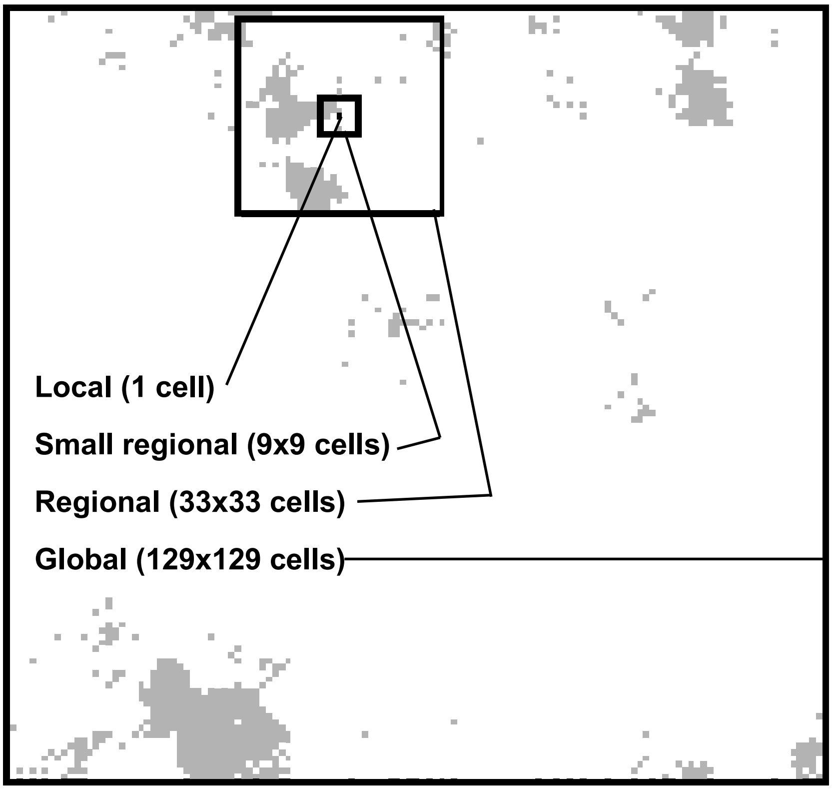

Figure 1. Setup used to study harvesting impacts at nested spatial scales in the sensitivity analysis. The entire model grid comprises 129 x 129 cells and suitable habitat is indicated in dark grey. For each one of the 100 landscapes a suitable focal cell (in black) is randomly chosen and used as the central cell of 9x 9 and 33 x 33 grid cell subregions (indicated by rectangular frames).

2.3.4 Plant dynamics and critical harvesting rates

We investigated two aspects of plant dynamics: persistence and overall abundance. Persistence was calculated for each parameter combination, spatial scale and harvesting rate as the proportion of the 100 simulation replicates that survived the entire simulation period (500 time steps). Thereafter, we calculated two critical harvesting rates (P_{90} and A_{90}) at which persistence and overall abundance, respectively, first dropped to or below 90% of the value without harvesting. Alternative critical rates at which persistence and abundance dropped to 50% and 10% showed similar behaviour to P_{90} and A_{90} (results not shown). We also calculated critical harvesting rate associated with occupied range, but this was highly correlated with P_{90} (Spearman's rank correlation: 0.945) and was not further analysed. For some parameter combinations of the sensitivity analysis (low local extinction and adult mortality), all simulation replicates persisted throughout the recording period, even at H = 100%. In these extreme cases we assumed P_{90} to be 100%.

Table 1. Model types and demographic properties used in the full-factorial sensitivity analysis and to simulate harvesting impacts on three species of Cape Proteaceae.

Model and parameters/demographic properties	Sensitivity analysis	Selected Cape Proteaceae		
		Protea compacta	*Protea neriifolia*	*Protea repens*
Local population model	Beverton-Holt + Allee effects	Beverton-Holt	Ricker + Allee effects	Ricker + Allee effects
Model parameters				
Local extinction probability (*E*)	0.001, 0.01, 0.1 and 0.25	0.1	0.002	0.0001
Mortality rate (*M*)	0.05, 0.25, 0.50, 0.75 and 1	1	1	1
Maximum reproductive rate (R_{max})	1.5, 5.5, 12.5 and 18.5	1.5	15.1	2
Carrying capacity (*K* – ind/ha)	174, 1744, 5000 and 10000	87	14764	15.6
Allee critical point (*C*– ind/ha)	-K (absent), -K/2 (weak) and 0.05K (strong)	-	-0.003K	0.08K
Dispersal kernel	Spatially-discretized generalized exponential kernel (Clark *et al.* 1998). Mean distance: 0.1 cell lengths; shape parameter: c=1 (thin-tailed kernel) dispersal) and c=0.5 (fat-tailed kernel).	From Schurr *et al.* (2007)		

2.3.5 Statistical analyses

Outcomes of the sensitivity analysis were summarized by fitting linear models with critical harvesting rates as response variable. The critical harvesting rates were arcsine square root transformed in order to ensure normality of errors. The maximal linear model for each analysis included all two-way interactions between scale and species characteristics (dispersal ability, Allee critical point, maximum reproductive rate, adult mortality rate, carrying capacity and local extinction probability). To obtain minimal adequate models, we removed terms from the maximal model as long as this caused no significant decrease in model fit at $P < 0.05$ (Crawley 2005).

2.3.6 Model application to selected CFR Proteaceae

We assessed how harvesting would affect persistence and global abundances of three Proteaceae species (*Protea compacta, P. neriifolia* and *P. repens*). These species are endemic to CFR and some populations are subjected to wildflower harvesting. The dispersal kernels of these species were derived from validated process-based models for primary and secondary seed dispersal by wind (Tackenberg 2003; Schurr *et al.* 2005, 2007). Using these dispersal kernels in combination with alternative local dynamics' models, Cabral and Schurr (in press) found that the range dynamics of *P. compacta* is best described if local dynamics follow the Beverton-Holt model (Beverton & Holt 1957). For this species we used the parameter estimates obtained by Cabral and Schurr (in press). *P. neriifolia* and *P. repens* were not studied by Cabral and Schurr (in press), but we used the same approach to fit models of range dynamics to abundance records from the Protea Atlas Database (Rebelo 2001). For both species we found the local dynamics is best described by the Ricker model with Allee effects (J.C. unpublished data; for the formulation of this model see Cabral and Schurr in press). The population models and the corresponding parameter estimates for the study species are summarized in Table 1. Although *P. neriifolia* and *P. repens* have similar vegetative architecture and would be expected to have carrying capacity around 4000-8000 ind/ha in suitable areas, our estimate of K is an average K over all suitable grid cells. These cells may include portions that are unsuitable and some that have underwent habitat loss. Note that R_{max} happens only in population densities between C and K. Suitable habitats were described by habitat models considering historical climate conditions (Midgley *et al.* 2002, 2003). 50 replicate simulations ran for 1000 time steps in order to reach the quasi-stationary state. Harvesting rates varied from 0 to 100% in steps of 1%.

For the study species we calculated not only A_{90} and P_{90} but also the harvesting rate at Maximum Sustainable Yield (MSY). This allowed us to compare our results for *P. neriifolia* and *P. repens* with existing MSY estimates (Maze & Bond 1996). Yield was calculated as the number of seeds (surrogating flower number) harvested across the species' global range. The yields at the last simulated time step were averaged over replicates. The harvesting rate that maximized the average yield was identified as the harvesting rate at MSY.

2.4 Results

2.4.1 Sensitivity analysis

Harvesting decreased persistence probability and abundance and - for most scales and parameter combinations - this decrease was rather abrupt (Fig. 2). This threshold behaviour was most pronounced at the largest scale whereas at smaller scales increased harvesting caused a more gradual decrease in persistence and abundance (Fig. 2). Spatial scale and all demographic properties except carrying capacity had significant effects on A_{90} and P_{90} ($P<0.05$). P_{90} was lowest at local scale (Fig. 3a), increased slightly under fat-tailed dispersal kernel (Fig. 3b), increased with R_{max} (Fig. 3d), and decreased with the strength of Allee effects (Fig. 3c), local extinction probability (Fig. 3e), and adult mortality rate (Fig. 3f). A_{90} was consistently lower than P_{90} and showed qualitatively similar but quantitatively less pronounced responses to variation in demographic properties and spatial scales (Fig. 4).

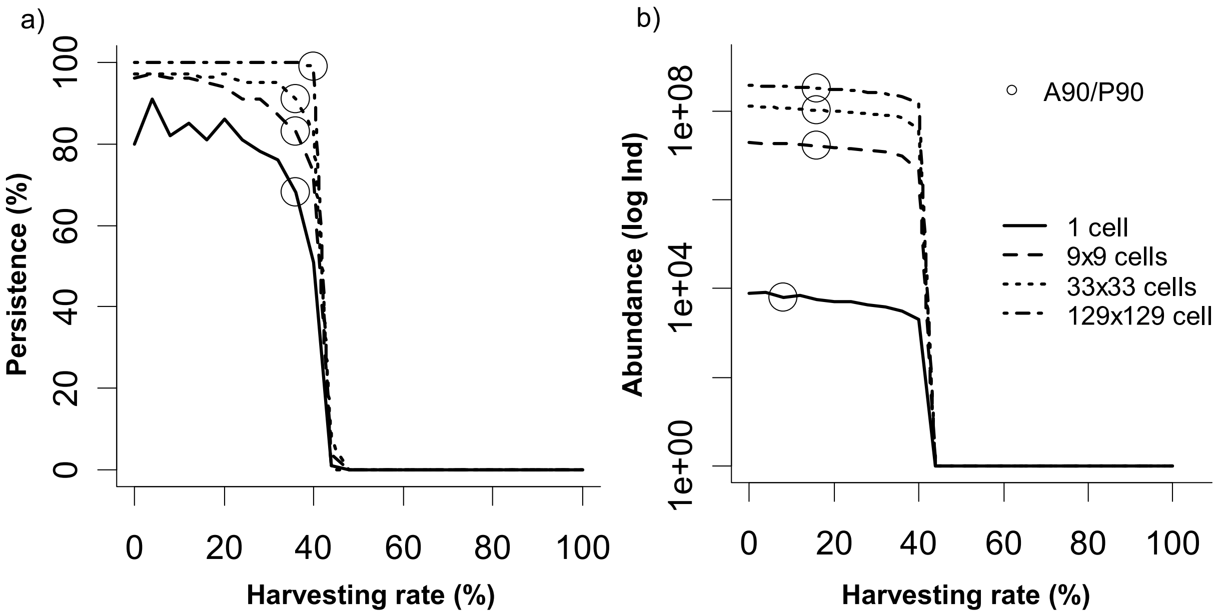

Figure 2. Effects of wildflower harvesting on persistence and abundance at different spatial scales (different line types). The figures show results for one combination of demographic parameters that makes the difference between scales more evident (E=0.1, Rmax=5.5, K=1744, C=0.05K, M=1, fat-tailed dispersal kernel). Note that the y-axis in (b) is plotted on a log scale. Circles indicate the critical harvesting rates P_{90} and A_{90} in (a) and (b), respectively.

The minimal adequate model for P_{90} also contained two-way interactions of spatial scale with Allee effects and local extinction probability, respectively. In absence of Allee effects, the difference within scales is basically between local scale and all the other scales. When increasing Allee effects, the difference among regional and large scales can be detected, but the difference between local scale and all the others is attenuated (Fig. 5a). Under low local extinction probabilities, there is no difference between scales, but under high local extinction probabilities, the scales start to differentiate with a pronounced drop of P_{90} at local scale (Fig. 5b). For the A_{90}, the minimal adequate model also included two-way interactions, but only of spatial scale with local extinction probability, showing a divergent trend from that of P_{90}. Although the local scale has always an evident lower A_{90} than all the other scales, small regional and larger scales get increasingly similar A_{90} by increasing the local extinction probability (Fig. 5c). Although all critical harvesting rates differed strongly between the local scale and the other scales, excluding the local scale did not qualitatively change the outcome of statistical analyses (results not shown).

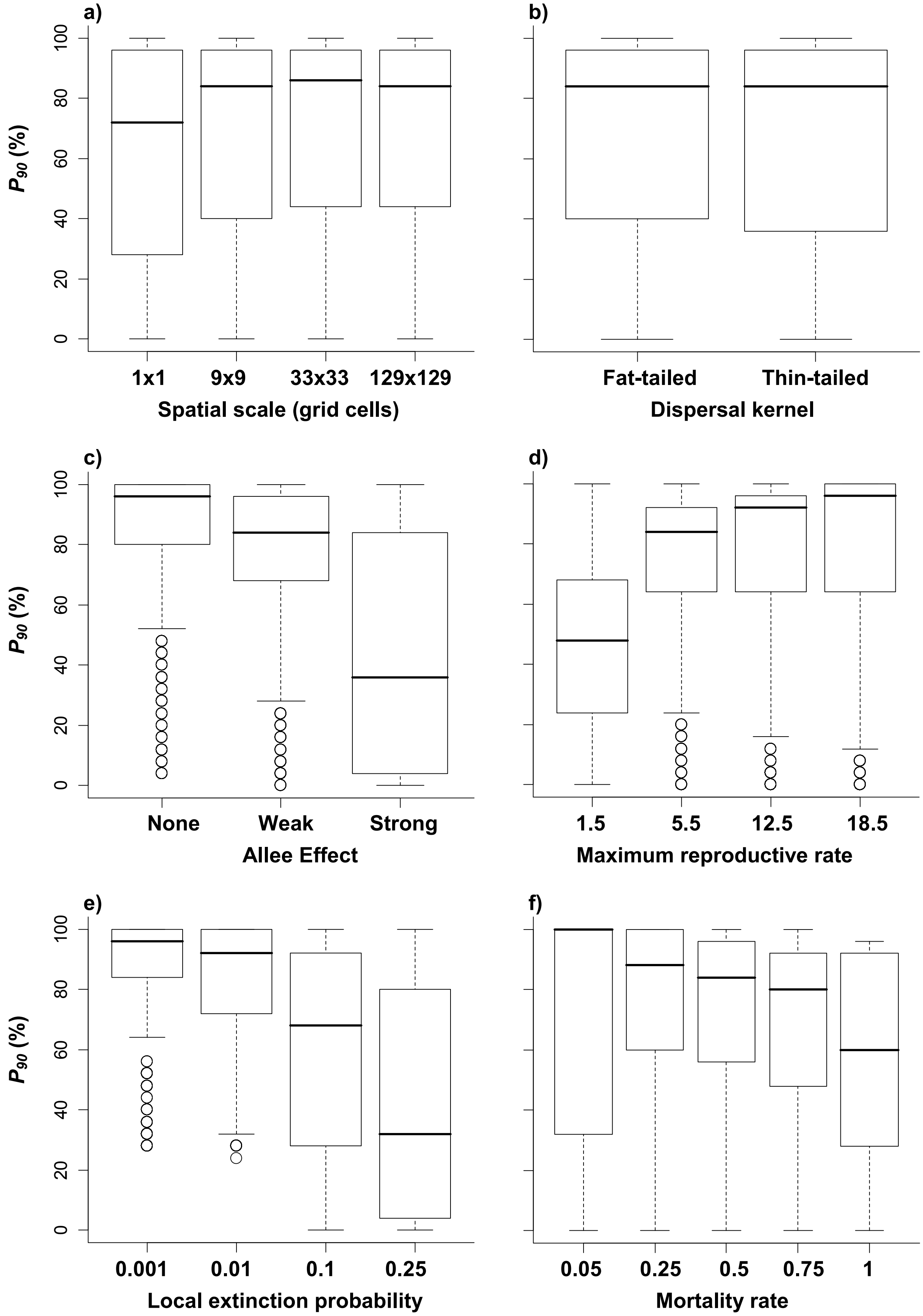

Figure 3. Effects of demographic properties and spatial scale on the critical harvesting rate P_{90} at which persistence is reduced to 90% of the level without harvesting. Boxplots depict variation arising from the other parameters varied in the sensitivity analysis (see Table 1).

