

**Seed dispersal and range dynamics of plants:
understanding and predicting
the spatial dynamics of serotinous Proteaceae**

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A cone of *Leucadendron rubrum* that is about to release its seeds.

Contents

1 General Introduction	1
1.1 Seed dispersal and large-scale dynamics of plants	1
1.2 Measuring and modelling seed dispersal	6
1.3 The study system	10
2 A process-based model for secondary seed dispersal by wind and its experimental validation	15
2.1 Introduction	16
2.2 Model description	17
2.3 Model parameterisation and validation	23
2.4 Results	27
2.5 Discussion	33
3 Can evolutionary age, colonization and persistence ability explain to which extent species fill their potential range?	38
3.1 Introduction	38
3.2 Methods	40
3.3 Results	47
3.4 Discussion	50
4 Long-distance dispersal need not save species threatened by climate driven range shifts	54
4.1 Introduction	54
4.2 Methods	55
4.3 Results	58
4.4 Discussion	60
5 General Discussion and Outlook	62
5.1 Ecological and methodological findings	62
5.2 Implications for conservation	64
5.3 Directions for further research	67
Summary	71
Zusammenfassung	72
Acknowledgements	74

References	76
Appendix 1 - Aggregation of the process-based model for secondary seed dispersal by wind	90
Appendix 2 - Simulation of seed dispersal by wind and estimates of parameters relevant for the range dynamics of serotinous Proteaceae	94
Appendix 3 - Simulating population-level migration rates and future range sizes of serotinous Proteaceae	99
List of figures	105
List of tables	106

1 General Introduction

The dynamics of populations depends on the four demographic processes of birth, death, immigration and emigration. This 'fact of life' defines - in the words of Begon, Harper and Townsend (1996) - 'the main aim of ecology: to describe, explain and understand the distribution and abundance of organisms'. Dispersal determines two of the four demographic processes, namely immigration and emigration. Consequently, it is difficult to imagine an ecological or evolutionary problem that is not influenced by dispersal (Dieckmann et al. 1999). It is less obvious, however, how strong the influence of dispersal is for a given ecological question in a given study system. In fact, Wiens (2001) claimed that 'dispersal is one of the most important, yet least understood, features of ecology, population biology and evolution'.

With this thesis, I aim to contribute to the understanding of seed dispersal and range dynamics of plant species. In this first Chapter, I review existing information on the importance of seed dispersal for the large-scale dynamics of plant species, discuss methods for measuring and modelling seed dispersal, and introduce the study system of this thesis: Proteaceae from the South African Cape Floristic Region. In Chapter 2, I develop and validate a model for a particular dispersal process (secondary seed dispersal by wind). In Chapter 3, I test whether the biogeographical distribution of Proteaceae can be explained by combining data on their abundance, life history and evolutionary age with process-based models for seed dispersal. In Chapter 4, I forecast the ability of Proteaceae to migrate in response to climate change and quantify the uncertainty in these forecasts. Finally, Chapter 5 summarizes the findings of this thesis with respect to ecology and conservation, and suggests directions for further research.

1.1 Seed dispersal and large-scale dynamics of plants

Seed dispersal is the premier spatial demographic process of plants (Nathan & Muller-Landau 2000) and therefore influences many different aspects of plant biology. Several authors have recently reviewed the consequences of seed dispersal for fields such as population dynamics and population genetics (Levin et al. 2003), evolutionary dynamics (Barton 2001), the structure and dynamics of communities (Zobel 1997, Hubbell 2001, Levin et al. 2003, Levine & Murrell 2003, Poschlod et al. 2004), or the conservation, restoration and management of natural systems (Bakker et al. 1996, Bonn & Poschlod 1998, Poschlod & Bonn 1998). I restrict the following overview to the main focus of this thesis: the consequences of seed dispersal for the migration and large-scale distribution of plant species. Some of the relevant

terms are defined in Table 1.1. Note that I am deliberately not using a fixed definition of long-distance dispersal: which distances are 'long' depends on the objective of a study (Higgins et al. 2003a).

Table 1.1. Definitions of terms relevant for seed dispersal and the spatial dynamics of plant species.

Term	Definition
Seed	A general expression for the reproductive dispersal unit of a plant (Levin et al. 2003). This definition follows the common use of the term 'seed' in the ecological literature (Bonn & Poschlod 1998), but differs from the morphological definition of a seed as the fertilized ovule of the spermatophytes that consists of embryo, endosperm, and testa (Wagenitz 1996). The ecological definition of a seed thus comprises a variety of structures that are morphologically referred to as seeds, fruits, infructescences or spores (compare Poschlod et al. 2004).
Seed shadow	The spatial distribution of seeds dispersed from a single plant (Nathan & Muller-Landau 2000).
Dispersal kernel	A two-dimensional probability density function of the location of seed deposition with respect to the seed source (Fig. 1.1, Nathan & Muller-Landau 2000).
Distance distribution	A one-dimensional frequency distribution of seed dispersal distances (Nathan & Muller-Landau 2000).
Colonization	The foundation of a new population as a consequence of the dispersal of offspring to an unoccupied site, and the subsequent establishment of a population in this site.
Migration	The spread of a species into a region that previously was not part of its range.

Seed dispersal and plant migration

The occurrence of one and the same plant species both on continental mainlands and oceanic islands seemed to provide an argument for the independent creation of species at several distant points. To counter this argument, Darwin (1859) conducted an early quantitative study of seed dispersal. He measured the germinability of seeds after prolonged soaking in sea water, combined this information with the velocity of ocean currents, and concluded that a number of plant species had the ability to colonize remote islands. Darwin also referred to shifting plant distributions in response to glacial cycles, but he regarded these shifts as limited by climatic conditions rather than the migration ability of species. A different view was taken by Reid (1899, cited in Skellam 1951) when he formulated what was later termed 'Reid's paradox' (Clark et al. 1998). Reid wondered how plants like oaks that 'merely scatter their seeds' could have migrated to northern Britain within a few thousand years after the end of the

last glaciation. Reid's paradox was one of the motivations for Skellam (1951) to develop a formal model for population spread. In his treatment of the problem, he integrated the life history of a species (reproductive rate and generation time) with a statistical description of dispersal distances (a 'dispersal kernel', Table 1.1). Skellam assumed that dispersal follows a diffusion process that is equivalent to a Gaussian dispersal kernel (Fig. 1.1). However, under this assumption, Reid's paradox could not be resolved: the rapid post-glacial spread of oaks was only possible if either mean dispersal distance or fecundity was unrealistically high. Skellam (as Reid before him) concluded that the rapid post-glacial spread of plants into northern Europe could only be explained by rare long-distance dispersal events. However, there were few data on the frequency of these events. Even 25 years after Skellam, Harper (1977) remarked on the 'desperate poverty of hard quantitative information' about both short- and long-distance seed dispersal.