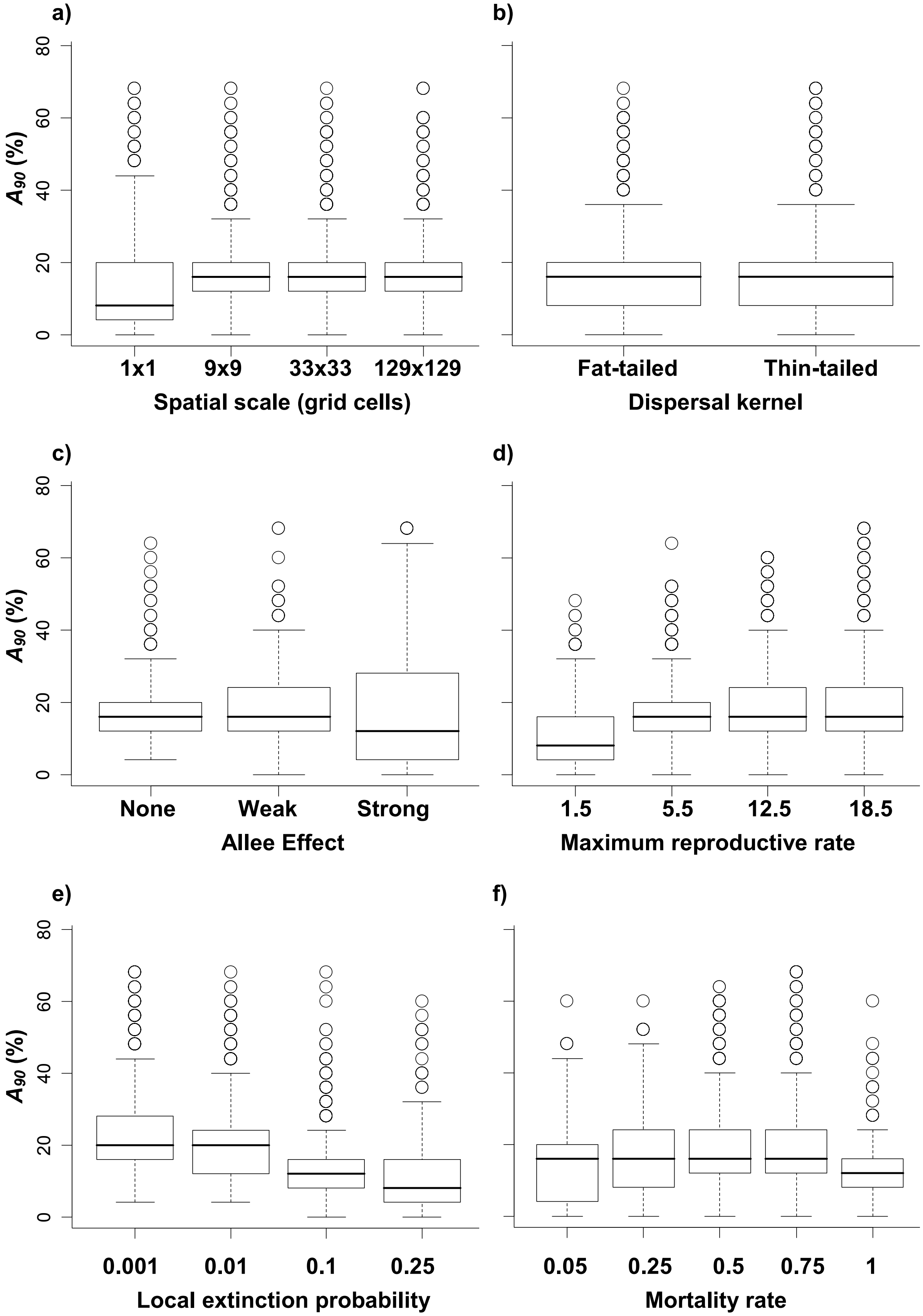

Figure 4. Effects of demographic properties and spatial scale on the critical harvesting rate A_{90} at which abundance is reduced to 90% of the level without harvesting. Boxplots depict variation arising from the other parameters varied in the sensitivity analysis (see Table 1).

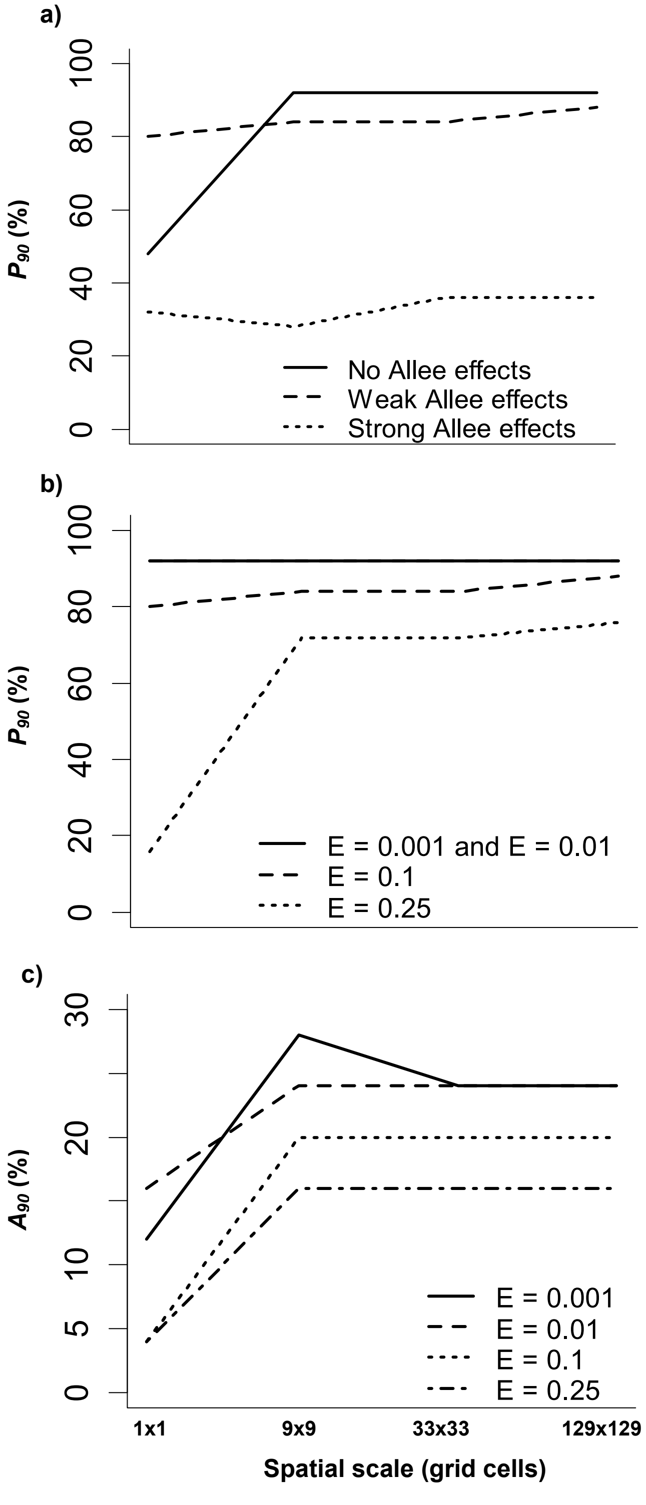

Figure 5. Interactions between spatial scale and demographic properties (different line types) on the critical harvesting rates P_{90} and A_{90}. The figures show results for one combination of demographic parameters (Rmax=5.5, K=1744, M=0.5, fat-tailed dispersal kernel). a) Interaction between scale and Allee effects on P_{90}. b) Interaction between scale and local extinction probability on P_{90}. c) Interaction between scale and local extinction probability on A_{90}.

2.4.2 Specific CFR Proteaceae

The three study species differ quantitatively in their predicted response to wildflower harvesting. *P. compacta* and *P. neriifolia* were predicted to tolerate only very low harvesting rates before their range-wide persistence and abundance were affected, whereas *P. repens* may support higher harvesting rate (Figs. 6a-b). The persistence of all species was projected to remain unaltered until showing a sharp threshold response to harvesting that coincided with the P_{90} detection (Fig. 6a). The persistence thresholds were more abrupt for *P. neriifolia* and *P. repens*, than for *P. compacta* (Fig. 6a). Abundance showed a similar threshold behaviour for *P. compacta* and *P. neriifolia*. By contrast, the abundance response of *P. repens* to harvesting pressure was more complex, as abundance initially decreased in response to increasing harvesting rate (reaching A_{90} at 5% harvesting), then increased with intermediate harvesting rates before dropping steeply to extinction (Fig. 6b).

The P_{90} values were 6%, 15% and 48%, and the A_{90} values were 1%, 2% and 5% for *P. neriifolia*, *P. compacta* and *P. repens*, respectively. For *P. compacta* we graphically depict the impact of the critical harvesting rates P_{90} and A_{90} on the predicted range at the last simulated time step (Figs. 6c-d). The resulting maps illustrate that a harvesting rate with a minor impact on range-wide persistence (P_{90}) can markedly decrease range size, and that the abundance-based critical harvesting rate A_{90} is more conservative. The harvesting rates at MSY were 4%, 7% and 45% for *P. neriifolia*, *P. compacta* and *P. repens*, respectively.

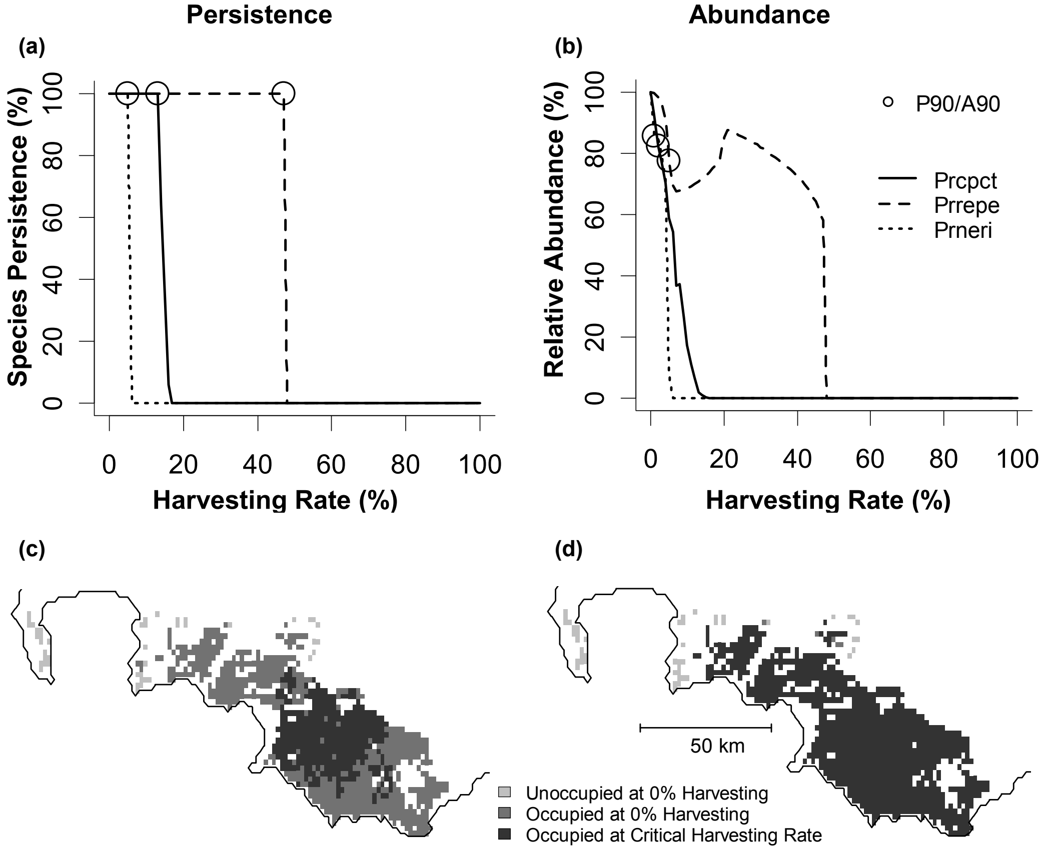

Figure 6. Effects of wildflower harvesting on three species of Cape Proteaceae on the last simulated time step. a) Persistence against harvesting rate under climate change. b) Relative effect of harvesting on abundance. Species were drawn in (a) and (b) with different line types under the names Prcpct = *P. compacta*, Prneri = *P. neriifolia* and Prrepe = *P. repens*. Circles indicate P_{90} in (a) and A_{90} (b). c-d) Example simulations showing the effects of wildflower harvesting on the range of *P. compacta*. Dark grey cells are occupied at the critical harvesting rates P_{90} (c) and A_{90} (d), respectively, and intermediate grey cells are additionally occupied at 0% harvesting. Light grey cells show portions of the potentially suitable range that are unoccupied.

2.5 Discussion

This study illustrates the potential impact of wildflower harvesting on plant persistence and abundance as it varies with species demographic properties and spatial scale (Figs. 2, 3, 4, 5). Despite this variation, however, abrupt thresholds in the response of persistence and abundance to harvesting emerged as a general pattern (Figs. 2, 6). Harvesting may thus have profound negative effects on persistence or abundance if it exceeds critical rates P_{90} and A_{90}, respectively. These critical harvesting rates are therefore important criteria for assessing harvesting impacts. In the following, we first discuss these critical harvesting rates for the three studied species of CFR Proteaceae before using the sensitivity analysis to draw more general conclusions.

2.5.1 Harvesting impacts on specific CFR Proteaceae

Results indicate that critical harvesting rate P_{90} can be very low for some species, such as *P. compacta* and *P. neriifolia*, with values for A_{90} being even lower (Fig. 6). The observed difference between P_{90} and A_{90} reveals that a harvesting rate with little apparent impact on persistence (P_{90}) may strongly reduce abundance and occupied range (Figs. 6c-d). This indicates that P_{90} is less suitable for harvesting and conservation management than A_{90}. Moreover, any practically implemented harvesting rate should be smaller than the critical rates identified here in order to account for stochasticity that is not included in the model and that can force species demographics beyond critical thresholds (Lande *et al.* 2001).

Our estimated harvesting rate at MSY for *P. repens* (45%) is close to independent experimental findings (~50%, Maze & Bond 1996). However, the very low estimate for *P. neriifolia* (4%) differs from the high estimate (~75%) obtained by Maze and Bond (1996). Three main reasons can explain this divergence: different scales, different demographic parameters and chaos. First, it is likely that MSY at larger scales is achieved with lower harvesting rates, because local recruitment gets more seed limited at increasing scales (Nathan & Muller-Landau 2000). Second, the demographic parameters used in our simulations seem to differ from those of Maze and Bond (1996), but how MSY varies with demographic parameters is still unclear and should be addressed in further research. Third, our demographic values cause strong overcompensation in the local dynamics, resulting in periodic or chaotic oscillations. Because harvesting may stabilize oscillatory local dynamics by controlling overcompensation (Sinha & Parthasaraty 1996), the harvesting-mediated inhibition of oscillations may result in more synchronized local populations. If local populations are synchronized, it is more likely that they go extinct simultaneously and, thus, also the metapopulation (Münkemüller & Johst 2007). Nevertheless, these explanations may jointly explain the large difference between MSY estimates for *P. neriifolia*. Hence, theoretical investigations are required to enlighten how MSY varies over complex interactions among oscillatory dynamics, Allee effects, metapopulation dynamics and spatial scale.

2.5.2 Harvesting impacts on metapopulations

It was expected that persistence and abundance at larger scales would be more negatively influenced by harvesting given higher seed limitation on colonization at larger scales (Nathan & Muller-Landau 2000). However, it seems that metapopulation dynamics buffer harvesting-induced increase in seed limitation through rescue effects and re-colonisations. The role of metapopulation dynamics on increasing spatial scale is indicated by increasing stability on persistence and abundance for higher harvesting rates at the global scale (Fig. 2). On the other hand, the sensitivity of metapopulations at larger scales to harvesting and to seed-limitation translates into sharper thresholds of persistence and abundance than those at smaller scales (Fig. 2). Sharp thresholds have indeed been observed in real (meta-)populations (Ludwig *et al.* 1993; Myers *et al.* 1995; Jackson *et al.* 2001). Harvesting may force metapopulations below a critical minimum size below which extinction is inevitable (Hanski *et al.* 1996; Bascompte *et al.* 2002). However, even if harvesting does not cause extinction, (meta-)population recovery after harvesting is ceased may be very slow (see Musick 1999), especially under Allee effects (Myers *et al.* 1995; Petersen & Levitan 2001). Moreover, (meta-)population recovery may cease at a lower stable size (Hanski *et al.* 1995) from which the former size may not be reached without external intervention. In practice, it might be difficult to observe metapopulation collapses because wildflower harvesting is spatially heterogeneous. Nevertheless, results suggest that careful monitoring and regulation of wildflower harvesting are needed in order to avoid irreversible thresholds.

Our sensitivity analysis showed that the critical harvesting rate P_{90}, and to a lesser extent also A_{90}, increase with the spatial scale of study: harvesting that compromises persistence or abundance in local populations may have little effect on large-scale persistence and abundance (Fig. 3 and 4). In this context, spatially-explicit models offer the possibility to simultaneously assess harvesting impacts at multiple spatial scales. Hence, these models enable conservation managers to study the consequences of spatio-temporally varying harvesting rates. This seems particularly valuable for species with high local extinction risk and no Allee effects, for which critical harvesting rates show the largest difference between local and larger scales (Fig. 5). This matches with the indication that minimum population size, which can be interpreted as the abundance size at a persistence threshold, is unrelated to global extinction risk (Brook *et al.* 2006). Indeed, Brook *et al.* (2006) obtained this result without considering Allee effects. In species that are not subject to Allee effects, harvesting assessments on local scale would lead to more precautionary harvesting rates because local scale supports lower rates than at larger scales. On the other hand, if the harvesting assessments are done over large scales, the harvesting rates implemented based on these assessments may lead to local population crashes. Hence, any assessment of harvesting effects on (meta-)populations and conservation monitoring should identify the spatial scales at which harvesting impacts and conservation options are to be evaluated. Nevertheless, at smaller scales, like in flower farms, population extinction thresholds showed to be more gradual than at larger scales (Fig. 2), which can induce alleviation of harvesting by the producer.

We found that plant species with frequent local extinction, low maximum reproductive rate, high adult mortality, and strong Allee effects are most vulnerable to wildflower harvesting (Fig. 3 and 4). This is because these demographic properties make plant dynamics more seed-dependent and hence more sensitive to seed removal by flower harvesting. Dispersal ability also influences the effects of harvesting on persistence (Fig. 3). This is because the species with thin-tailed dispersal kernels are more seed limited at long-distance dispersal, which is fundamental for metapopulation dynamics, than species with fat-tailed dispersal kernels (Nathan & Muller-Landau 2000). The obtained effects of dispersal ability on P_{90} reflect the properties of metapopulation dynamics, whose persistence depends on dispersal between patches (e.g. Levins 1969; Lindenmayer & Possingham 1996; Casagrandi & Gatto 2002; James *et al.* 2002). The importance of demographic properties for species response to harvesting shows that harvesting management based on good demographic knowledge is necessary to meet conservation targets.

Although the current paper focuses on wildflower harvesting, the simulated seed removal can be interpreted to mimic other processes. The simulated seed removal acts similar to any process that reduces the number of dispersal units between seed production and seedling establishment. Examples of such processes are pre-dispersal seed mortality through predation or diseases, seed mortality during dispersal or even a combination of these processes.

2.5.3 Potential applications

Our approach to assess harvesting impacts can be applied to other exploited species of CFR Proteaceae, for which sustainable yields and critical harvesting rates have not yet been evaluated (Turpie *et al.* 2003). This is of high importance given that the CFR Proteaceae is predicted to suffer strong rearrangements of their distribution under climate change (Bomhard *et al.* 2005; Midgley *et al.* 2006; Keith *et al.* 2008) and harvesting may decrease species migration ability, specially for the low-spreading sprouter species (Higgins *et al.* 2008). Process-based models, like our approach, are able to assess the impact of climate change impacts given direct simulation of range dynamics (Travis 2003; Keith *et al.* 2008; Cabral & Schurr in press). Furthermore, the generic nature of our process-based framework allows it to be applied to other systems. The framework can accommodate species-specific knowledge on key demographic processes as a prerequisite for the quantification of critical harvesting rates. However, even if the biological knowledge is incomplete, our general sensitivity analysis can help to qualitatively assess possible species responses and to assign species to harvesting risk categories. Such assessments would help conservation planners and policy makers to implement and monitor harvesting rates that are in accordance with species conservation.

Link to the next chapter

In the Chapter 2 I applied the model developed and introduced in Chapter 1 in order to assess the impact of wildflower harvesting on species range size and global abundance. I first performed a sensitivity analysis in order to gain theoretical knowledge about the role of demographic properties on the species response to wildflower harvesting. Additionally, I assessed the impact of wildflower directly on selected CFR Proteaceae species, for which it was possible to utilize the most suitable model for local dynamics and its parameter estimates. This information was made available by the fitting approach presented in Chapter 1.

Similarly, in Chapter 3 I applied the demographic model presented in Chapter 1 in order to assess species response to environmental change, namely past habitat loss and future climate change. I focused also in the interaction of both environmental change drivers, which has been scarcely attempted by other studies applying process-based models. For this end, I used also the best model for local dynamics and its parameter estimates obtained for all eight CFR Proteaceae species in Chapter 1.

Chapter 3 – Impacts of past habitat loss and future climate change on the range dynamics of South African Proteaceae [1]

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[1] In preparation as **Cabral JS**, Jeltsch F, Midgley GF, Higgins SI, Phillips SI, Rebelo AG, Rouget M, Thuiller W, Schurr FM. Impacts of past habitat loss and future climate change on the range dynamics of South African Proteaceae. To be submitted to *Global Change Biology*.

3.1 Abstract

Habitat loss and climate change have severe impacts on biodiversity and may interact in their negative effects on species. Responses to environmental change may differ between species because of differences in demographic properties and in the strength of environmental change. An appropriate approach to assess responses to environmental change is process-based modelling, which can integrate demographic properties and track changes in range size, occupancy and abundances. Here we use process-based models for range dynamics to assess the impacts of past habitat loss and future climate change on the dynamics of eight Proteaceae species endemic to the South African Cape Floristic Region. Our approach combines spatio-temporal distributions of suitable habitat with process-based demographic models that simulate reproduction, seed dispersal, recruitment, individual mortality and population extinction. Range size, range filling and local abundances varied over scenarios and species. Habitat loss and, principally, climate change had generally strong negative effects on species performance. Climate change affected mainly range size and range filling due to range reductions and the combination of range shifts with low colonization of new habitat. Habitat loss affected mostly local abundances of some species. The combination of habitat loss and climate change was worst for most species responses. However, this combined effect was less than the addition of individual habitat loss and climate change effects. This is because climate change shifts the suitable habitats to areas less affected by habitat loss. Relative changes in range size were predicted well by the strength of environmental change, whereas changes in range filling and local abundance depended mostly on demographic properties. Most of the surviving populations were in overlapping habitat between original and future ranges, serving as biodiversity refugia and key conservation focus. These findings highlight the need for process-based demographic assessments of species responses to habitat loss and climate change.

3.2 Introduction

Habitat loss and climate change are major drivers of biodiversity loss (Sala *et al.* 2006). While habitat loss has already seriously impacted biodiversity in the past (e.g. Tabarelli *et al.* 1999; Helm *et al.* 2006), the negative impacts of climate change are expected to worsen biodiversity loss in the future (e.g. Bakkenes *et al.* 2002; Thomas *et al.* 2004; Thuiller *et al.* 2005). Climate change and habitat loss are likely to mutually reinforce their negative effects on the persistence of species and (meta-)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). This is because habitat loss reduces population sizes, which may also lower the ability of species to evolutionarily adapt *in situ* to climate change (Pearson & Dawson 2003). Moreover, climate change forces species to migrate in order to keep up with their habitat shifts (Huntley 1991). Species that cannot migrate fast enough to follow the pace of such environmental change will either go extinct or will have to be saved through assisted migration (Hoegh-Guldberg *et al.* 2008) or ex-situ conservation. Higgins *et al.* (2003a) and Opdam and Wascher (2004) suggested that reduced habitat connectivity may lower migration rates. However, it is not clear by how much decreased habitat connectivity caused by habitat transformation will lower migration rates under climate change.

Plant response to habitat loss and climate change may vary substantially with species traits (Morin *et al.* 2008). For example, dispersal ability is a key factor determining species responses to environmental change (Travis 2003; Brooker *et al.* 2006; Midgley *et al.* 2006). Large-scale species responses under environmental change depend tightly on rare long-distance seed dispersal events (Nathan *et al.* 2008). Moreover, species may suffer from reduced reproduction in small populations, so-called positive density-dependence or Allee effects (Allee *et al.* 1949; Courchamp *et al.* 2008). Species subject to Allee effects are expected to be more affected by global change, by having higher rates of population extinction (e.g. Stephens & Sutherland 1999, Courchamp *et al.* 2008) and lower, migration rates (Kot *et al.* 1996; Keitt *et al.* 2001). Moreover, Allee effects proved to play a role on range dynamics of plant species (Keitt *et al.* 2001; Cabral & Schurr in press). The influence of other demographic properties, like reproductive rate, persistence ability and local extinction, on species range dynamics (Schurr *et al.* 2007) and on species response to environmental change is only starting to emerge in the literature (Keith *et al.* 2008).

In order to reliably assess the impacts of environmental change on species distributions, we thus need models that describe key demographic processes based on species traits or properties. This requires replacing widely used correlative species distribution models by process-based alternatives. Approaches in this direction are offered by 'hybrid' models (Thuiller *et al.* 2008) which link habitat models with process-based demographic models (Jeltsch *et al.* 2008; Keith *et al.* 2008; Cabral & Schurr in press). Hybrid process-based demographic models incorporate changes in suitable habitats and can predict also changes in habitat occupancy, range size, local and global abundances (e.g. Keith *et al.* 2008, Cabral & Schurr in press). The possibility to assess abundance dynamics in space and time may, for example, help conservation planners to categorize populations and species into risk categories (IUCN 2001). Moreover, process-based models can be used to describe species dynamics under non-equilibrium conditions like habitat loss and climate change (Keith *et al.* 2008; Morin *et al.* 2008; Cabral & Schurr in press). The framework presented by Cabral and Schurr (in press) enables species-specific predictions by fitting alternative process-based demographic models to species-specific abundance data. This opens the possibility to assess which species properties and processes play in fact a role for the range dynamics of a target study species.

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. Ecological forecasts are urgently needed for a great amount of species, especially in the threatened biodiversity hotspots, which concentrate thousands of endemic and endangered species (Myers *et al.* 2000). Therefore, we have to find ways of generalizing predictions for well-studied species to the many other species for which species-level assessments are impossible. 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 shift, and how much is explained by species properties. If species responses mostly depend on the strength of habitat change, correlative habitat models that consider habitat loss may be sufficient to assess species response. However, if responses depend on species properties, then models incorporating explicitly these properties are required.

In the present study, we use the hybrid model approach presented by Cabral & Schurr (in press) to investigate how habitat loss and climate change affect the large-scale dynamics of selected Proteaceae species endemic to the Cape Floristic Region (CFR). The biodiversity hotspot of the CFR, South Africa (Myers *et al.* 2000), has already undergone about 30% of habitat transformation, due to urbanization, alien species and agriculture (Rouget *et al.* 2003). Additionally, climate change is predicted to have a large impact in the CFR, reducing and shifting the habitat of many Proteaceae (Midgley *et al.* 2002, 2003, 2006; Thomas *et al.* 2004;

Bomhard *et al.* 2005; Keith *et al.* 2008). Our approach predicts not only future range sizes, but also changes in abundance and in range filling (the proportion of suitable habitat that is occupied, Svenning & Skov 2004). In summary, the present work aims 1) to assess effects of habitat loss, climate change and the their interaction on species dynamics; 2) to investigate the role of the demographic properties on species response to environmental change; 3) to address the usefulness of process-based models on predicting future species dynamics and biodiversity refugia over pure correlative habitat models.

3.3 Materials and Methods

To assess the impact of past habitat loss and climate change on range size, range filling and local abundance, we applied spatially-explicit process-based models that include key demographic processes. We selected study species for which parameters describing local demography, long-distance dispersal and habitat distribution were estimated previously (Midgley *et al.* 2003; Schurr *et al.* 2005, 2007; Cabral & Schurr in press). Furthermore, we calculated indexes of the strength of environmental change and analysed the relative role of these indexes and species demographic properties on species responses. Finally, we overlaid future species ranges in order to assess the usefulness of the process-based approach in identifying biodiversity refugia under different scenarios. A description of the implemented models and of the analyses of simulation results follows below.

3.3.1 Study system and model assumptions

We selected eight Proteaceae species that are endemic to the Cape Floristic Region (CFR), South Africa. Recurrent wild fires determine the population dynamics of CFR Proteaceae species (Bond & van Wilgen 1996). The study species do not build persistent soil seed banks but are serotinous which means that they store their seeds in cones on the canopy (Rebelo 2001). Seed release from the canopy, seed dispersal and sequential recruitment happen after fires (Bond 1988; Cowling 1992; Le Maitre & Midgley 1992; Bond & van Wilgen 1996; Rebelo 2001; Schurr *et al.* 2005, 2007).

CFR Proteaceae show two distinct strategies of fire persistence: adult individuals of sprouter species can survive fire, whereas nonsprouter species survive fire only as seeds (Bond & van Wilgen, 1996; Bond & Midgley, 2001, 2003; Schurr *et al.*, 2007). We considered four pairs of related sprouter and nonsprouter species (Rebelo, 2001; Reeves, 2001). Because inter-fire recruitment and inter-fire adult mortality are negligible, population dynamics can be assumed to follow 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 local catastrophic extinction by burning populations that are not sexually mature yet. Such 'irregular' fires that generate catastrophic extinctions tend to be small due to slow post-fire accumulation of biomass. The susceptibility to catastrophic extinction is much higher for nonsprouters and increases with age of first reproduction (Rebelo 2008; Cabral & Schurr in press).

3.3.2 Process-based demographic models and simulation design

To simulate spatial dynamics of CFR Proteaceae, we used the demographic model described by Cabral and Schurr (in press) with minor modifications in order to incorporate habitat loss and climate change. The model is grid-based and combines a habitat model with a process-based model of local dynamics and long-distance dispersal (Cabral & Schurr in press). Grid cell size is 1’ x 1’ (1.55 km x 1.85 km) and each cell holds one population. The modelled processes are local reproduction, dispersal, recruitment, individual mortality and local extinction. Model parameters are maximum reproductive rate (R_{max}), carrying capacity (K), per-fire mortality of adults (M), local extinction probability (E) and Allee critical point (C, for species subject to Allee effects). Most of the study species coexist in nature and, therefore, difference in these parameters are rather due to species traits than to environmental conditions. A general description of the demographic model is given below (for a detailed description see Cabral & Schurr in press). In the model, local population dynamics proceed in discrete time steps following

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

where the vectors $\mathbf{N}(t+1)$ and $\mathbf{N}(t)$ describe local abundances in all cells at time t and $t+1$, S is a function describing adult survival, and G is a function describing dispersal and recruitment. 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 nonsprouters, 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

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

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 E, local populations suffer catastrophic extinction which sets local abundance to 0. We also assumed that catastrophic extinction occurs independently for individual grid cells.

We used a species-specific habitat model describing a grid of suitable and unsuitable patches and a species-specific two-dimensional discrete dispersal kernel. The dispersal kernel gives the probability of seed dispersal from a source cell into each of the neighbouring cells in a 5x5 cells neighbourhood, which is the typical size of a regular fire. The species-specific dispersal kernels were produced by validated mechanistic models for primary (airborne) and secondary (tumble) seed dispersal by wind (Tackenberg 2003; Schurr *et al.* 2005, 2007). When combining these dispersal kernels with alternative models for local population dynamics (see Appendix 3.A of the supporting information), Cabral and Schurr (in press) found that different local population models perform best at explaining the abundance distributions of our study species (Table 1). For each species we thus used the best model and the corresponding parameter estimates (Cabral & Schurr (in press), Table 1). The dispersal ability calculated by Schurr *et al.* (2007) is also given in Table 1.

For each species we ran 100 simulation replicates. Each simulation was initialized by setting the initial local abundances of all suitable cells to carrying capacity *K*. The initial habitat model represented climatic conditions in 2000 (Midgley *et al.* 2002, 2003). We then ran the simulations for 1000 model time steps in order to reach a quasi-stationary state. Subsequently, environmental change scenarios were applied (see Fig. 1). The first time step under environmental change scenarios was assumed to be 1960. In this time step, we split the simulations 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 was subject to climate change. Hence, we assessed four scenarios: no environmental change (Control), habitat loss only (HL), climate change only (CC), or habitat loss and climate change (HL/CC) (Fig. 1). Simulations under all scenarios were run until 2050.

Table 1. Models of local population dynamics, associated parameter estimates and dispersal ability of eight species of CFR Proteaceae. The best models and parameter values of each species were identified by Cabral & Schurr (in press). Brackets besides species names indicate the persistence ability of species (n: non-sprouter, s: sprouter), which are grouped as related pairs (Rebelo, 2001). Local population models are: Beverton-Holt (B-H), Ricker (R), Beverton-Holt with Allee effect (B-H + A) and Ricker with Allee Effect (R + A) (see Appendix 3.A). Parameters are the per-fire probability of adult mortality (*M*), and local extinction (E), the maximum reproductive rate (R_{max}), carrying capacity (*K*), and Allee critical point (*C*). Note that *M* was set to be 1 for non-sprouter species. Dispersal ability is given as the percentage of seeds that are dispersed over 1 km and was calculated by a mechanistic model simulating the wind dispersal of 10000 seeds in 10000 environments (Schurr *et al.* 2007).