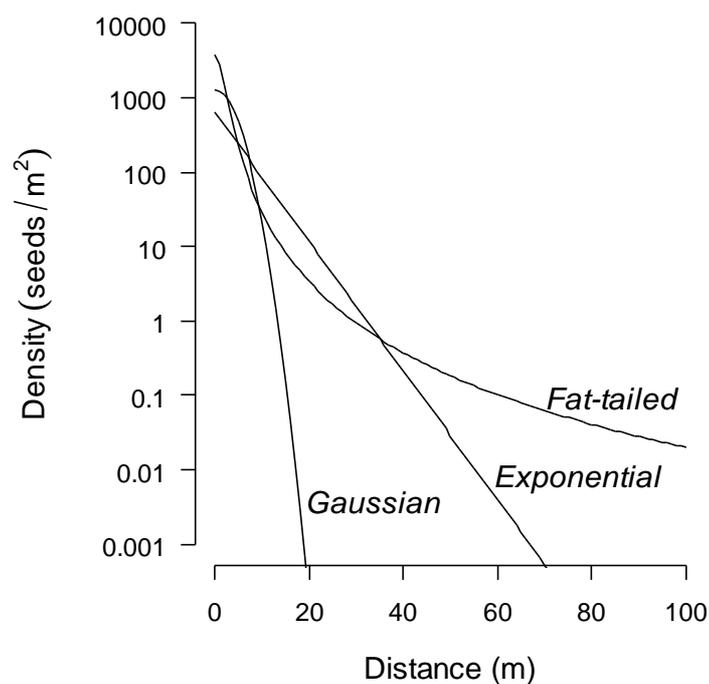


Fig. 1.1. Examples of Gaussian, exponential and fat-tailed seed dispersal kernels. The graph shows the change in expected seed density as a function of the distance from a mother plant that produces 10^5 seeds. A Gaussian dispersal kernel is assumed in diffusion models (e.g. Skellam 1951). For fat-tailed dispersal kernels, the seed density decreases less rapidly with distance than for an exponential kernel. The fat-tailed kernel shown is Clark's $2Dt$ (Clark et al. 1999). Note that seed density is plotted on a log scale.

In recent years, the rapid spread of invasive plant species and forecasts of global warming have revived the interest in plant migration and long-distance seed dispersal (Pitelka et al.

1997). Empirical studies found that many plant species have 'fat-tailed' dispersal kernels (Fig. 1.1): most of their seeds are deposited near the mother plant but a few are dispersed over long distances (Portnoy & Willson 1993, Clark et al. 1999). The incorporation of empirically estimated fat-tailed dispersal kernels into models for plant migration seems to resolve Reid's paradox: rare long-distance dispersal produces migration rates that can be reconciled with the palaeo-record (Cain et al. 1998, Clark 1998, Clark et al. 1998, 2001a, Higgins & Richardson 1999). However, the apparent resolution of Reid's paradox highlighted a problem for the prediction of future plant migrations (Clark et al. 2003): the migration rates of species with fat-tailed dispersal kernels strongly depend on extreme dispersal events (Clark et al. 2001a). Even if the dispersal kernel is known exactly, the magnitude of these extreme dispersal events is subject to strong stochasticity. Therefore, the predicted migration rates involve a substantial proportion of inherent uncertainty that cannot be reduced by better quantification of long-distance dispersal (Clark et al. 2003). From this, one might conclude that predictions of future migration are futile. On the other hand, there are so far no studies that predict the future range of a species by combining estimates of its migration ability with the predicted shift of its climatically determined potential range (Higgins et al. 2003b). It is therefore not clear to what extent forecasts of future ranges will be affected by the uncertainty in predicted migration rates. In Chapter 4, I derive forecasts of the future range sizes of plant species under climate change and quantify the uncertainty in these forecasts.

Seed dispersal and the spatial distribution of plant species

The importance of dispersal for the spatial distribution of species was emphasized by the theories of island biogeography and metapopulation ecology. The theory of island biogeography (MacArthur & Wilson 1967) predicts the species richness of islands by assuming a dynamic equilibrium between colonization (a function of the island's distance from the mainland) and extinction (a function of island size). A similar view was taken by Levins (1969, 1970) when he formulated the concept of a metapopulation as a 'population of populations' that occupies discrete habitat patches. In Levins' model, each population may go extinct and the metapopulation can only persist if the colonization of empty habitat patches compensates for the extinction of local populations.

The development of island biogeography and metapopulation biology coincided with an increasing awareness amongst conservationists that the destruction and fragmentation of habitat could cause the extinction of species. Island biogeography was applied to conservation biology under the premise that a reserve constitutes a 'habitat island' (Hanski & Simberloff

1997). This resulted in an extensive literature on reserve design, such as the SLOSS debate on the superiority of single large or several small reserves (Soulé & Simberloff 1986). In the late 1980s, the metapopulation concept replaced the theory of island biogeography as the dominant conservation paradigm (Hanski & Simberloff 1997). This paradigm shift has been explained by a shift from an equilibrium to a nonequilibrium view of ecological dynamics (Hanski & Simberloff 1997). However, the two paradigms also differ in an important conservation message: in contrast to island biogeography, the Levins model suggests that conservation of small and unoccupied habitat patches is necessary to ensure the regional persistence of a species (Hanski & Simberloff 1997).