Species (persistence ability)	Model	Parameter					Dispersal ability (%)
		M	*E*	R_{max}	*K* (ind/ha)	*C* (ind/ha)	
Protea compacta (n)	B-H	(1)	0.1	1.5	87	-	0.067
P. scorzonerifolia (s)	B-H + A	0.2	0.1	9	523	-174	0.0034
P. stokoei (n)	R	(1)	0.15	1.5	83	-	0.203
P. speciosa (s)	B-H	0.001	0.005	1	131	-	0.0039
Leucadendron modestum (n)	R + A	(1)	0.1	9	3487	- 174	0.00002
L. lanigerum lanigerum (s)	B-H + A	0.675	0.005	4	9024	105	0.00002
L. xanthoconus (n)	R + A	(1)	0.0025	14.5	2790	-1308	0
L. salignum (s)	B-H +A	0.4	0.0005	7.5	872	17	0.00025

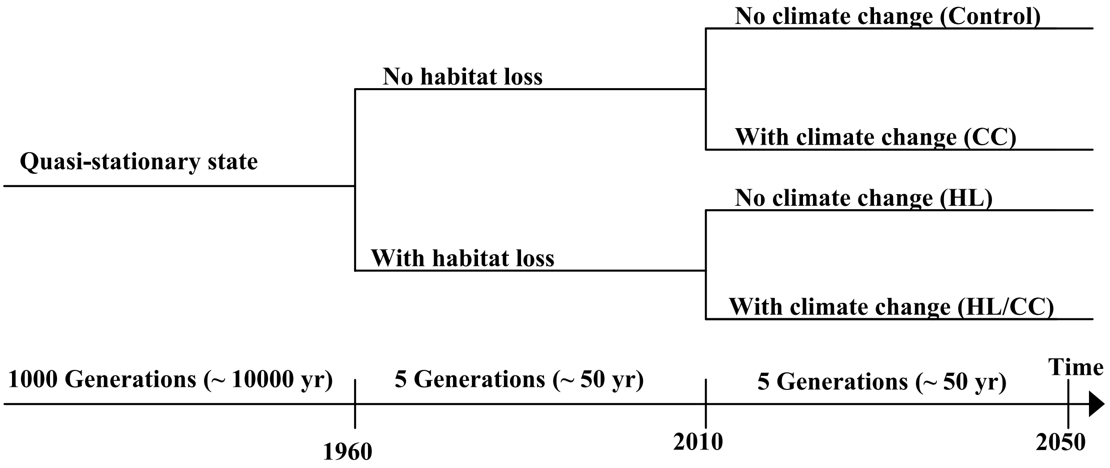

Figure 1. Time schedule for the simulation of past habitat loss and future climate change scenarios. Each simulation is first run for 1000 time step in order to reach quasi-equilibrium with its habitat. Thereafter the simulation is split into two parallel simulations, of which one simulation undergoes habitat loss (HL) on 1960. Subsequently, each of the two parallel simulations is again split into two simulations, of which one is exposed to climate change (CC) for five generations (~ 50 years), from 2010 to 2050. The scenario abbreviations are given in the right end of the time schedule.

Past habitat loss was implemented as a sudden habitat transformation in 1960 (Fig. 1). To describe the spatial distribution of past habitat loss, we used spatially explicit data on transformed habitat available for the entire CFR (Rouget *et al.* 2003). This transformation map contains the proportion of past habitat lost in each grid cell due to alien species, agriculture and urbanization (Rouget *et al.* 2003). In total, 30% of the entire CFR has already been transformed (Rouget *et al.* 2003). We assumed that habitat transformation affects population dynamics by altering the carrying capacity according to

$$K_{eff,i} = H_i K, \tag{3}$$

where $K_{eff,i}$ is the effective carrying capacity after habitat transformation in cell i, H_i is the proportion of suitable habitat after habitat transformation in this cell, and K is the maximum carrying capacity that would be reached if the entire cell was untransformed.

To describe climate change, we used habitat forecasts for ten-year time slices from 2010 to 2050 predicted by the HadCM2 global circulation model under the IS92a climate scenario (Houghton *et al.* 1996; Bomhard *et al.* 2005; Keith *et al.* 2008). These five sequential habitat time slices were applied to the grid in sequential simulation time steps (Fig. 1). However, in some parts of the CFR the fire interval can be as long as 28 years (Polakow & Dunne 1999). In general, our predictions might still underestimate rather than overestimate the negative effects of environmental change. This is a consequence of the following assumptions and model features: a) fire interval (and hence generation time of nonsprouters) of 10 years; b) no further habitat is lost in the future; c) dispersal in the coarse resolution of 1' grid cells, which might bias migration upwards.

To measure the degree of environmental change a species faces in each scenario, we calculated a Habitat Loss Index (*HLI*) and a Habitat Shift Index (*HSI*). We calculated the *HLI* as follow:

$$HLI = (H_{control}-H_{2050})/H_{control}, \tag{4}$$

where H_{2050} is the amount of suitable habitat area at 2050 and $H_{control}$ is the suitable habitat of the control scenario, which is equivalent to the suitable habitat prior any environmental change. A value of 1 for *HLI* means complete habitat loss, whereas 0 means no habitat loss and negative values represent gain of suitable habitat area.

HSI was calculated as

$$HSI = (H_{control}-O_{2050})/H_{control}, \tag{5}$$

where O_{2050} is the total amount of overlapping area between the suitable habitat at 2050 and the control scenario. The *HSI* values can vary from 0 (all initial habitat was retained) to 1 (complete habitat shift). H_{2050}, O_{2050} and $H_{control}$ are given as the sum of H_i over all cells with suitable habitat.

To compare predictions of our process-based approach and of habitat models, we overlaid the predicted ranges of all species for each scenario. With this procedure, we could visualize whether predictions including demographic processes were substantially different from predictions based solely on correlative habitat models. This overlaid ranges showed also biodiversity picks, where the greatest number of the study species coexist.

3.3.3 Analyses of simulation results

For all scenarios we recorded from 2010 to 2050 the range size (number of grid cells), range filling, local and global abundances. Results were averaged over the 100 simulation replicates. Since global abundance was strongly correlated with range size (Spearman's rho = 0.876), we omitted it from further analyses. For climate change scenarios, we additionally assessed whether the study species were able to colonize habitat that became suitable. To this end, we also recorded range size and local abundances in the habitat becoming climatically suitable (in the following termed as 'novel habitat'). To quantify interactions between climate change and habitat loss, we used Two-Way-ANOVAs that estimate the main effects and the interaction effect of both drivers of environmental change on species responses (range size, range filling and local abundance). All statistical analyses were conducted in 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 to the control scenario) we fitted statistical models that included as explanatory variables 1) only the strength of environmental change (*HSI* and *HLI*), 2) only demographic properties (dispersal ability, reproductive parameter, carrying capacity, mortality rate, local extinction probability and Allee critical point) and 3) both the strength of environmental change and demographic properties. Initially, we used linear mixed-effects models (R-library nlme, Pinheiro *et al.* 2007) with random effects of species for these analyses. However, the random effect of species was invariably insignificant (P = 1 for all analyses) and estimated to be close to 0. Hence, we subsequently report the results of linear models without random effects.

3.4 Results

There was a general negative effect of environmental change on species dynamics. Except for *P. stokoei*, the habitat of all study species was predicted to contract under climate change and to undergo moderate to strong shifts. *Leucadendron modestum* is the only study species predicted to experience a complete habitat shift under climate change (Fig. 2). Nevertheless, six species exhibited 100% survival probability in all scenarios. A smaller survival probability was found for *P. stokoei* (97% for all scenarios, including the control) and *L. modestum* (7%

under climate change against 100% without climate change). The example of *L. modestum* shows that climate change and habitat loss can have strong negative effects on large-scale dynamics (Fig. 2). The combination of both drivers of environmental change is predicted to cause a rapid drop in the range size and mean local abundance of this species. This drop restricted, in average, *L. modestum* to one single very small population for the year 2050 (Fig. 2).

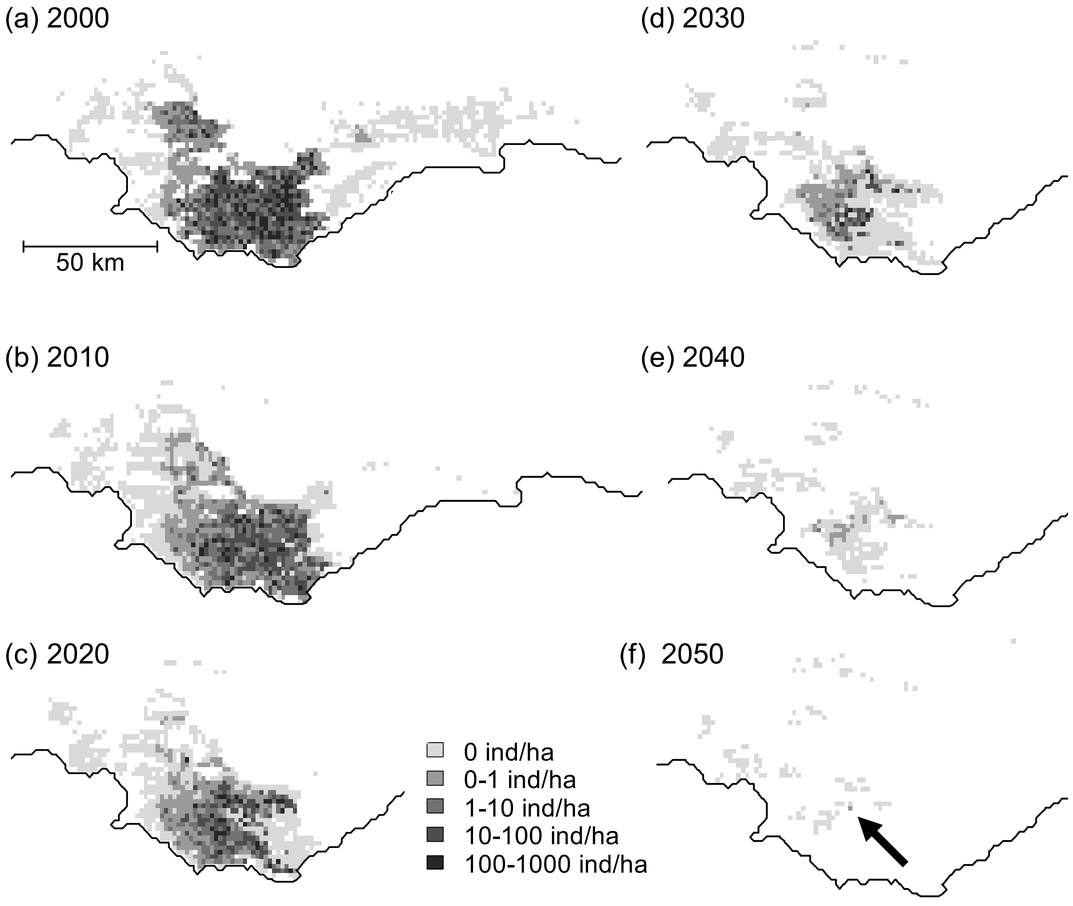

Figure 2. Time-series maps for *Leucadendron modestum* under climate change and habitat loss. (a) year 2000 for the control scenario, without climate change and without habitat loss . (b) year 2010. (c) 2020. (d) 2030. (e) 2040. (f) 2050. The legend at the centre bottom of the figure indicates the average local abundance over the 100 replicate simulations. Note that the light grey area with 0 individual illustrates the unoccupied but suitable habitat. There was complete habitat shift in 2050 and the only surviving population with an average abundance of less than 1 ind/ha is indicated by an arrow in (f).

Despite the general negative effect of environmental change, we found differences between response variables, scenarios and species (Fig. 3). Future range size and local abundances of all species decreased under all three environmental change scenarios (Fig. 3). The range filling decreased for all species under scenarios with past habitat loss. Under climate change, however, range filling increased for two species (*Protea scorzonerifolia* and *P. speciosa*) and decreased for the remaining species (Fig. 3). For details on simulations results see Appendix 3.B of the supporting information. The worst scenario was the combination of past habitat loss and climate change, resulting in a mean general decrease of 46.7% for the response variables over all study species. The scenario only with climate change was slightly better, with a mean general decrease of 39.5%. The scenario only with habitat loss provoked a general decreased of 14.5%. The results of the Two-Way-ANOVAs indicate that impacts of the past habitat loss scenarios were strongest for the local abundances (Table 2). The most remarkable impact of habitat loss was a 78% decrease in the local abundances of *L. xanthoconus* (see Appendix 3.C for the ranking of the scenarios' impacts for each species and response). Differently, climate change affected mainly the range filling and range size (Table 2), mostly due to range shrinkage and shift combined with a low colonization of the novel habitat. Moreover, climate change was often responsible for more than 50% decrease in range size for all species except *P. stokoei* (see Appendix 3.C). The different impacts of the environmental change drivers are exemplified for *P. compacta* (Fig. 4). This species showed an evident decrease in local abundances without changing range size under scenario with habitat loss and a dramatic drop on range size under climate change scenarios (Fig. 4).

Although the scenario combining past habitat loss and climate change posed the most negative impacts, the interaction estimate between habitat loss and climate change was almost always positive for all species (Table 2). The only exception was for the local abundance of *P. stokoei* (Table 2). This positive interaction means that when combined, habitat loss and climate change effects on species responses were better than the sum of the effects caused separately by climate change and past habitat loss. The positive interaction was more conspicuous for local abundances (Fig. 3). Figure 5 illustrates that the past habitat loss experienced by the study species within grid cells was highest in areas predicted to turn unsuitable due to climate change (median 14%, mean 13.1%), intermediate in areas predicted to remain climatically suitable (median 10%, mean 13.1%) and lowest in areas predicted to become climatically suitable (median 9.5%, mean 10%). Moreover, total past habitat loss varied between study species from 20% to 76% (mean 38%) for the habitat without considering climate change. Interestingly, the past habitat loss that has occurred in the grid cells predicted to be suitable under future climate change was substantially lower, varying from 8% to 48% (mean 20%).

Over all scenarios with environmental change, *L. modestum* was the most affected species, followed by *L. lanigerum lanigerum* and *P. compacta* (Fig. 3, Appendix 3.D). *Leucadendron salignum* and *P. stokoei* tended to react least strongly. Some species showed strong interactions for some responses. For example, range filling of *P. scorzonerifolia* decreased quite strongly under past habitat loss but strongly increased under climate change and under both habitat loss and climate change (Fig. 3). The relative change in the species response is given in detail in Appendix 3.D.

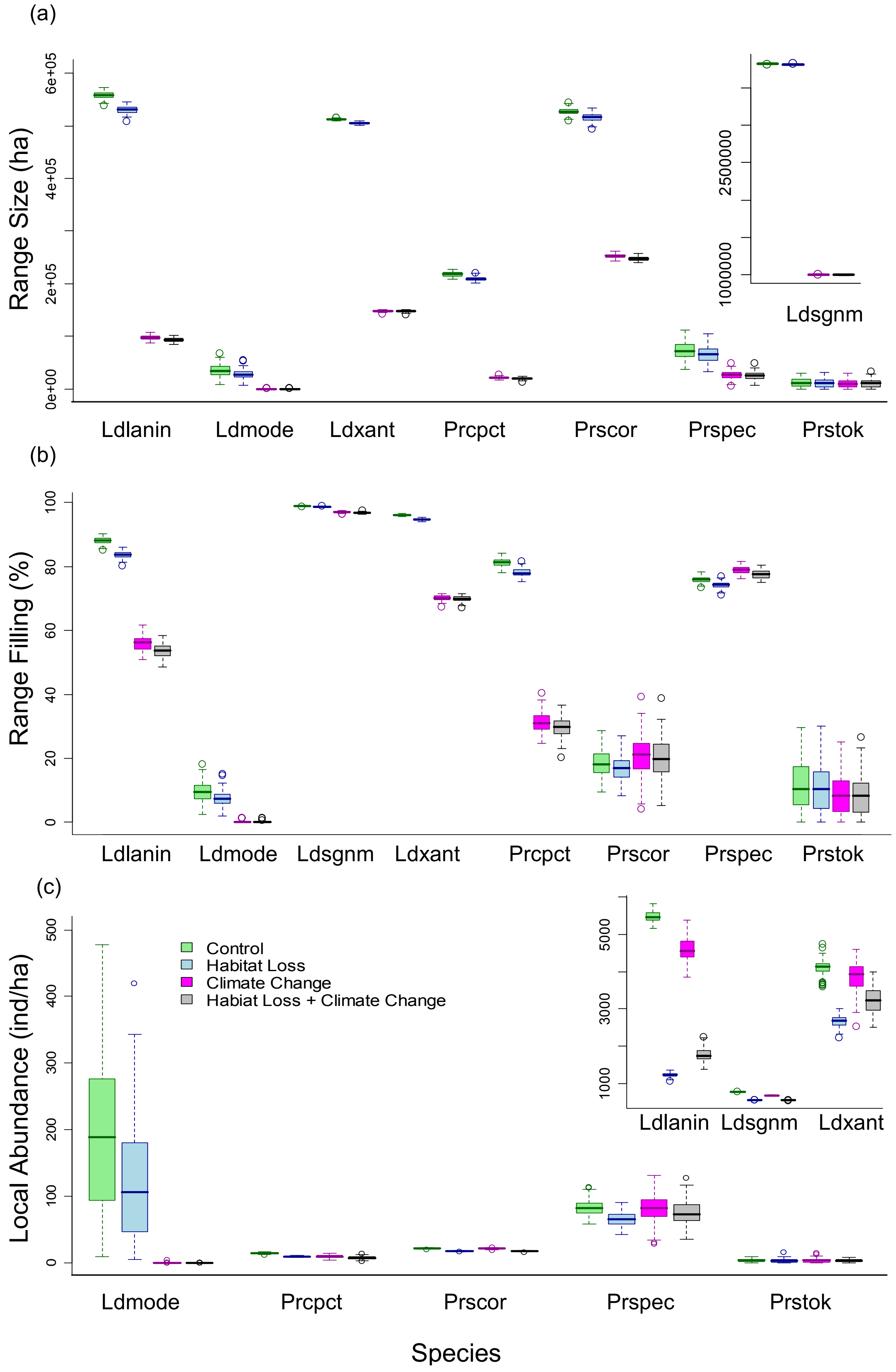

Figure 3. Range size (a), range filling (b) and local abundance (c) in 2050 for all species and scenarios. Box-plots show variation between 100 simulation replicates. Species acronyms are Ldlanin: *Leucadendron lanigerum lanigerum*, ldmode: *L. modestum*; Ldsgnm: *L. salignum*, Ldxant: *L. xanthoconus*, Prcpct: *Protea compacta*, Prscor: *P. scorzonerifolia*, Prspec: *P. speciosa*, Prstok: *P. stokoei*. Legend in (c) indicates the scenarios, where Control represents the scenario without habitat loss and without climate change.