Until recently, most empirical and theoretical studies of island biogeography and metapopulations dynamics have focussed on animals. In contrast, there was little empirical evidence for island or metapopulation effects in plants (Husband & Barrett 1996, Poschlod 1996, Hanski 1999, for exceptions see Bond et al. 1988, Menges 1990). Over the last decade, however, there has been an increase in studies applying the metapopulation concept to regional dynamics of plants (Freckleton & Watkinson 2002). In response, it has been criticized that most of these studies claimed the existence of plant metapopulations without providing conclusive evidence (Bullock et al. 2002, Freckleton & Watkinson 2002). One argument against the usefulness of metapopulation theory for plants is that many plant species face a very low risk of local extinction because they have persistent life history stages, e.g. soil seed banks (Poschlod 1996, Bullock et al. 2002, Freckleton & Watkinson 2002). Such species may form 'regional ensembles' of unconnected local populations (Freckleton & Watkinson 2002). Freckleton and Watkinson (2002) also criticize that metapopulation theory had been applied inadequately to 'spatially extended populations', that is to continuous populations that occur on a large area of suitable habitat. Metapopulations, regional ensembles and spatially extended populations differ in the relative importance of regional and local processes, with important consequences for conservation (Freckleton & Watkinson 2002). If regional processes are important (as in metapopulations), then conservation efforts should be directed towards the regional availability of suitable habitat; if regional processes are weak then effort should be directed at the conservation of existing populations (Hanski 1999, Freckleton & Watkinson 2002).

There are at least three reasons why plant conservation requires a good understanding of long-distance seed dispersal: (1) estimates of long-distance dispersal are necessary to assess whether a species shows metapopulation-like dynamics (Freckleton & Watkinson 2002); (2) the dynamics of those species that form metapopulations depends on long-distance seed

dispersal rather than mean dispersal distance (Higgins & Cain 2002); (3) anthropogenic influences can strongly affect seed dispersal and the ability of plant species to colonize habitat patches (Poschlod 1996, Pitelka et al. 1997, Bonn & Poschlod 1998). Currently, however, long-distance seed dispersal is a major unknown in most studies of the regional dynamics of plant species (Poschlod 1996, Cain et al. 2000, Freckleton & Watkinson 2002, Higgins & Cain 2002; but see Tackenberg 2001).

While the estimation of dispersal is already difficult at the regional scale, it is even more difficult at the large spatial scales relevant for biogeography. It is therefore largely untested whether metapopulation theory can explain biogeographical processes, although a number of theoretical studies have used metapopulation models to address biogeographical questions (e.g. Hanski & Gyllenberg 1997, Holt & Keitt 2000). In Chapter 3, I test whether the biogeographical distribution of plant species can be predicted by metapopulation models that are parameterized with estimates of long distance seed dispersal.

1.2 Measuring and modelling seed dispersal

As shown above, predictions of the migration and spatial distribution of plant species require quantitative descriptions of demographic processes in general and of long-distance seed dispersal in particular. Terrestrial plants are in principle well suited for demographic studies: for most of their lives 'plants stand still and wait to be counted' (Harper 1977). The seeds of many plant species, however, are small, mobile and difficult to track. Due to the difficulties of measuring seed dispersal, classical plant ecology has mostly used morphological traits to classify plant species into dispersal syndromes (e.g. Hildebrand 1873, Ridley 1938, van der Pijl 1982; for a discussion of this approach see Higgins et al. 2003a, Tackenberg et al. 2003). Nevertheless, there is a large (and growing) number of methods for measuring and modelling seed dispersal (Cain et al. 2000, Nathan et al. 2003).

Measuring seed dispersal

A direct method of measuring seed dispersal is to track the dispersal trajectories of experimentally released seeds. However, the seeds of most plant species cannot be tracked during dispersal because of their small size and/or the nature of their dispersal vector (Nathan et al. 2003). Most studies have therefore inferred seed dispersal from the post-dispersal location of seeds or seedlings (Nathan et al. 2003). Since this is straightforward when the source of all seeds is known, many studies have estimated the seed shadows of isolated plants (e.g. examples in Harper 1977, Bullock & Clarke 2000). Yet, isolated plants may disperse

their seeds under conditions that are very different from those in closed populations, where most seeds are dispersed (e.g. Nathan et al. 2002b). In populations of several mother plants, labels such as radioisotopes or dye can be used to identify the source from which a seed originated (e.g. Watkinson 1978, Winn 1989, Fischer et al. 1996). An elegant method is the use of the maternal genotype as a 'natural label': Godoy and Jordano (2001) genotyped all trees in a stand of *Prunus mahaleb* and used the genotype of the endocarp (which is of maternal origin) to assign diaspores to their mother plants.

All these approaches face the problem that the direct measurement of long-distance seed dispersal requires extensive sampling (Bullock & Clarke 2000). This is because long-distance dispersal events are rare, so that they can only be detected and quantified if sampling effort is high. For most practical applications, the direct measurement of long-distance seed dispersal will therefore be too labour-intensive (Greene & Calogeropoulos 2002).

In principle, it is possible to indirectly estimate long-distance seed dispersal from genetic variation within and between populations (so called 'long-term genetic analyses', Cain et al. 2000). However, these analyses cannot estimate seed dispersal independent from the past dynamics of the studied populations, which are often poorly known (Ouborg et al. 1999, Rousset 2001a,b, Nathan et al. 2003). Since long-term genetic analyses are sensitive to assumptions about past population dynamics, they are of limited use for obtaining quantitative estimates of long-distance seed dispersal (Rousset 2001a,b Nathan et al. 2003).

Modelling seed dispersal

Any quantitative interpretation of empirical data requires a model - be it a statistical, an analytical or a simulation model (Wissel 1989). These quantitative models can be classified into two broad categories: phenomenological models and process-based (or mechanistic) models. Phenomenological models aim at describing observed data without considering the underlying processes. In contrast, process-based models aim at predicting a phenomenon by describing some of the processes that generate it. In this thesis, I develop and use process-based models for seed dispersal, habitat colonization, plant migration and range dynamics. The following overview of seed dispersal models therefore focuses on process-based models and how they can be parameterized, validated and extrapolated. For the purpose of comparison, I briefly also discuss phenomenological dispersal models.