Table 2. Effects of habitat loss, climate change and their interaction on range size, range filling and mean local abundance of eight CFR Proteaceae. The table shows parameters of Two-Way-ANOVAs fitted to 100 replicate simulations for each scenario. Related nonsprouter and sprouter species are shown pair wise with the nonsprouter at the top.

Species	Species Response	Habitat Loss	Climate Change	Interaction
Protea compacta	Range Size	-30.19	-688.14	26.2
	Range Filling	-0.032	-0.5	0.015
	Local Abundance	-1413.83	-1457.53	807.72
P. scorzonerifolia	Range Size	-21.01	-161.71	17.55
	Range Filling	-0.015	0.023	0.008
	Local Abundance	-4690.3	-162.3	2851.2
P. stokoei	Range Size	-1.2	-4.1	0.16
	Range Filling	-0.0034	-0.024	0.0005
	Local Abundance	-108.257	-48.038	-6.953
P. speciosa	Range Size	-39.35	-958.63	22.33
	Range Filling	-0.016	0.031	0.0011
	Local Abundance	-1079.28	-56.39	29.55
Leucadendron modestum	Range Size	-25.56	-120.48	25.52
	Range Filling	-0.019	-0.09	0.019
	Local Abundance	-20488	-57277	20476
L. lanigerum lanigerum	Range Size	-97.36	-1609.37	82.54
	Range Filling	-0.044	-0.32	0.019
	Local Abundance	-121875	-252678	405043
L. xanthoconus	Range Size	-23.8	-1269.74	22.52
	Range Filling	-0.0127	-0.259	0.011
	Local Abundance	-414029	-68285	232692
L. salignum	Range Size	-47.41	-9843.76	42.7
	Range Filling	-0.0035	-0.02	0.002
	Local Abundance	-62218.27	-26744.19	24362.92

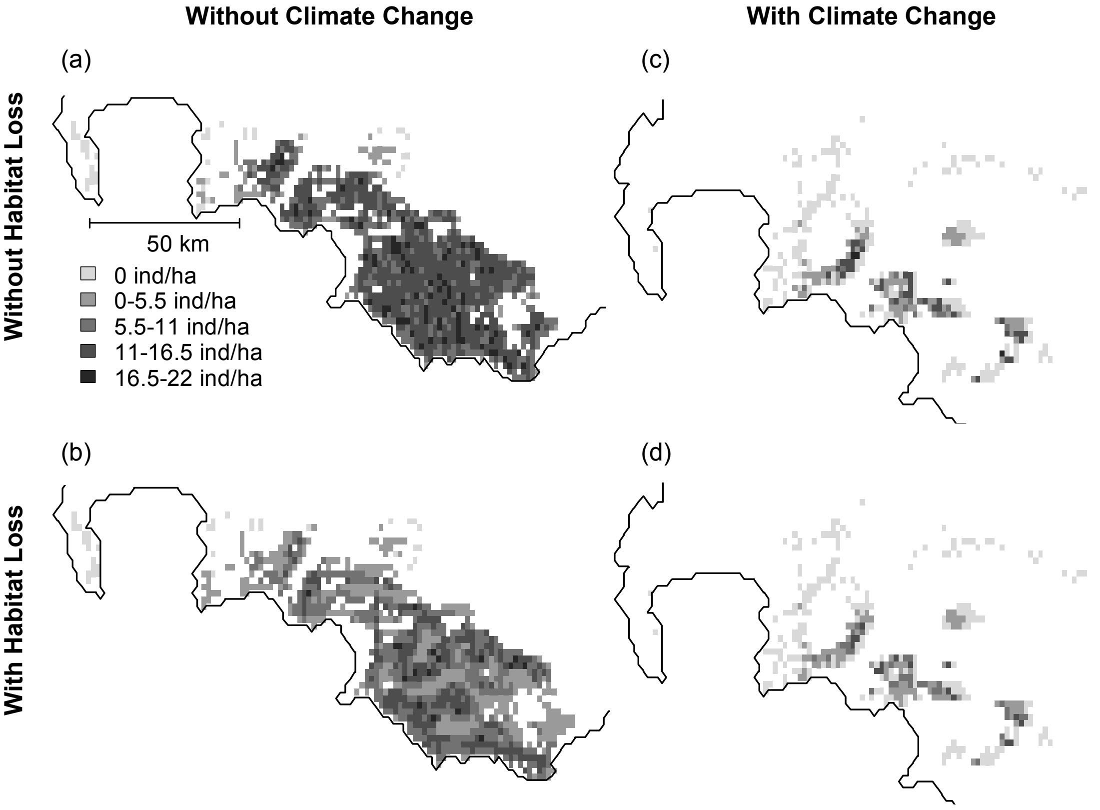

Figure 4. Maps for *Protea compacta* for the year 2050 for all four scenarios. (a) control scenario without climate change and without habitat loss. (b) habitat loss only. (c) climate change only. (d) climate change and habitat loss. The legend in (a) indicates the average local abundance over the 100 replicate simulations. Note that the light grey area with 0 individual/ha illustrates the unoccupied but suitable habitat. Most of the range size in (c) and (d) corresponds to the habitat retained as suitable under climate change forecasts for year 2050.

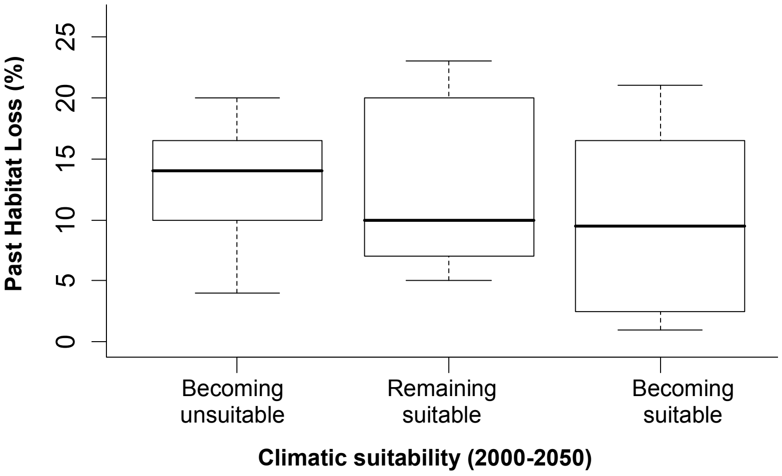

Figure 5. Past habitat loss in areas becoming climatically unsuitable, areas remaining climatically suitable and areas becoming climatically suitable. Climatic suitability was derived from climate projection for the eight study species in 2050. Box-plots represent variation between the study species on the mean past habitat loss within individual grid cells.

Such differences among species were partially due to the ability of colonizing the novel habitat. In this habitat, range size, range filling and local abundances were very low for all *Protea* species and for *L. modestum* (see Appendix 3.B). *Leucadendron xanthoconus*, *L. salignum* and, to a lesser extent, *L. lanigerum lanigerum* were able to colonize a considerable amount of the novel habitat and even to establish high local abundances in this habitat (Appendix 3.B). When comparing the ability to colonize the novel habitat, sprouter species achieved a higher range filling (mean 23% and a mean range size equals to 32976 ha) than nonsprouter species (mean 9% and a mean range size equals to 6595 ha). When considering related species, the nonsprouter *Protea* species had higher range size in the novel habitat comparatively to their sprouter pairs. The opposite happened for the *Leucadendron* species. Therefore, this higher range filing in the novel habitat for the sprouter species was due to *Leucadendron*. However, the nonsprouter species were able to colonize the novel habitat in higher densities (mean 52510 ind/ha) than sprouter species (mean 111 ind/ha). In general, however, the study species survived mostly in the habitat retained as suitable (see Appendix 3.B).

Taking into account the entire future habitat, demographic properties and the strength of environmental change could reasonably also well explain the variation on species responses. Considering all explanatory variables, it was possible to explain 90%, 70% and 63% of the variance of range size, range filling and local abundance, respectively (Table 3). The calculated *HLI* and *HSI* were as high as 0.95 and 1, respectively. *HLI* and *HSI* had negative effects on relative changes in all species responses (Table 3, Fig. 6a-b). The range size variance was mostly explained by the habitat indexes (Table 3). Indeed, the partial R^2 for range size indicated that the *HSI* was the most important variable to explain its variance (partial R^2=0.13 of the variance), followed by carrying capacity (partial R^2=0.02) and *HLI* (partial R^2=0.01), with negligible contribution of other variables. Relative changes in range filling and local abundances were less closely related to HLI and HSI (Figs. 6c-f). This is because range filling and local abundance depended more strongly on demographic properties than on habitat change indexes (Table 3). The variance in range filling across species and scenarios was best explained by adult mortality rate (partial R^2=0.20), followed by dispersal ability (partial R^2=0.10), *HSI* (partial R^2=0.09), maximum reproductive rate (partial R^2=0.06), and local extinction probability (partial R^2=0.05). Variance in local abundance was best explained by adult mortality rate (partial R^2=0.18), maximum reproductive rate (partial R^2=0.09), and dispersal ability (partial R^2=0.06).

Table 3. Contribution of demographic properties, habitat indexes and their combination to explain range size, range filling and abundance responses across species and scenarios. Response was measured as relative change compared to the control scenario. Values are proportions of explained variance (R^2).

Species Responses	Demographic Properties	Habitat Indexes	Both
Range Size	0.25	0.86	0.90
Range Filling	0.57	0.38	0.70
Local Abundance	0.62	0.24	0.63

The importance of incorporating demographic properties was confirmed by overlaying future species ranges. The diversity pick detected by our process-based approach were only slightly different than considering only habitat models under climate conditions for 2000. However, under climate change, with past habitat loss or not, the biodiversity picks detected by our process-based approach diverged substantially from the results based solely on habitat models (Figs. 7 a-b). This difference arises from the low colonization of the novel habitat. In some grid cells, the number of species considering demographic processes can be half of the maximum obtained number (six species) considering only habitat models (Figs. 7 c).

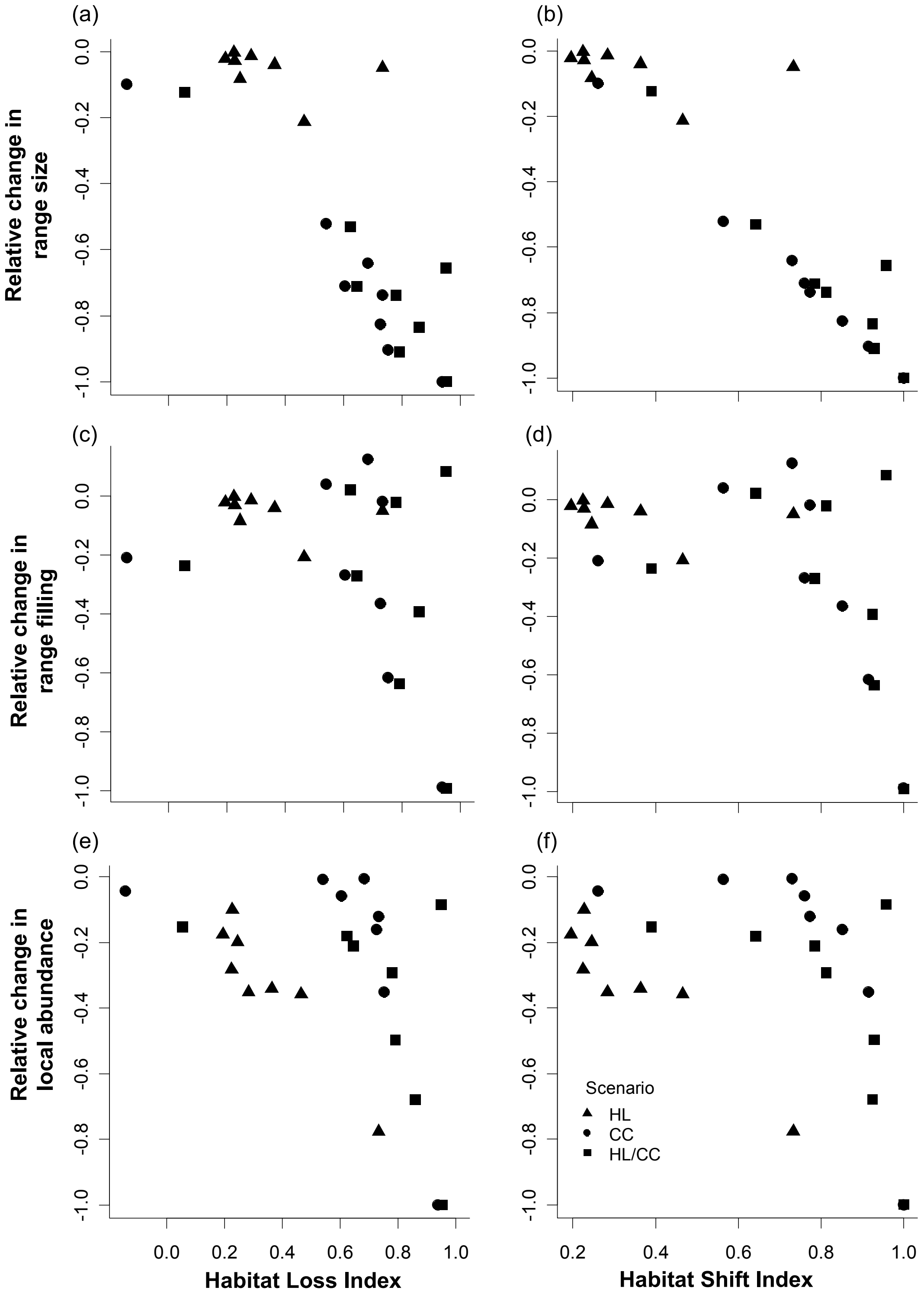

Figure 6. Plot with the relative changes in range size, range filling and local abundances of the environmental changes scenarios across Habitat Loss and Habitat Shift Indexes. Points were taken from the year 2050. (a)-(b) range size. (c)-(d) range filling. (e)-(f) local abundances.

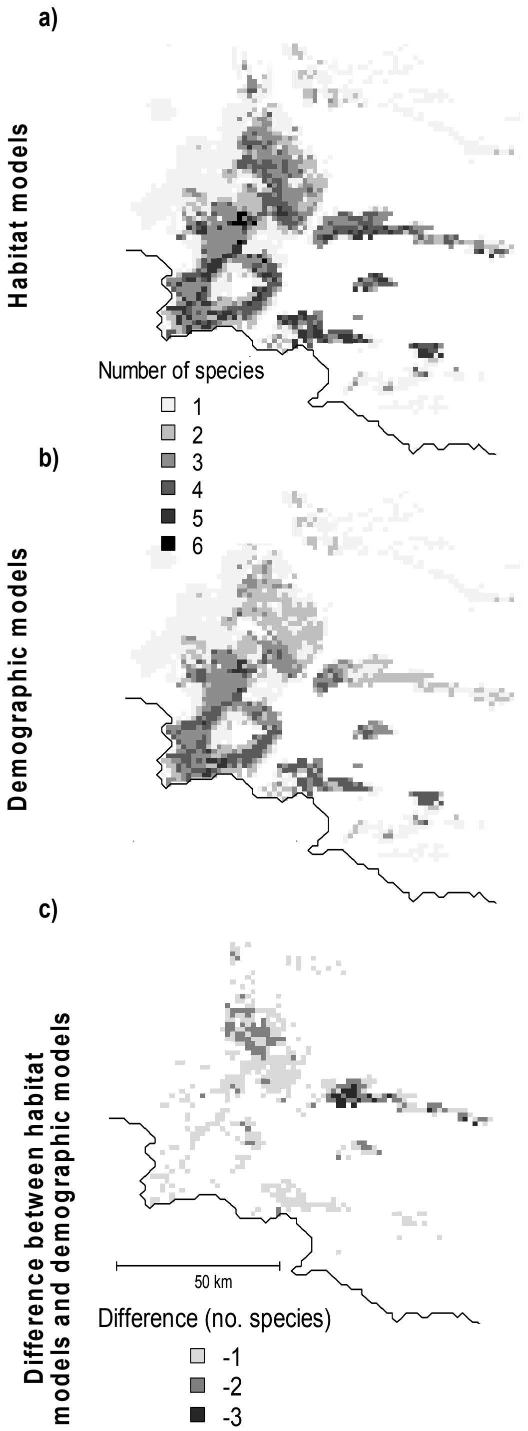

Figure 7. Overlapping study species ranges maps under climate change for the year 2050 in a species-rich section of the CFR. (a) takes into account only the habitat models. (b) shows results of the demographic models considering habitat loss. (c) shows the difference in number of species between the predictions based solely on the habitat models and predictions of the demographic models considering habitat loss. The legend between (a) and (b) indicates the number of species in these figures. The legend in (c) indicates the difference in number of species.