The most widely used phenomenological models of seed dispersal are exponential, lognormal, and $2Dt$ kernels (Clark et al. 1999, Stoyan & Wagner 2001, Fig. 1.1). A simple way of parameterising these models is to fit them to frequency distributions of observed dispersal

distances. However, phenomenological dispersal models can also be fitted in situations where the sources of individual seeds are not known. This is done by searching the dispersal kernel for which the observed distribution of seed sources has the highest likelihood of producing the observed distribution of seeds (Ribbens et al. 1994).

While phenomenological models describe the joint outcome of all dispersal processes, process-based models focus on a particular dispersal process. This process is described by combining information on a dispersal vector with information on dispersal-relevant traits of the seed and its mother plant. Potentially, process-based models may also describe the effect of environmental variables that interact with properties of the seed, the mother plant or the dispersal vector.

In principle, process-based models can be developed for any dispersal process; but in practice, they exist only for a limited set of processes. For instance, I am not aware of a process-based model for seed dispersal by water (*hydrochory*), apart from the early work by Darwin (1859, see above) and others (Schimper 1908). Process-based models for seed dispersal by animals (*epi-* and *endozoochory*) are rare and have mostly been developed for specific study systems (e.g. Sun et al. 1997, Hickey et al. 1999, Holbrook & Smith 2000, Westcott & Graham 2000). Some recently formulated models, however, are more generic and can therefore be applied to a wider range of systems (Higgins et al. 2003c, Levin et al. 2003, Powell & Zimmermann 2004, O. Tackenberg, S. Kahmen & P. Poschlod *unpublished data*).

The vast majority of process-based models for seed dispersal describe seed movement by wind (*anemochory*). Virtually all of these models describe only airborne seed movement and ignore seed dispersal along the ground (see Chapter 2). Most of the earlier models for airborne wind dispersal have a closed analytical form (e.g. Schmidt 1918, Greene & Johnson 1989, Okubo & Levin 1989). These models generally provide a good description of short-distance dispersal but underestimate long-distance dispersal (for reviews see Nathan et al. 2001, Tackenberg 2003). Long-distance seed dispersal through the air is predicted more reliably by two recently developed models that incorporate temporal and spatial heterogeneity in wind conditions (in particular turbulence; Nathan et al. 2002a, Tackenberg 2003). A disadvantage of these advanced models is that their parameterization requires extensive wind measurements and that their simulation is computer-intensive.

The parameters of process-based dispersal models have a biological or physical meaning. For instance, models of airborne seed dispersal by wind typically have a parameter describing the terminal falling velocity of seeds. Thus, while phenomenological models can only be

parameterized by fitting to observed dispersal data, the parameters of process-based models can be measured independent of dispersal data.

The validity of dispersal models can be assessed by comparing their predictions to empirical patterns of seed distribution observed in natural environments (e.g. Nathan et al. 2001, 2002a) or experimental seed releases (e.g. Tackenberg 2003). Since the direct measurement of long-distance seed dispersal is usually impossible (see above), dispersal models typically cannot be validated at large spatial scales (but see Nathan et al. 2002a and Chapter 2). Predictions of long-distance seed dispersal therefore require the extrapolation of dispersal models beyond the relatively small spatial scales at which validation is possible.

Process-based and phenomenological models differ with respect to such extrapolation. A process-based model seeks to understand a pattern in terms of the processes that produce it. This understanding is the scientific basis for extrapolation of the model to other systems in which the same processes are acting (Levin 1992). For instance, a process-based dispersal model that has been validated in a certain system may be extrapolated to other systems in which the modelled processes dominate dispersal. These other systems may comprise other species, other environmental conditions, or larger spatial and temporal scales. The extrapolation of phenomenological models is more problematic: since phenomenological models are 'blind' to the underlying processes, it cannot be judged whether these processes also operate in a system for which the model was not fitted. It is therefore impossible to assess whether the extrapolation of a phenomenological dispersal model is permissible (Nathan et al. 2003).

The assumptions of process-based models can be stated clearly and can therefore be compared to independent information on the conditions in a certain system. Such a comparison can be used to assess whether a process-based dispersal model will tend to overestimate or underestimate seed dispersal in a given system. In the model simulations presented in Chapter 3 and 4, I make use of this property of process-based models. The objective of Chapter 3 is to explain observed biogeographical distributions of plant species. The model simulations for this chapter are therefore based on assumptions that seem realistic. For the forecasts presented in Chapter 4, however, I make assumptions that tend to overestimate the migration ability of plants. The resulting forecasts can therefore be interpreted as upper limits of true migration abilities.

The understanding of seed dispersal ultimately requires the development of process-based models that can explain observed patterns (Levin et al. 2003). So far, however, process-based

models exist only for a limited set of dispersal processes (see above). In Chapter 2, I extend the domain of process-based dispersal models by developing and validating a model for secondary seed dispersal by wind.

1.3 The study system

Study region

The study area of this thesis is the Cape Floristic Region (CFR), an area of ca. 90000 km² at the south-west tip of Africa that is also known as the Capensis Floral Kingdom (see also Fig 3.1). Topographically, the CFR is a mosaic of plains and rugged mountainous areas; it ranges in elevation from sea level to more than 2000 m altitude (Linder 2003). The two main soil types are nutrient-poor sands, and clays of intermediate nutrient status (Goldblatt & Manning 2002). The western part of the CFR has a mediterranean-type climate with cool, wet winters and hot, dry summers; the eastern part has a smaller annual temperature range and a bimodal rainfall regime with precipitation peaking in spring and autumn (Deacon et al. 1992). Mean annual rainfall ranges from 200 mm/yr on the leeward slopes of interior ranges to 2000 mm/yr on high coastal mountains (Goldblatt & Manning 2002).