3.5 Discussion

This study investigates how different scenarios of environmental change may affect the range size, range filling and local abundances of South African Proteaceae (Figs. 2, 3, 4). Predicted differences of species responses (Fig. 3) could be partially explained by the strength of environmental change and partially by demographic properties (Fig. 6, Table 3). It was also possible to assess future biodiversity refugia (Fig. 7). In the following, we first discuss the potentials, usefulness and limitations of our process-based approach. Subsequently, we assess the role of demographic properties and the strength of environmental change for the large-scale dynamics of CFR Proteaceae species. Finally, we show how the presented approach can aid climate-integrated conservation management.

The process-based approach for range dynamics used here improves our understanding of species responses to global change. Among the advantages of the process-based approach over pure correlative habitat models is the assessment of persistence, occupancy, local and global abundances. With such assessments, more complete information is provided for conservation planners than information based solely on habitat models. Forecasts based solely on habitat models provide only habitat predictions and must assume species-habitat equilibrium in order to give information on species responses (Guisan & Thuiler 2005). However, readers that are not familiarized with these models may tend to assimilate results as automatic migration with consequent underestimated extinction risks (Botkin *et al.* 2007). In contrast, process-based models relax the species-habitat equilibrium assumption and proved to be useful to investigate the species response under multiple environmental change drivers. However, similar process-based approaches to modelling species distributions (Keith *et al.* 2008; Morin *et al.* 2008) have not investigated interactions between different drivers of environmental change. Process-based approaches can also be used to identify migration pathways, contributing to the detection of possible migration corridors (Williams *et al.* 2005).

Although predictions of our process-based approach can be used to forecast species dynamics under environmental change, it is important to emphasize that our predictions ignore parameter and model uncertainty. We do not vary the model of local dynamics and its parameter values, which are important sources of uncertainty (Higgins *et al.* 2003b). Hence, potential improvements would be confidence intervals for the parameter estimates. Moreover, our results might be optimistic for species with low dispersal ability (see Table 1). This is caused by the discretization of the dispersal kernel into the coarse resolution of minutes. The discretization requires an integration of the amount of seeds dispersed within the area. This can lead to an upward bias for poor disperser species in a coarse resolution, which is a general limitation of grid-based simulations. Nevertheless, the predictions of our approach could be further enhanced with the implementation of other processes, like interspecific competition (Higgins *et al.* 2008), and/or other impacts, such as wildflower harvesting (Maze & Bond 1996; Turpie *et al.* 2003; Chapter 2).

The results revealed that most of the study species could survive past habitat loss and future climate change up to 2050. Species survival seems possible even under strong habitat shrinkage and shift. For example, habitat models for *P. compacta* predict a decrease in suitable area in more than 75% and only 9% of original habitat remains suitable (see Fig. 4). Yet, *P. compacta* persisted in 100% of the replicate simulations for all scenarios. In contrast, an example involving complete habitat shift is given by *L. modestum*, which had only 7% change of survival under climate change scenarios. Hence, complete habitat shift enlarges extinction risks. Midgley *et al.* (2002) predicted that, similar to *L. modestum*, more than one third of all 330 species of Cape Proteaceae will experience complete habitat shifts by 2050 under climate scenario HadCM2n=GGa[IS92a]. It is important to emphasize that, although already quite severe, our results probably underestimate the negative impacts of climate change. Reasons for this conclusion is that we used a relatively mild scenario of climate change and that climate change will not probably cease at 2050.

When comparing the effects of both environmental change drivers on species dynamics, we found clear differences. The main effect of climate change was a reduction of range size and simultaneous changes in range filling. Range filling increased or decreased depending on the spatial configuration of the future habitat and the species' migration ability. The main reason for a lower range size under climate change is the small area of the habitat retained as suitable, where the species mostly survived. Differently to climate change, the main effect of past habitat loss was on local abundances, especially by the direct decrease on the carrying capacity of the individual grid cells. However, most of the cells still sustain a local population, as indicated by the small impact of past habitat loss on range size. It is important to emphasize that Rouget *et al.* (2003) indicated a loss of 30% in remaining natural habitat within 20 years, which would result in over 50% of habitat loss from the original extent of the natural vegetation in the CFR. Such extent of total habitat loss may worsen the species responses obtained in this study.

Additionally to the differential impacts on species response, both environmental change drivers interacted in our results. The positive interaction between past habitat loss and climate change obtained in the present work indicates that although a scenario combining both drivers of environmental change is the worst, it can still be better than expected by simple addition of separate effects. Interestingly, under combined climate change and habitat loss, the mean local abundance for some species, namely *L. lanigerum lanigerum*, *L. xanthoconus* and *P. scorzonerifolia*, was even higher than under past habitat loss only. This is a consequence of lower levels of past habitat loss in the habitat that is retained suitable and in the novel habitat (Fig. 5). Such possible interaction indicates that a general negative impact of environmental change can not be assumed straightforward. Remarkably, studies tend to ignore the possibility of a differential portion of habitat that has been already lost when comparing current and future habitat areas (Travis 2003). Nevertheless, for most species and responses, the scenario combining climate change and past habitat loss was worse than scenarios with only one driver of environmental change (see also Travis 2003). Moreover, our results support the findings that the relative role of both drivers of environmental change on range dynamics is species-specific (Warren *et al.* 2001; Franco *et al.* 2006).

Species responses vary not only with the strength of environmental change but also with demographic properties (Table 3, Fig. 6). The fact that the variance in relative changes of range size is mostly explained by the presented habitat indexes suggests that range size responses can be reliably assessed from information on habitat loss and shift (Table 3, Fig. 6). In addition to habitat indexes, carrying capacity is the most important demographic property that influences the variance of range size. This is probably because higher carrying capacities make the maintenance of local populations possible even in patches with high percentages of habitat loss. Furthermore, conservation planners may be also interested in how range filling and local abundances react to environmental change. These responses are better predicted by demographic properties than by the strength of environmental change (Table 3, Fig. 6). For this purpose, models that incorporate demographic processes are ideal. Among the demographic properties, mortality rate, dispersal ability and maximum reproductive rate proved to be very important for explaining the variance in range filling and local abundance. In addiction to our findings, Morin *et al.* (2008) also suggested through a process-based approach that differences in species responses are caused by differences in dispersal rates. Although dispersal rates, and thus also migration rates, depend on the characteristics of the landscape fragmentation, habitat loss and dispersal agent (Higgins *et al.* 2003a), they proved to strongly depend on species properties in our simulations. Higgins *et al.* (2003a) showed also that migration rates' responses to habitat loss varies according to the model species. Moreover, Clark *et al.* (2001a) also showed that migration rates depend on reproduction and that variable reproduction rates among individuals generate lower migration rates. Hence, our results on species response may be optimistic due to the fact that we assume a constant net reproductive rate. Therefore, the role of demographic properties on species persistence under environmental change deserves further attention (Dullinger *et al.* 2004; Morin *et al.* 2008).

The low migration ability of our study species is made evident by limited colonisation of the novel habitat. A reason for a low colonisation in this habitat can be that the total suitable habitat in 2050 of some species gets patchier and less connected than the original habitat in 2000 (Higgins *et al.* 2003a; Opdam & Wascher 2004). Indeed, Honnay *et al.* (2002) found for forest plant species higher colonization of new suitable habitat under higher forest connectivity. Furthermore, the migration rate of plant species can be greatly reduced if the habitat availability decreases too much proportionally to the matrix (Collingham & Huntley 2000). In addition, species with thin-tailed dispersal kernel are more sensitive to this decrease (Schwartz 1992). Interestingly, *Protea* species confirm the expectation that sprouting species should have lower colonisation ability than nonsprouters (Higgins *et al.* 2008), but *Leucadendron* species do not. It is not clear how the study sprouting *Leucadendron* species achieve a higher colonization in the novel habitat, but they have equal or higher dispersal ability and a lot larger habitat, and therefore source populations, than their related nonsprouter species. However, further studies are necessary in order to better explain the higher colonisation ability observed for sprouting *Leucadendron* species. Furthermore, stronger Allee effects and lower maximum reproductive rates of sprouter species in comparison to nonsprouter species might explain the lower abundances observed for sprouters in the colonized habitat.

Another important finding of our study was that the maintenance of Proteaceae populations under climate change will take place mostly in the habitat retained as suitable. This type of habitat consists of more pristine areas (Fig. 5) that concentrate in the cooler mountain ranges (Midgley *et al.* 2002), where little anthropogenic impact has occurred (Midgley *et al.* 2003; Rouget *et al.* 2003). Key areas containing upland-lowland gradients have already been identified for conservation efforts considering their importance on migration of biota (Cowling *et al.* 2003). Moreover, the habitats retained as suitable with sustainable populations constitute very important biodiversity refugia for species survival and evolution and serve as important conservation focus (Kitching 2000). The need of detecting such refugia is urgent for the biodiversity-hotspots Mediterranean-climate biomes, like the CFR. In the habitat area predicted to be retained under climate change for the world's Mediterranean-climate biomes, around a third of the natural vegetation has been already lost (Klausmeyer & Shaw 2009). Furthermore, identification of refugia that support sustainable populations of the largest number of species can help better conservation efforts in detecting areas where populations can persist. The simple superposition of correlative habitat models of several species may not indicate correctly the actual biodiversity refugia under impending climate change. This happens because such superpositions cannot account for the areas that species cannot colonize or where they are unable to persist due to demographic or metapopulation constraints (Figs. 2, 4 and 7; Cabral & Schurr in press; Hanski 1998).

Summarizing, the process-based approach for range dynamics offers the possibility to describe range size, range filling and local abundance responses, providing a powerful tool for more complete predictions. It was shown that range size can be reasonably predicted by habitat models. However, further key information on species responses to environmental change is gained if demographic properties are taken into account by simulating demographic processes. Moreover, given the large impacts on species' habitats predicted under climate change (Midgley *et al.* 2002, 2003, 2006; Thomas *et al.* 2004; Bomhard *et al.* 2005), information about the actual migration ability derived from demographic properties as well as the identification of refugia is most needed (Huntley 1991). Therefore, the retained habitat should be one of the focuses of conservation efforts. The present process-based model is able to identify species refugia that sustain viable populations. These refugia would also function as a source of emigrants to colonize the nearby novel habitat. Furthermore, for species that are predicted to face complete range shifts, like many Proteaceae (Midgley *et al.* 2002), alternative conservation actions are needed. Assisted migration has been discussed as an option for species highly threatened by climate change (Hunter Jr. 2007; Hoegh-Guldberg *et al.* 2008). However, there is currently intense debate about the pros and cons of this management option (McLachlan *et al.* 2007; Mueller & Hellmann 2007; Ricciardi & Simberloff 2009; Sax *et al.* 2009). In any case, risk assessments of assisted migration require us to quantify the migration ability of species (Hoegh-Guldberg *et al.* 2008). The process-based demographic approach presented here also provides a powerful method for this purpose.

3.6 Appendix 3.A - Reproduction Functions

The equations describing the per-capita reproduction function for a cell *i* at time step *t*, $R(N_i(t))$, were the same as implemented by Cabral & Schurr (in press). Model parameters are maximum reproductive rate, R_{mod}, carrying capacity, *K*, and Allee critical threshold *C*. For a better biological interpretation of the parameter, the maximum reproductive rate presented in the article is the maximum of the reproduction functions for $N_i(t)>0$ (termed R_{max}). The equations are indicated in the following.

The first function is the Beverton-Holt model (Beverton & Holt 1957) which can be used to describe reproduction of species with overlapping and non-overlapping generations,

$$R(N_i(t)) = \frac{R_{\mathrm{mod}}}{1+\frac{R_{\mathrm{mod}} N_i(t)}{K_p}} \tag{1}$$

where K_p is a parameter related to the carrying capacity. The carrying capacity *K* itself can be calculated using the following formula:

$$K = \frac{(R_{\mathrm{mod}} - M)K_p}{R_{\mathrm{mod}} M} .$$

The second function is an extension of the Beverton-Holt model that describes an Allee effect on reproduction:

$$R(N_i(t)) = \frac{R_{\mathrm{mod}}}{1+k(N_i(t)-c)^2} , \tag{2}$$

where *c* gives the population size at which maximum reproductive rate R_{max} is reached, and k is a parameter related to carrying capacity. For this model, the carrying capacity is given by

$$K = c + \sqrt{\frac{(R_{\mathrm{mod}} - M)}{Mk}} ,$$

and the Allee critical point (the population size below which the population shrinks) is given by

$$C = c - \sqrt{\frac{(R_{\mathrm{mod}} - M)}{Mk}} .$$

The third reproduction function we consider is the logistic Ricker model (Ricker 1954).

$$R(N_i(t)) = R_{\mathrm{mod}}^{\,1-\frac{N_i(t)}{K}} \tag{3}$$

The fourth function is an extension of the Ricker model that describes Allee effects

$$R(N_i(t)) = R_{\mathrm{mod}}^{\frac{4(K - N_i(t))(N_i(t) - C)}{(K-C)^2}} \qquad (4)$$

3.7 Appendix 3.B - Complete results for year 2050.

Table 3.B.1. Range size, colonized novel habitat, range filling, range filling within novel habitat, local abundance and local abundance within novel habitat for all species and scenarios in year 2050. The relative differences in range size, range filling and local abundance are also given for all scenarios with environmental change in comparison to the control scenario. Species acronyms are: Prcpct, *Protea compacta*; Prstok, *P. stokoei*; Prspec, *P. speciosa*; Prscor, *P. scorzonerifolia*; Ldxant, *L. xanthoconus*; Ldmode, *L. modestum*; Ldlanin, *Leucadendron lanigerum* lanigerum; Ldsgnm, *L. salignum*. The control scenario means without climate change and without habitat loss. The other scenarios are habitat loss (HL), climate change (CC) and both habitat loss and climate change (HL/CC). Results show the average over 100 replicate simulations. Related nonsprouter and sprouter species are shown pair wise with the nonsprouter at the top.

Species	Scenario	Range size (ha)	Colonized novel habitat (ha)	Relative difference in range size	Range filling (%)	Range filling in novel habitat (%)	Relative difference in range filling	Local abundance (ind/ha)	Local abundance in novel habitat (ind/ha)	Relative difference in local abundance
Prcpct	Control	218150.8	-	-	81.3	-	-	14.48	-	-
	HL	209493.8	-	-0.04	78.1	-	-0.04	9.55	-	-0.34
	CC	20826.6	3719.15	-0.9	31.3	8.1	-0.61	9.40	0.3	-0.35
	HL/CC	19682.52	3498.35	-0.9	29.6	0.076	-0.64	7.29	0.25	-0.5
Prscor	Control	72252.4	-	-	18.5	-	-	82	-	-
	HL	66227.8	-	-0.08	17	-	-0.08	65.7	-	-0.2
	CC	25882	504.7	-0.64	20.7	2.6	0.12	81.5	0.07	-0.007
	HL/CC	24889.9	464.53	-0.65	20	2.4	0.08	75.0	0.08	-0.08
Prstok	Control	11905.9	-	-	11.4	-	-	3.7	-	-
	HL	11561.76	-	-0.03	11	-	-0.03	3.4	-	-0.10
	CC	10730.18	131.9	-0.1	9	0.29	-0.21	3.6	0.03	-0.04
	HL/CC	10431.97	169.18	-0.12	8.7	0.37	-0.24	3.7	0.04	-0.15
Prspec	Control	527281.6	-	-	76	-	-	21.3	-	-
	HL	515998	-	-0.02	74.3	-	-0.02	17.56	-	-0.18
	CC	252394.5	31.54	-0.52	79	0.2	0.04	21.1	0.03	-0.01
	HL/CC	247514	37.3	-0.53	77.5	0.23	0.02	17.5	0.04	-0.18

Table 3.B.1. Continuation.

Species	Scenario	Range size (ha)	Colonized novel habitat (ha)	Relative difference in range size	Range filling (%)	Range filling in novel habitat (%)	Relative difference in range filling	Local abundance (ind/ha)	Local abundance in novel habitat (ind/ha)	Relative difference in local abundance
Ldmode	Control	34576	-	-	9.4	-	-	199.8	-	-
	HL	27247	-	-0.21	7.4	-	-0.21	128.3	-	-0.36
	CC	28.7	28.7	-0.999	0.1	0.1	-0.99	0.04	0.04	-0.999
	HL/CC	17.2	17.2	-0.999	0.075	0.075	-0.99	0.003	0.003	-0.999
Ldlanin	Control	558465	-	-	88	-	-	5476.8	-	-
	HL	530547	-	-0.05	84	-	-0.05	1226.5	-	-0.78
	CC	96979	11034	-0.82	56	14	-0.36	4595.6	4.8	-0.16
	HL/CC	92729	8892	-0.83	53	11	-0.39	1757.89	2.5	-0.68
Ldxant	Control	512201.5	-	-	96	-	-	4108	-	-
	HL	505376.8	-	-0.01	95	-	-0.01	2664	-	-0.35
	CC	148103.5	22119.90	-0.71	70	27	-0.27	3870	2762	-0.06
	HL/CC	147736	22068	-0.71	70	26	-0.27	3237	2690	-0.21
Ldsgnm	Control	3826547	-	-	99	-	-	768	-	-
	HL	3812952	-	-0.004	98	-	-0.004	551	-	-0.28
	CC	1003849	121496	-0.74	97	77	-0.02	674.8	0.78	-0.12
	HL/CC	1002498	120566	-0.74	97	76	-0.02	542.8	0.7	-0.29

3.8 Appendix 3.C - Ranking of the effects caused by different environmental change scenarios.

Table 3.C.1. Ranking of the effects caused by environmental chance scenarios according to study species and species response. The species responses are range filling (RF), local abundance (Abundance) and range size (Range). The most affecting scenario is at the top and the least at the bottom, with the respective change relative to the scenario without any environmental change in parenthesis. The losses greater than 50% are indicated in bold. Scenario acronyms are CC: climate change only, HL: habitat loss only, HL/CC: habitat loss and climate change. Related nonsprouter and sprouter species are shown pair wise with the nonsprouter at the left side.