The Cape has an extremely species-rich flora with a high level of endemism: it hosts ca. 9030 species of vascular plants, 69% of which are endemic (Goldblatt & Manning 2002). The species richness of the Cape Flora matches that of tropical regions, whereas the degree of endemism is comparable to oceanic islands (Linder 2003). Due to its exceptional flora, the CFR has been listed as one of the 25 global biodiversity hotspots (Myers et al. 2000). The species richness of the CFR is under threat from agriculture, urbanization and the spread of alien plants (Rouget et al. 2003, Latimer et al. 2004), as well as from climate change (Midgley et al. 2002a, 2003, Thomas et al. 2004). A systematic conservation strategy, the Cape Action Plan for the Environment, has recently been developed to counter these threats (Cowling et al. 2001, 2003).

Most of the CFR's plant diversity is concentrated in the Fynbos Biome. Fynbos is a fire-prone sclerophyllous shrubland that is dominated by Ericaceae, Restionaceae, and by the family studied in this thesis - the Proteaceae.

Study species

The CFR hosts ca. 330 species of Proteaceae (Rebelo 2001). As Proteaceae dominate the overstorey of fynbos vegetation, they play an important role for the functioning of this ecosystem (Stock & Allsopp 1992), and for the composition of its communities (Cowling & Gxaba 1990). Proteaceae also have aesthetic value: many species produce large and attractive inflorescences, and one of these species (*Protea cynaroides*) has been designated as South Africa's National Flower. Moreover, fynbos Proteaceae are of considerable economic importance: in 1999 the fynbos flower industry generated a gross income of 149.3 million South African Rands, and most of this income was realized through the sale of Proteaceae inflorescences (Turpie et al. 2003).

The 41 Proteaceae species studied in this thesis belong to three genera: *Aulax*, *Leucadendron* and *Protea*. Their life history and demography is closely linked to fire, a recurrent phenomenon in fynbos (Fig. 1.2). All study species are serotinous: they form woody cones in which the seeds are stored for a prolonged period of time. The period of seed storage ranges from one year in weakly serotinous species to about 7 years in strongly serotinous species (Bond & van Wilgen 1996, Rebelo 2001). The cones are fire-safe and release their seeds when the water supply to them stops (Rebelo 2001). This occurs when the branch carrying the cone is killed by fire, so that the seeds are released into the post-fire landscape. After being released, the seeds germinate readily when conditions are suitable (Bond 1985). Serotinous Proteaceae therefore have a 'canopy seed bank', and 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 are discrete events that are largely restricted to the first year after a fire (Fig. 1.2, Rebelo 2001). This has four reasons (Bond & van Wilgen 1996): (1) fire triggers seed release; (2) fire decreases rodent densities and hence seed predation; (3) fire increases levels of light, water and nutrients; and (4) fire reduces the competition from established plants that precludes seedling establishment in unburnt vegetation. Although serotinous Cape Proteaceae show density-dependent establishment (Bond et al. 1984, 1995), seedlings seem to suffer little mortality once they have survived their first summer drought (Le Maitre & Midgley 1992, Bond & van Wilgen 1996). The density and spatial structure of Proteaceae stands is thus largely determined during the relatively short period of seed dispersal and establishment (Bond et al. 1984).

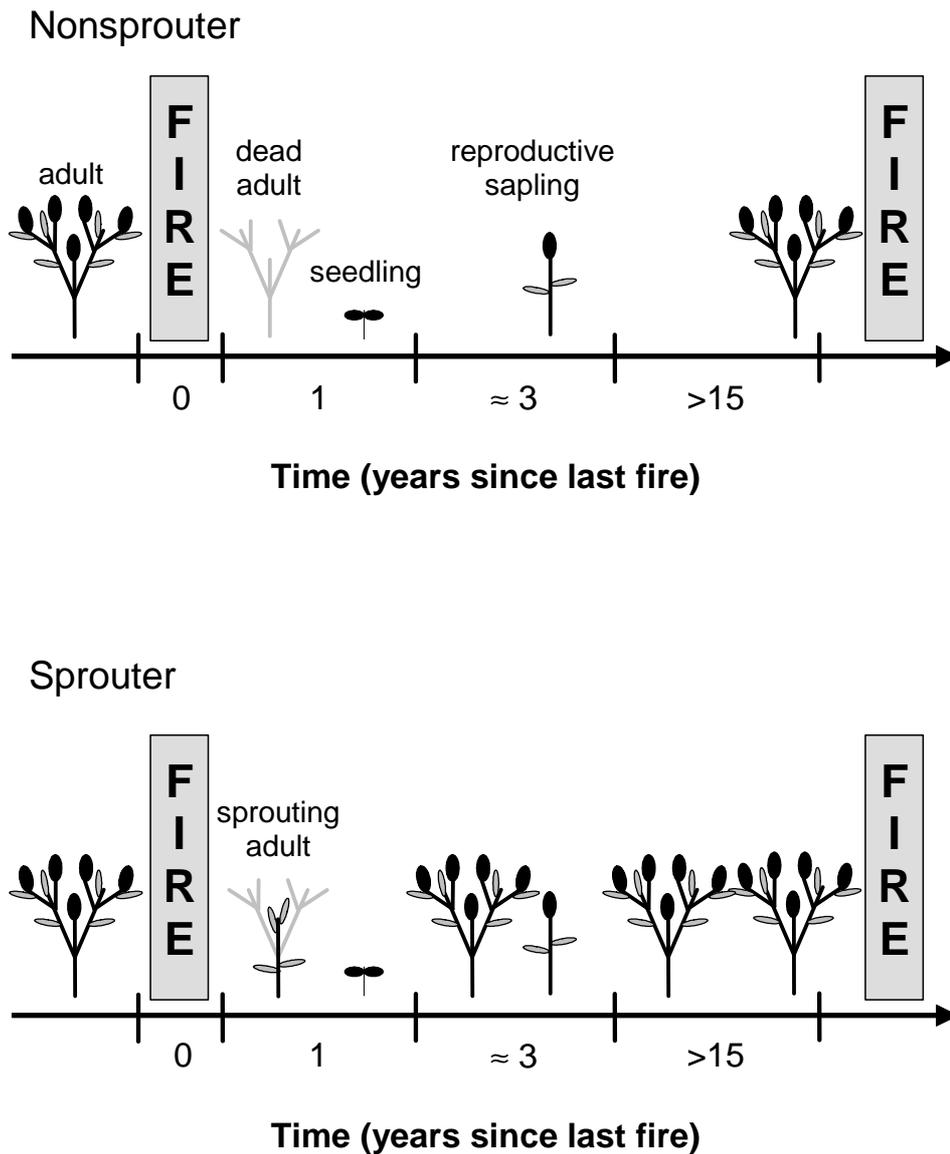


Fig. 1.2. The life cycle of serotinous Proteaceae in response to a typical fire cycle. Serotinous species store their seeds in cones (black ovals) which open after the mother plant has burnt. Seed dispersal and successful establishment are largely restricted to the first year after a fire. Upon establishment, saplings need a few years to become reproductively mature. In sprouting species (bottom), both seeds and adults can survive fires. In nonsprouting species (top), only seeds can survive fire, whereas adults are killed by fire. Therefore nonsprouters can go locally extinct if fire intervals are shorter than the time they need to become reproductively mature. (Note that the periods indicated on the time scale are approximate and may vary between species and environmental conditions.)

Wind is the predominant dispersal vector in the post-fire landscapes in which serotinous Proteaceae disperse their seeds (Bond 1988, Le Maitre & Midgley 1992, Rebelo 2001). The wind dispersal of Proteaceae seeds is a two-phased process in which primary seed dispersal through the air is followed by secondary seed dispersal along the ground surface (Bond 1988).

Secondary seed dispersal by wind has the potential to move Proteaceae seeds over long distances (Bond 1988). This is because high intensity fynbos fires create extensive obstacle-poor surfaces. In these environments, ants and rodents, the other main dispersal vectors of Fynbos Proteaceae, appear to be of minor importance, probably because their densities are drastically reduced by fire (Bond & van Wilgen 1996). Moreover, no seed movement further than a dozen metres was detected in field measurements of Proteaceae seed dispersal by ants (Slingsby & Bond 1985) and rodents (Midgley et al. 2002b).

The study species can be grouped into sprouters and nonsprouters, two distinct life history strategies that differ in the fire susceptibility of adult plants (Fig. 1.2). The adults of nonsprouting species are killed by fire, whereas the adults of sprouting species have an underground rootstock or a thick bark that allows them to survive fires (Bond & van Wilgen 1996, Bond & Midgley 2001, 2003). Sprouters and nonsprouters have markedly different life histories (Bond & van Wilgen 1996, Bond & Midgley 2003): sprouters are long-lived, iteroparous, and have overlapping generations. Nonsprouters are short-lived, effectively semelparous, and have non-overlapping generations. Moreover, populations of nonsprouters can go locally extinct if fire intervals are shorter than the time they need to become reproductively mature (ca. 3 years for most of the study species, Fig. 1.2, Le Maitre & Midgley 1992, Rebelo 2001).

The fynbos Proteaceae are exceptionally well-studied - not only with respect to their life history and demography (summarized above for serotinous species) but also with respect to their spatial distribution, local abundance and phylogeny. Species-level molecular phylogenies include *Protea* and *Aulax*, as well as some species of *Leucadendron* (Reeves 2001, Gail Reeves *unpublished data*). Spatial distributions and local abundances of all Southern African Proteaceae species were recorded by the Protea Atlas Project (Rebelo 2001). This massive mapping effort resulted in what Gelfand et al. (2005) identified as one of the largest and highest quality datasets in the world for studying biodiversity. Midgley et al. (2002a, 2003) used the Protea Atlas Database to develop statistical models that describe the current distribution of Proteaceae from climatic variables. They combined these bioclimatic models with scenarios of climate change to predict the location of potential ranges in the year 2050. Williams et al. (*in press*) developed a method that uses these predictions to identify 'migration corridors': networks of conservation areas designed to facilitate the migration of Proteaceae in response to climate change. However, the use of this method in conservation planning requires better estimates of the migration ability of species (Williams et al. *in press*).

In the following chapters, I seek to quantify the seed dispersal of serotinous Proteaceae and its consequences for the biogeographical distribution and the migration ability of these species. I measured traits relevant for anemochorous seed dispersal in a total of 41 species. However, each of the subsequent chapters uses only a subset of these species. For the validation of the dispersal model presented in Chapter 2, I selected 7 species that span the range of seed sizes and morphologies typical of serotinous fynbos Proteaceae. For the comparative study of biogeographical distributions (Chapter 3), I used the 37 species that are included in molecular phylogenies (Table A2.1). Finally, the migration forecasts in Chapter 4 are restricted to 26 species of nonsprouters (Table A3.1) since for this group there are data on reproductive rates.

2 A process-based model for secondary seed dispersal by wind and its experimental validation

Abstract

Secondary seed dispersal by wind, the wind-driven movement of seeds along the ground surface, is an important dispersal mechanism for plant species in a range of environments. I formulate a process-based model that describes how secondary dispersal by wind is affected by seed traits, wind conditions and obstacles to seed movement. The model simulates the movement paths of individual seeds and can be fully specified using independently measured parameters. I develop an explicit version of the model that uses a spatially explicit representation of obstacle patterns, and also an aggregated version that uses probability distributions to model seed retention at obstacles and seed movement between obstacles. The aggregated version is computationally efficient and therefore suited to large-scale simulations. It provides a very good approximation of the explicit version ($R^2 > 0.99$) if initial seed positions vary randomly relative to the obstacle pattern.

To validate the model, I conducted a field experiment in which I released seeds of seven South African Proteaceae species that differ in seed size and morphology into an arena in which I systematically varied obstacle patterns. When parameterised with maximum likelihood estimates obtained from independent measurements, the explicit model version explained 70-77% of the observed variation in the proportion of seeds dispersed over 25 m and 67-69% of the observed variation in the direction of seed dispersal. The model tended to underestimate dispersal rates, possibly due to the omission of turbulence from the model, although this could also be explained by imprecise estimation of one model parameter (the aerodynamic roughness length).