Protea compacta			*P. scorzonerifolia*			*P. stokoei*			*P. speciosa*		
RF	Abundance	Range	RF	Abundance	Range	RF	Abundance	Range	RF	Abundance	Range
HL/CC **(-64%)**	**HL/CC** **(-50%)**	**HL/CC** **(-91%)**	HL (-8%)	HL (-20%)	**HL/CC** **(-66%)**	HL/CC (-24%)	HL/CC (-15%)	HL/CC (-12%)	HL (-2%)	HL/CC (-18%)	**HL/CC** **(-53%)**
CC **(-62%)**	CC (-35%)	**CC** **(-90%)**	HL/CC (+8%)	HL/CC (-8%)	**CC** **(-64%)**	CC (-21%)	HL (-10%)	CC (-10%)	HLCC (+2%)	HL (-18%)	**CC** **(-52%)**
HL (-4%)	HL (-34%)	HL (-4%)	CC (+12%)	CC (-0.7%)	HL (-8%)	HL (-3%)	CC (-4%)	HL (-3%)	CC (+4%)	CC (-1%)	HL (-2%)

Table 3.C.1. Continuation.

Leucadendron modestum			*L. lanigerum lanigerum*			*L. xanthoconus*			*L. salignum*		
RF	Abundance	Range	RF	Abundance	Range	RF	Abundance	Range	RF	Abundance	Range
HL/CC **(-99%)**	**HL/CC** **(-99%)**	**HL/CC** **(-99%)**	HL/CC (-39%)	**HL** **(-78%)**	**HL/CC** **(-83%)**	HL/CC (-27%)	HL (-35%)	**HL/CC** **(-71%)**	HL/CC (-21%)	HL/CC (-29%)	**HL/CC** **(-74%)**
CC **(-99%)**	**CC** **(-99%)**	**CC** **(-99%)**	CC (-36%)	**HL/CC** **(-68%)**	**CC** **(-83%)**	CC (-27%)	HL/CC (-21%)	**CC** **(-71%)**	CC (-2%)	HL (-28%)	**CC** **(-74%)**
HL (-21%)	HL (-36%)	HL (-21%)	HL (-5%)	CC (-16%)	HL (-5%)	HL (-1%)	CC (-6%)	HL (-1%)	HL (-0.4%)	CC (-12%)	HL (-0.4%)

3.9 Appendix 3.D - Ranking of most affected species.

Table 3.D.1. Ranking of most affected species according to environmental change scenario and species response. The species responses are range filling (RF), local abundance (Abundance) and range size (Range). The most affect species is at the top and the least at the bottom, with the respective change relative to the scenario without any environmental change in parenthesis. The losses > 50% are indicated in bold. Species acronyms are Ldmode: *Leucadendron modestum*, Ldlanin: *L. lanigerum lanigerum*, Ldsgnm: *L. salignum*, Ldxant: *L. xanthoconus*, Prcpct: *Protea compacta*, Prscor: *P. scorzonerifolia*, Prspec: *P. speciosa* and Prstok: *P. stokoei*.

Habitat Loss			Climate Change			Habitat Loss + Climate Change		
RF	Abundance	Range	RF	Abundance	Range	RF	Abundance	Range
Ldmode (-21%)	**Ldlanin (-78%)**	Ldmode (-21%)	**Ldmode (-99%)**	**Ldmode (-99%)**	**Ldmode (-99%)**	**Ldmode (-99%)**	**Ldmode (-99%)**	**Ldmode (-99%)**
Prscor (-8%)	Ldmode (-36%)	Prscor (-8%)	**Prcpct (-62%)**	Prcpct (-35%)	**Prcpct (-90%)**	**Prcpct (-64%)**	**Ldlanin (-68%)**	**Prcpct (-91%)**
Ldlanin (-5%)	Ldxant (-35%)	Ldlanin (-5%)	Ldlanin (-36%)	Ldlanin (-16%)	**Ldlanin (-83%)**	Ldlanin (-39%)	**Prcpct (-50%)**	**Ldlanin (-83%)**
Prcpct (-4%)	Prcpct (-34%)	Prcpct (-4%)	Ldxant (-27%)	Ldsgnm (-12%)	**Ldsgnm (-74%)**	Ldxant (-27%)	Ldsgnm (-29%)	**Ldsgnm (-74%)**
Prstok (-3%)	Ldsgnm (-28%)	Prstok (-3%)	Prstok (-21%)	Ldxant (-6%)	**Ldxant (-71%)**	Prstok (-24%)	Ldxant (-21%)	**Ldxant (-71%)**
Prspec (-2%)	Prscor (-20%)	Prspec (-2%)	Ldsgnm (-2%)	Prstok (-4%)	**Prscor (-64%)**	Ldsgnm (-2%)	Prspec (-18%)	**Prscor (-66%)**
Ldxant (-1%)	Prspec (-18%)	Ldxant (-1%)	Prspec (+4%)	Prspec (-1%)	**Prspec (-52%)**	Prspec (+2%)	Prstok (-15%)	**Prspec -53%)**
Ldsgnm (-0.3%)	Prstok (-10%)	Ldsgnm (-0.4%)	Prscor (+12 %)	Prscor (-0.7%)	Prstok (-10%)	Prscor (+8 %)	Prscor (-8%)	Prstok (-12%)

General Discussion

With this thesis, species distribution models move towards process-based models that are able to generate more complete predictions and forecasts. The incorporation of demographic processes that underpin range dynamics is an important step to link species distribution models more completely to the niche theory than how pure habitat models are linked to it (see Peterson 2006). Chapter 1 shows that process-based models of range dynamics can be fitted to data (see Fig. 1 of Chapter 1). This statistical framework finally allows for model selection and appreciation of relevant processes for a target species. For example, the simulation of different mechanisms that play a role in species distribution was achieved by implementing key demographic processes with alternative models describing local population dynamics. Furthermore, once fitted, these models can then be used to assess species responses to different non-equilibrium scenarios (Chapters 2 and 3). Hence, the understanding of mechanisms governing range dynamics is enhanced, including a large potential of the approach to further enlarge the knowledge about how species distribute themselves in space and time.

In the first part of this chapter, I will discuss the findings obtained in Chapters 1, 2, and 3 for the study system – Proteaceae species from the Cape Floristic Region (CFR). Afterwards, I will discuss the limitations, advantages and the potential of process-based models for species distribution, before outlining some promising directions for future research.

4.1 CFR Proteaceae

4.1.1 CFR Proteaceae in a changing world

The simulated range dynamics of CFR Proteaceae showed good spatial agreement with observed populations (Chapter 1). The simulation of demographic models demonstrated that small and isolated patches cannot be occupied due to dispersal or demographic constraints (see Fig. 3 of Chapter 1). After simulating the demographic models, the resulting abundance distribution was used as input for the observation model in order to generate more comparable abundances to the actual observations. There was an evident difference between the results of the demographic models and the results of the observation models (see Fig. 3 of Chapter 1). This has several implications. For example, there can be a substantial lack of observation effort in the areas predicted to be occupied by the demographic model. The extensive sampling effort of the Protea Atlas Project makes this implication less likely. Nevertheless, some few parts of CFR were not sampled and constitute areas for further field investigation and possibly validation of model predictions (Guisan *et al.* 2006; Dormann 2007). Further implications include the lack of other mechanisms, like habitat loss or fire dynamics.

An on-going anthropogenic factor that can influence the range dynamics of CFR Proteaceae is wildflower harvesting (Chapter 2). The results of Chapter 2 suggest that wildflower harvesting can quickly cause extinction at the metapopulation level once persistence thresholds are exceeded. The results obtained for *P. compacta* and *P. neriifolia* indicate that these thresholds may be reached at rather low harvesting rates. Therefore, a management plan based on cautious assessments, as indicated in Chapter 2, is urgently needed for wildflower conservation and harvesting monitoring and regulation.

Climate change may decrease, fragment and/or shift the suitable habitat of Proteaceae species (Midgley *et al.* 2002, 2003, 2006). As a consequence, impacts of habitat loss and future climate change on the red list status of 227 CFR Proteaceae suggest a rise in the percentage of critically endangered species from 1% up to 7% as well as extinction of up to 2% of the species (Bomhard *et al.* 2005). Considering that these alarming predictions were generated solely by correlative habitat models, the actual numbers should be even higher due to the limited migration ability of the species (Chapter 3). Moreover, results from Chapter 3 seem still to be optimistic (see the method section of Chapter 3). It was also shown in Chapter 3 that most species will survive mainly in the habitat that remains suitable. Furthermore, only some species will still be able to colonize habitat becoming suitable in the time frame considered for climate change (Chapter 3).

4.1.2. Directions for future research

Open questions still need investigation and can be address by the presented process-based model for range dynamics. For example, one could assess whether the species will eventually be able to colonize the habitat becoming climatic suitable if time is given (e.g., if climate change slows or ceases) and to which extent and at which pace such colonization will take place. It is also still unclear how wildflower harvesting impacts on species dynamics will influence species response to climate change. Climate change may also influence the occurrence of wild fires, a key factor triggering dispersal and recruitment (see the General

Introduction). If wild fires happen more frequently due to the expected drier and hotter conditions (Bowman *et al.* 2009), species that need longer to start reproduction will have higher extinction probability. On the other hand, species that reproduce more frequently will be able to migrate faster. It is important to emphasize, however, that Rouget *et al.* (2003) also indicates that the habitat is predicted to be further lost in the near future, which might worsen the impacts of habitat loss on range dynamics of CFR species. Furthermore, the model is also promising to identify possible migration corridors (Williams *et al.* 2005) more precisely. Another interesting research direction would be to investigate speciation due to geographical isolation cause by climate shifts. There is the evidence of recent fast hyperdiversification of CFR Proteaceae (Sauquet *et al.* 2009). Such speciation may have taken place among species whose range went fragmented due to past changes in climate and the resulting isolated refugia might have favoured species divergence. Therefore, it would be interesting to test if the presented demographic model for range dynamics is able to predict isolated refugia that eventually generated separate species.

Other process and mechanisms not accounted in the present thesis or in single chapters could be incorporated in future works related to the CFR Proteaceae. For example, past habitat loss, which was not accounted for in Chapter 1, could enhance the predictions of demographic models, including the parameter's values during model fittings. Although biological interactions and the role of competitors and facilitators have been partially investigated for CFR Proteaceae (Higgins *et al.* 2008), approaches integrating biological interactions into species distribution models are largely lacking.

4.2 Process-based models of range dynamics

As a step towards more complete range predictions, process-based models are a natural direction of the research focusing on modelling species distributions. Process-based approaches including physiological (Kearney & Porter 2004) and demographic processes (Keith *et al.* 2008; Morin *et al.* 2008; this thesis) can improve predictions of species distribution models. The present thesis shows that process-based models for species distribution have advantages and limitations, but can be further ameliorated.

4.2.1 Advantages

The presented approach opens a new avenue for species distribution modelling because it 1) incorporates demographical processes into predictions of species ranges; 2) can be fitted to abundance data; 3) can use the resulting fitted models to derive species-specific predictions, which thus take into account the relevant mechanisms for the studied species; 4) enables model selection between alternative models; 5) is dynamic and therefore able to simulate transient responses to non-equilibrium scenarios, such as habitat turnover and climate change.

Simulation of processes within the suitable habitat described by habitat models improves predictions by indicating where the species can actually occur due to demographic constraints. It is thus also possible to assess whether the species absence of regions predicted to be suitable can be attributed to demographic and/or dispersal limitation, for example. Isolated suitable habitat may simply be unreachable or a small group of suitable patches may not be able to support viable populations (Hanski *et al.* 1996).

The relevant demographic processes for a given study species can be also evaluated when fitting process-based models to abundance data. By fitting alternative models with the same dataset, it is also possible to do model selection (Akaike 1973, 1974) and then indicate which processes indeed play a role for the species' range dynamics. This is of special value given that some demographic processes are hardly considered in extinction risk assessments under climate change, even though such processes underpin species response. Risk assessments under climate change eventually incorporate some demographic constraints by considering alternative scenarios of migration, for example (see Midgley *et al.* 2006). In these types of assessments, however, migration is not provided as a system behaviour emerging from demographic processes. Moreover, other processes that are directly related to population dynamics cannot easily be accounted for by assessments based solely on habitat models. Examples of these processes are given by compensation strength in local dynamics and Allee effects, which have been largely neglected in species-specific forecasts and risk assessments.

The dynamic nature of the presented process-based demographic models makes it straightforward to investigate transient responses to deviations from the habitat-species equilibrium, like climate change and habitat loss (Travis 2003; Keith *et al.* 2008; Zurell *et al.* 2009). With such dynamic models it is possible not only to simulate species response under a non-equilibrium scenario but also to detect whether the species is currently in equilibrium or still in a transient phase (Ovaskainen & Hanski 2002; Zurell *et al.* 2009). Furthermore, the process-based approach coupled with a sensitivity analysis is useful for detecting demographic thresholds (Chapter 2). Such ecological thresholds and regime shifts has not been investigated as much as wanted (Anderson *et al.* 2009), although many modelling tools are already available (Anderson *et al.* 2009). With the presented approach, it is possible not only to assess thresholds but also the associated hysteresis when the perturbation ceases or is relaxed (Anderson *et al.* 2009). Hysteresis is a property of systems that can follow different routes when a perturbation is increased or decreased (e.g. how the species' range behaves after wildflower harvesting is ceased).

4.2.2 Limitations

Despite the given advantages, the presented process-based model for range dynamics has some limitations. Part of the limitations is direct related to the assignment of the potential habitat by the habitat models. The quality of habitat models on describing potential range has been largely debated (Heikkinen *et al.* 2006; Austin 2007; Beale *et al.* 2008). Such correlative models may not comprise actual correlations between species distribution and climatic variables (Beale *et al.* 2008). Although this might be a major limitation for models describing the distribution of animal species, it might be less relevant for plants. In contrast to most animals, established plant individuals cannot simply move if environmental conditions become unsuitable. Because of this, plants might have a more critical dependence on climatic and edaphic variables, such as precipitation and soil type, than animals. Moreover, habitat models generated for a geographical region may not be transferable, even to neighbouring regions (Randin *et al.* 2006). For CFR Proteaceae, the habitat models used take into account the global distribution of species (Midgley *et al.* 2002) and this limitation is thus less relevant for my study species. However, transferability limitations should be considered when analysing only partial ranges of a given study species.

Other limitations of process-based models concern the framework of fitting models to data. When parameterization of process-based models to data is already computational demanding, models that include more processes and parameters might impose elevated time and computational demands or be unfeasible. Moreover, because of the general trade-off between bias and variance of statistically estimated models, an increase in the number of parameters increases the variance of parameter estimates (e.g. Burnham & Anderson 1998). This can result in biologically unrealistic results, some of which may be difficult to recognize if appropriate independent data for validation is lacking. Nevertheless, the virtual ecologist approach provides a solution in order to evaluate the models and fitting procedure (Zurell *et al.* 2009; Zurell *et al.* submitted). The main limitation of the presented fitting procedure is the lack of confidence intervals or posterior distribution for the parameter values. The requirement of high-quality data (Thuiller *et al.* 2008) is another major limitation associated with fitting methods. The general scarcity of appropriate data to fit process-based models restricts, at least for the moment, their fully application to many other systems.

4.2.3 Directions for future research

A way to deal with limitations coming from the habitat models, process-based approaches should directly correlate environmental variables with the ecological parameters, eliminating the necessity of habitat models to describe the potential habitat (Thuiller *et al.* 2008). The statistical tools for fitting a model that relates processes to environmental variables might be already available, namely hierarchical Bayesian framework (Clark 2005). However, fitting this kind of complex approach is even more computer-intensive and demands high-quality data on spatial-temporal dynamics (Thuiller *et al.* 2008). Nevertheless, once adequate data are available, the fast advance of computation power should make it feasible to apply the hierarchical Bayesian framework to process-based species distribution models (Jeltsch *et al.* 2008; Thuiller *et al.* 2008).