The analysis of the aggregated model predicts a unimodal relationship between the distance of secondary dispersal by wind and seed size. The model can also be used to identify species with the potential for long-distance seed transport by secondary wind dispersal. The validated model expands the domain of process-based dispersal models, contributes to a functional understanding of seed dispersal, and provides a tool for predicting the distances that seeds move.

2.1 Introduction

Seed dispersal by wind consists of two phases (Watkinson 1978). Following primary seed dispersal (the airborne movement of seeds from the mother plant to the ground surface), a seed may be blown along the surface until it germinates, until it is permanently entrapped, or until its dispersal structure has deteriorated (Johnson & Fryer 1992, Greene & Johnson 1997). This wind-driven movement along the ground surface is often termed secondary wind dispersal (e.g. Greene & Johnson 1997) but it has also been referred to as phase II dispersal (Watkinson 1978) or tumble dispersal (e.g. Bond 1988).

Secondary dispersal by wind is effective when seeds remain mobile for sufficient periods of time, when the ground surface is smooth, when few obstacles impede seed movement, and when the vertical wind velocity profile (Monteith & Unsworth 1990) results in high wind velocities close to the ground. Such conditions are found in various environments (Chambers & MacMahon 1994). Indeed, wind-driven seed dispersal along the ground has been observed in temperate grasslands (van Tooren 1988), coastal environments (Watkinson 1978, Redbo-Torstensson & Telenius 1995), tundra (Glaser 1981), alpine habitats (Chambers et al. 1991), arid and semiarid environments (Reichman 1984, Milton 1995, Aguiar & Sala 1997), on snow (Matlack 1989, Greene & Johnson 1997), as well as in environments disturbed by fire (Bond 1988, Hammill et al. 1998), human activities (Chambers et al. 1991, Campbell et al. 2003) or volcanic eruptions (e.g. Fuller & del Moral 2003).

Secondary wind dispersal can markedly alter the seed shadows resulting from primary dispersal (Harper 1977, Chambers & MacMahon 1994, Nathan & Muller-Landau 2000) and may be more important than primary dispersal with respect to the spatial patterning of plant populations (Chambers & MacMahon 1994) and the long-distance movement of seeds (Higgins et al. 2003a). Consequently, secondary wind dispersal is considered important for processes as diverse as plant migration in response to climate change (Midgley et al. 2002a), species persistence in fragmented landscapes (Bond 1988), succession after natural or anthropogenic disturbances (Chambers et al. 1991, Campbell et al. 2003, Fuller & del Moral 2003), and ecosystem functioning (Wiegand et al. 1995, Aguiar & Sala 1997).

To understand and forecast these processes, we need a quantitative description of secondary wind dispersal (Chambers & MacMahon 1994). The quantitative study of other seed dispersal mechanisms has been advanced by the development of process-based models (Chapter 1, Nathan & Muller-Landau 2000). Such models describe the processes underlying seed movement and predict seed dispersal from properties of species and their dispersal agents.

Many process-based models have been developed to describe primary wind dispersal (e.g. Greene & Johnson 1989, 1996, Okubo & Levin 1989, Andersen 1991), and some of them (Nathan et al. 2002a, Tackenberg 2003) reliably predict the airborne long-distance dispersal of seeds. In contrast, few authors have studied the mechanisms determining secondary wind dispersal, although Greene & Johnson (1997) developed a model for secondary wind dispersal over snow, based on Johnson & Fryer's (1992) detailed treatment of the physics of secondary seed movement by wind. However, this model has to be calibrated with data from experimental seed releases.

Here I develop a process-based model for secondary wind dispersal that builds on the principles outlined by Johnson & Fryer (1992) but, unlike Greene & Johnson (1997), describes the effects of both obstacles and the vertical wind velocity profile and can be fully specified with independently measured parameters. I formulate the model, derive an aggregated model version suitable for large-scale simulations and describe a protocol for estimating model parameters. In addition, I show that the model reliably describes seed movement in field experiments and explore model behaviour through extensive parameter variation. Finally, I explore the implications of the model for long-distance seed dispersal and for the relationship between seed size and dispersal distance.

2.2 Model description

Physical background

The physical forces considered in the model are drag and friction, with friction being a function of lift and gravity (Johnson & Fryer 1992). The wind drag on a seed (\vec{D}) acts in the direction of the horizontal wind vector experienced by the seed (\vec{U}). The strength of this drag force is

$$|\vec{D}| = \frac{1}{2} C_D \rho A (\vec{U} - \vec{v})^2 \quad (\text{Eq. 2.1}),$$

where C_D is the seed's coefficient of drag, ρ is air density, A is the planform area of the seed, and \vec{v} is the seed velocity vector (Monteith & Unsworth 1990, Johnson & Fryer 1992). Opposed to the drag force is friction, \vec{F} whose maximum absolute value depends on the balance of seed weight (\vec{W}) and lift (\vec{L})

$$|\vec{F}| \leq \mu (|\vec{W}| - |\vec{L}|) \quad (\text{Eq. 2.2}),$$

where μ is the seed's coefficient of friction on the surface (Johnson & Fryer 1992). When the seed is stationary, $\mu = \mu_s$ (coefficient of static friction), and when it is moving $\mu = \mu_k$ (coefficient of kinetic friction). The strength of the weight force acting on the seed is

$$|\vec{W}| = mg \quad (\text{Eq. 2.3}),$$

where m is seed mass and g is gravitational acceleration. The strength of the lift force experienced by the seed is

$$|\vec{L}| = \frac{1}{2} C_L \rho A (\vec{U} - \vec{v})^2 \quad (\text{Eq. 2.4}),$$

where C_L is the seed's coefficient of lift (Landau & Lifschitz 1991, Johnson & Fryer 1992).