The application of the presented approach to other study systems can be attempted despite possible lack of appropriate data to fit the models or to describe the dispersal kernels. However, for example, even if dispersal kernels are not well-know as for the CFR Proteaceae, alternative dispersal kernels can be used as scenarios and model selection could be performed (Chapter 1). While habitat models can readily be fitted to (absence/)presence data (Thomas *et al.* 2004; Thuiller *et al.* 2005; Araújo *et al.* 2006; Thuiller *et al.* 2006), the need for abundance data constitutes a major limitation to the fitting of demographic models. This necessity indicates that efforts on collecting such data must be pursued, especially in a monitoring scheme (Thuiller *et al.* 2008; Lindenmeyer & Likens 2009). Moreover, abundance monitoring generates time-series data, which enables proper parameterization of demographic models, especially through a hierarchical Bayesian framework (Clark 2005; Jeltsch *et al.* 2008; Thuiller *et al.* 2008). Nevertheless, the process-based models can still be applied to other systems in a sensitivity analysis or scenario-based study design (e.g. Chapter 2; Keith *et al.* 2008). Probably the South-West Australian Proteaceae offers the most suitable system to which the presented approach can be direct applied to.

Furthermore, other biological processes can be implemented in order to improve the presented model and make it more suitable to other study systems. In the most advanced phase of mechanic species distribution modelling, physiological and demographic processes should be considered along with biotic interactions (Soberón & Nakamura 2009). Such full-fledged mechanistic model would ultimately allow for a better appraisal of distribution models based on niche theory (Soberón & Nakamura 2009). Complete mechanistic species distribution models could be thus used to separately address fundamental and realized ecological niches (Soberón & Peterson 2005; Kearney 2006; Peterson 2006). For example, the fundamental niche can be predicted by physiological process-based models, which link physiological processes directly with relevant environmental variables (Kearney & Porter 2004, Kearney 2006; Kearney & Porter 2009). These physiological species distribution models offer a mechanistic alternative for habitat models in order to predict the suitable habitat. Eventually, however, correlative habitat models may come close to a description of fundamental niche, if considering species fitness in controlled lab experiments in order to check the species ecological amplitude (Soberón & Nakamura 2009). Hence, the predictions of the present thesis may be improved by simply using better habitat models or physiological distribution models. This could constitute a nice investigation about the quality of models describing fundamental niche: by fitting hybrid models with alternative descriptors of the suitable habitat, the model selection would indicate the approach that best describes the range dynamics of a target species.

Once the fundamental niche is known, demographic models can account for demographic constraints and dispersal limitation (Soberón & Peterson 2005; Peterson 2006). The present thesis contributes with such demographic processes. Models that explicit simulate biotic interactions can, finally, assess the role of these ecological processes in determining the realized niche (Soberón & Peterson 2005; Peterson 2006). Therefore, future research should focus on implementing process-based models that link physiological and demographic processes with biotic interactions. The role of biological interaction on determination realized niche may vary. For example, inter-specific competition may largely limit the realized niche compared to the fundamental niche (Bruno *et al.* 2003; Soberón & Peterson 2005; Soberón & Nakamura 2009). On the other hand, facilitation can make survival possible even in otherwise unsuitable conditions and, thus, the realized niche is enlarged to environmental conditions not predicted by the fundamental niche (Bruno *et al.* 2003). Moreover, biological interactions should play an important role on the species response to global change (Zurell *et al.* 2009). Interactions that might influence range dynamics and, thus, species ability to cope with global change include, for example, competition, predation, parasitism, pollination and zoochoric dispersal. These interactions are important because the interacting species should respond to climate change in a concerted fashion with the focus species. Nevertheless, demographic processes like those implemented in the present thesis may in some extent already account for biological interactions. For example, the estimated carrying capacity may indirectly compensate the effects of interspecific competition, whereas Allee effects may represent pollination failure at low densities.

Moreover, phenotypic plasticity and genetic variability can also be investigated, principally under environmental change. A genetic approach might enlighten our understanding on species' fundamental and realized niches by addressing niche evolution. Furthermore, such complex mechanistic models would have complicated parameter interactions and feedbacks. For example, not only physiological processes may depend on environmental variables, but also demographic processes and biotic interactions. Therefore, stepwise complexity levels may be implemented along the development of a full-fledged mechanistic models for species distribution. The optimal complexity can only be assessed and achieved if the different models can be statistically compared in a framework allowing for model selection. The present thesis contributes in this matter, by showing that it is possible to develop demographic species distribution models that can be fitted to data.

Besides physiological, ecological and evolutionary processes, the simulation of abiotic processes may produce more realistic predictions. For example, in Mediterranean-type ecosystems, process-based models of fire dynamics would make the range dynamics more realistic. Recent studies confirmed the usefulness of existing models describing fire dynamics for ecological research and suggested alternative models that are able to reflect empirical data of fire dynamics (Zinck & Grimm 2008; Zinck *et al.* in press). With fires simulated mechanistically, local extinction probability caused by fire could be directly estimated from simulation, resulting in an emergent property rather than a free parameter. Moreover, when applying the presented process-based model to other systems, perturbations like droughts, hurricanes, land slides might be enough relevant to be implemented in the model.

Finally, studies focusing on a more theoretical understanding can be designed aiming to address the complex interactions between metapopulation dynamics, dispersal ability, Allee effects, demographic stochasticity, deterministic chaos and harvesting (Chapters 1 and 2). Allee effects can either enhance chaotic oscillations (Morozov *et al.* 2004) or stabilize chaotic or oscillatory local dynamics (Scheuring 1999; Fowler & Ruxon 2002). These contradictory results might be due the fact that different equations for local dynamics were used. Therefore, what determines which impact Allee effects will have on local dynamics, if stabilizing or destabilizing, is still unclear. Moreover, chaotic oscillating populations can be also stabilized through harvesting (Sinha & Parthasaraty 1996). The harvesting-mediated inhibition of inherent chaos may result in lower or higher metapopulation-level extinction risk. If dispersal between populations is low, then the stabilization of local populations by inhibition of chaos might result in less local extinction risk and, consequently, less metapopulation-level extinction risk. On the other hand, if dispersal between populations is high, then the stabilization of local populations by inhibition of chaos increases synchronization between local populations, which results in higher metapopulation-level extinction risk (Münkemüller & Johst 2007). Furthermore, the interaction between model's stochasticity (see Chapter 1) and inherent deterministic chaos at local dynamics can contribute to the persistence of the metapopulations (Dennis *et al.*, 2003; Greenman & Benton, 2003). Such effect of this interaction occurs due to the amplification of the local population's noise, which increases decorrelation of local populations (Allen *et al.*, 1993). Interestingly, one type of noise present in our model, the demographic stochasticity (see Chapter 1), may be directly amplified by local chaotic oscillations, avoiding synchronization of local dynamics. Nevertheless, it is still lacking a comprehensive study that considers these complex interactions altogether. Hence, studies investigating such complex interplay are still necessary in order to improve the understanding of results from models predicting range dynamics.

4.3 Conclusions

In this thesis, I developed spatial-explicit process-based models for range dynamics that can be fitted to abundance data. The fitting approach can be used to do evaluate alternative models and to perform model selection. Additionally, these models can assess species responses to non-equilibrium scenarios caused by wildflower harvesting, habitat loss and climate change. General conclusions derived from the application of process-based models indicate that 1) the inclusion of demographic processes improves predictions of species distribution models; 2) the range dynamics of closely-related species may be shaped by different processes, and may thus respond differently to environmental change and exploitation; 3) Allee effects and the type of density regulation should be considered when investigating range dynamics of species; 4) wildflower harvesting, habitat loss and climate change might have strong negative consequences for CFR Proteaceae, but the sensitivity of individual species varies with their demographic properties; 5) wildflower harvesting impacts vary with spatial scale; 6) The effects of habitat loss and climate change are not always additive.

In summary, process-based models improve our understanding of the mechanisms that determine the range dynamics of plant species and are powerful tools for further investigations.

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Zusammenfassung

Der Einfluss demographischer Prozesse auf die Verbreitungsdynamik von Pflanzenarten ist noch kaum untersucht, da wenige geeignete prozess-basierte Modelle für die Verbreitung von Arten zur Verfügung stehen. Außerdem sind Modelle, die demographische Prozesse einbeziehen, geeigneter zur Untersuchung der Reaktion der Arten auf Störungen des Art-Habitat-Gleichgewichts durch beispielsweise Ausbeutung oder Umweltwandel als korrelative Habitatmodelle. Allerdings sind die wenigen verfügbaren prozess-basierten Modelle für die Verbreitung von Arten nicht mit Daten parametrisierbar. Das Ziel dieser Studie bestand daher darin, prozess-basierte Modelle zu entwickeln, die mit Daten zur Abundanz von Arten parametrisiert werden können. Die außergewöhnlich gut erforschten Proteaceen der südafrikanischen Kapregion (CFR), für die ein umfangreicher Datensatz zur Verfügung steht, stellen ein sehr geeignetes Untersuchungssystem zur Erstellung derartiger prozess-basierter Modelle dar. Diese Pflanzenarten sind durch den aktuellen Umweltwandel ernsthaft bedroht und ihre Infloreszenzen werden in Wildbeständen geerntet. Angesichts dieser Bedrohungen zeigt die vorliegende Arbeit den Nutzen prozess-basierter Modelle für die Untersuchung der Reaktion der Arten auf die Beerntung der Wildbestände, Habitatverlust und Klimawandel auf.

Die allgemeine Einleitung der These stellt zunächst die verfügbaren Modelle für die Verbreitung von Arten vor. Daraufhin wird der Nutzen und die Realisierbarkeit des auf Prozessen basierten Modellierens erläutert. Abschließend stelle ich das Untersuchungssystem, meine Ziele und den Aufbau der These detailliert dar.

In Kapitel 1 beschreibe ich ein prozess-basiertes Modell für die Verbreitungsdynamik sowie die Methoden zur Parametrisierung des Modells mit Daten zu Abundanzverteilungen. Das Modell umfasst ein räumlich-explizites demographisches Modul, das Fortpflanzung, Ausbreitung, Mortalität und lokales Aussterben beschreibt, und ein Beobachtungsmodul, das die ungenaue Beobachtung von Individuen berücksichtigt. Das demographische Modul verbindet artspezifische Habitatmodelle, die das geeignete Habitat beschreiben, und prozess-basierte demographische Modelle, die die lokale Dynamik und die Windausbreitung von Samen zwischen Populationen umfassen. Nach der Überprüfung der Parametrisierungsmethoden mit simulierten Daten, wende ich die Modelle auf acht Proteaceenarten mit unterschiedlichen demographischen Eigenschaften an. Außerdem untersuche ich die Rolle

zweier weiterer demographischer Mechanismen, die in Verbreitungsmodellen normalerweise vernachlässigt werden: positive (Allee-Effekte) und negative Dichte-Abhängigkeit. Die Ergebnisse zeigen, dass Allee-Effekte und überkompensatorische Dynamik (einschließlich chaotischen Verhaltens in der Lokaldynamik) für viele Arten tatsächlich eine Rolle spielen. Der Großteil der geschätzten Parameter stimmt quantitativ mit unabhängigen Daten überein. und beschreibt erfolgreich, wie die Abundanzverteilung aus der Bewegung und Interaktion der Individuen entsteht. Die vorgestellten Methoden scheinen daher zur Untersuchung von Ungleichgewichtsszenarien geeignet, die die Ernte von Infloreszenzen in Wildbeständen (Kapitel 2) und Umweltwandel (Kapitel 3) einschließen.

In Kapitel 2 untersuche ich einen für die Kapregion wichtigen Wirtschaftsfaktor, dessen Effekte auf die Dynamik von Pflanzenarten bisher kaum erforscht wurden – die Ernte von Infloreszenzen in Wildbeständen. Das Kapitel beinhaltet eine Sensitivitätsanalyse über mehrere räumliche Skalen sowie die folgenden demographischen Eigenschaften: Stärke der Allee-Effekte, maximale Reproduktionsrate, Mortalität erwachsener Individuen, Wahrscheinlicht lokalen Aussterbens und Kapazität des Habitats. Darauf folgend wurden die Effekte der Ernte anhand von drei realen Arten als Fallbeispiele untersucht. Die Reaktion der Pflanzen auf die Ernte zeigte ein Verhalten mit abrupten Schwellenwerten. Die durch die Ernte am stärksten gefährdeten Arten zeichneten sich durch kurze Samenausbreitungsdistanzen, starke Allee Effekte, geringe maximale Reproduktionsrate, hohe Mortalität und hohe lokale Aussterbewahrscheinlichkeit aus. Die Betrachtung größerer räumlicher Skalen wirkte sich trotz schärferer Grenzwerte positiv auf die Reaktion der Arten aus. Hierbei traten außerdem Interaktionen der räumlichen Skala mit der Stärke der Allee-Effekte und der lokalen Aussterbewahrscheinlichkeit auf. Die drei beispielhaft untersuchten realen Arten konnten sehr geringe bis mittlere nachhaltige Ernteraten ertragen. Zusammenfassend lässt sich sagen, dass Kenntnisse über die Demographie des Untersuchungssystems und die umsichtige Identifizierung der zu betrachtenden räumlichen Skala zu einer besseren Einschätzung der vertretbaren Ernteintensität und der für die gefährdeten Arten notwendigen Naturschutzziele führen sollten. Nichtsdestoweniger können die Ergebnisse der Sensitivitätsanalyse verwendet werden, um auch den Einfluss der Ernte auf unzureichend untersuchte Arten qualitativ abzuschätzen.

In Kapitel 3 wird die Reaktion der Arten auf vergangene Habitatverluste und zukünftigen Klimawandel sowie die Interaktion der beiden untersucht. Hierzu wurde nicht nur das zuvor entwickelte prozess-basierte Modell, sondern auch die in Kapitel 1 ermittelten Parameterschätzungen der besten Modelle für die lokale Dynamik verwendet. Sowohl

Habitatverlust als auch Klimawandel hatten starke negative Effekte auf die Dynamik der Arten. Der Klimawandel wirkte sich dabei vornehmlich negativ auf die Größe des Verbreitungsgebiets und die Ausnutzung des potentiellen Habitats (‚Range Filling') aus, wobei es zu einer Reduzierung und Verschiebung des Habitats ohne erfolgreiche Kolonisierung kam. Der Habitatverlust reduzierte vor allem die lokalen Abundanzen. Die meisten Arten wurden vor allem durch das Szenario mit beiden Klimawandel und Habitatsverlust stark beeinträchtigt. Der negative Effekt war allerdings geringer als nach einer einfachen Aufsummierung der Einzeleffekte zu erwarten wäre. Dies erklärt sich aus einer Verschiebung des Verbreitungsgebiets der Arten in Regionen, in denen es in der Vergangenheit zu geringeren Habitatverlusten kam. Die Größe des Verbreitungsgebiets wurde am besten durch die Stärke des Umweltwandels vorhergesagt, wogegen das Range Filling und die lokalen Abundanzen hauptsächlich von den demographischen Eigenschaften abhingen. Aus diesen Ergebnissen lässt sich schließen, dass Abschätzungen des Aussterbensrisikos unter Umweltwandel demographische Eigenschaften einbeziehen sollten. Die meisten überlebenden Populationen waren auf Refugien reduziert, die im Fokus der Naturschutzmaßnahmen stehen sollten.

Neben den Ergebnissen für das untersuchte System werden die Vor- und Nachteile sowie das Potential des vorgestellten prozess-basierten Modells in der allgemeinen Diskussion kommentiert. Zusammenfassend zeigen die Ergebnisse, dass 1) prozess-basierte demographische Modelle für die Verbreitungsdynamik von Arten mit Daten parametrisierbar sind; 2) die Einbeziehung demographischer Prozesse die Modelle für die Verbreitung von Arten verbessert; 3) verschiedene Arten von unterschiedlichen Prozessen beeinflusst werden und unterschiedlich auf Umweltwandel und Beerntung reagieren; 4) Dichteregulierung und Allee-Effekte bei der Untersuchung der Verbreitungsdynamik von Arten berücksichtigt werden sollten; 5) die Ernte von Infloreszenzen in Wildbeständen, sowie Habitatverlust und Klimawandel für manche Arten katastrophale Folgen haben können, deren Effekte aber von den demographischen Eigenschaften abhängen; 6) der Einfluss der Beerntung in Abhängigkeit von der betrachteten räumlichen Skala variiert; 7) die Effekte von Habitatverlust und Klimawandel nicht additiv sind.

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Declaration

This thesis comprises three scientific studies that investigate the role of demographic processes and the associated demographic properties on species range dynamics. This work also address species response to non-equilibrium scenario between species and habitat caused by wildflower harvesting, habitat loss and climate change. I carried out the investigations presented throughout this thesis and I wrote all contents of this thesis by myself. I also indicated in the text where I used published or unpublished data by others.

The three chapters were written as independent articles in cooperation with co-authors. Therefore, there is an overlap of information between chapters, which were also improved by the suggestions and comments of the co-authors. The Chapter 1 is already in press (Global Ecology & Biogeography) and thus was improved following comments of the referees and editors. The General Introduction and General Discussion as well as the rest of this thesis I wrote by myself.