The wind vector experienced by a seed, \vec{U} , depends on the vertical wind velocity profile. This profile describes how wind velocity decreases with the height above ground. On open ground, the horizontal wind velocity $|\vec{U}(z)|$ at height z above the ground typically follows a logarithmic profile:

$$|\vec{U}(z)| = \begin{cases} \frac{U_*}{K} \ln \frac{z}{z_0} & z > z_0 \\ 0 & z \leq z_0 \end{cases},$$

where z_0 is the aerodynamic roughness length, U_* is the friction velocity and K the von Karman constant (Monteith & Unsworth 1990). This logarithmic wind velocity profile can be expressed as a function of $|\vec{U}_{ref}|$, the wind velocity measured at a reference height z_{ref} (Monteith & Unsworth 1990)

$$|\vec{U}(z)| = \begin{cases} |\vec{U}_{ref}| \frac{\ln z - \ln z_0}{\ln z_{ref} - \ln z_0} & z > z_0 \\ 0 & z \leq z_0 \end{cases} \quad (\text{Eq. 2.5}).$$

The wind velocity experienced by a seed, $|\vec{U}|$, is calculated as $|\vec{U}(z)|$ averaged over the vertical seed projection, h

$$|\vec{U}| = \frac{1}{h} \int_0^h |\vec{U}(z)| dz = |\vec{U}_{ref}| p \quad (\text{Eq. 2.6})$$

where p is the 'wind interception parameter', a dimensionless ratio between the wind velocity experienced by the seed and the wind velocity at reference height. p summarises the effects of

the vertical seed projection and the wind velocity profile. For a logarithmic profile, the interception parameter is

$$p = \begin{cases} \frac{h(\ln h - \ln z_0) - h + z_0}{h(\ln z_{ref} - \ln z_0)} & h > z_0 \\ 0 & h \leq z_0 \end{cases} \quad (\text{Eq. 2.7}).$$

Explicit model version

The above equations are used to formulate a process-based model for secondary wind dispersal that represents obstacles in a spatially explicit fashion. This explicit version was implemented in Pascal (using Borland Delphi 5, Borland Software Co., Scotts Valley, USA). For a given time t , the model first determines whether seed movement is possible. If it is, the seed position at time $t + \Delta t$ is calculated from

$$\vec{S}(t + \Delta t) = \vec{S}(t) + \vec{v}(t)\Delta t,$$

where $\vec{S}(t)$ and $\vec{v}(t)$ are the position and the velocity of the seed's centre at time t , respectively. If T is the period of secondary wind dispersal (the amount of time for which a seed remains mobile) the seed's post-dispersal location is $\vec{S}(T)$.

Conditions for seed movement

A stationary seed ($\vec{v} = \vec{0}$) that is not retained by an obstacle starts moving if drag overcomes friction, that is if $|\vec{D}| > |\vec{F}|$. Using Eqs. 2.1-2.4 and Eq. 2.6 one can write down the condition for the start of seed movement in the absence of obstacles in terms of a threshold lift-off velocity, U_{lift} (Johnson & Fryer 1992)

$$p|\vec{U}_{ref}| = |\vec{U}| > U_{lift} = \sqrt{\frac{2mg}{\rho A \left(C_L + \frac{C_D}{\mu_s} \right)}} \quad (\text{Eq. 2.8}).$$

U_{lift} is thus an aggregated parameter that summarises seed properties (the wing loading m/A , Norberg 1973), seed-surface interactions (μ_s , C_D , C_L), and physical constants (g , ρ). Note that I define U_{lift} in terms of the wind velocity experienced by the seed ($|\vec{U}|$), whereas Johnson & Fryer (1992) express it in terms of a wind velocity at some arbitrary reference height ($|\vec{U}_{ref}|$). The definition used here allows a separation of the effects of a seed's lift-off velocity from the effects of its wind interception, p . I assume that U_{lift} is constant for a given seed on a given

surface. Ignoring seed momentum, I furthermore assume that seed movement stops as soon as the condition for the start of movement is no longer fulfilled.

Speed of seed movement

Kinetic friction experienced by a moving seed is assumed to be small and I therefore ignore it in the model ($\vec{F} = \vec{0}$ for a moving seed). Moreover, I assume that seeds accelerate and decelerate instantaneously. Under these assumptions, it follows from Eq. 2.1 that at any time a moving seed has the same speed as the wind it experiences,

$$\vec{v} = \vec{U} = p\vec{U}_{ref} \quad (\text{Eq. 2.9}).$$

This assumption is in agreement with field observations: 25 *Protea repens* seeds released on a 50 m long section of a sandy, obstacle free beach moved at 96% (standard deviation 15%) of the estimated wind velocity they experienced (F. Schurr, *unpublished data*).

Interaction with obstacles

I assume that the horizontal cross-sections of seeds are circular (with diameter s) and that the horizontal cross-sections of obstacles are elliptical (with diameters a and b). The centre (\vec{S}) of a seed situated at an obstacle then approximately lies on an ellipse E with diameters $a+s$ and $b+s$ (Fig. 2.1A). If E intersects the movement vector of a seed, the seed is either stopped or it changes its direction of movement. In the model, the outcome of this seed-obstacle interaction depends on the effects of the obstacle on wind conditions in its neighbourhood. While such effects are complex, I describe them with a simple rule: a seed situated at an obstacle experiences a wind vector that is the projection of \vec{U} on the tangent on ellipse E in seed location \vec{S} (Fig. 2.1A). If ω is the angle between \vec{U} and this obstacle tangent, the wind velocity experienced by the seed is $|\vec{U}|\cos\omega$. At an obstacle, the condition for seed movement is thus

$$p|\vec{U}_{ref}| > \frac{U_{lift}}{\cos\omega} \quad (\text{Eq. 2.10}).$$

If this condition is met, the seed moves along the obstacle tangent with velocity

$$|\vec{v}| = p|\vec{U}_{ref}|\cos\omega \quad (\text{Eq. 2.11}).$$

Once the seed has moved 'past' the obstacle (see Fig. 2.1B), seed velocity is again calculated from Eq. 2.9.

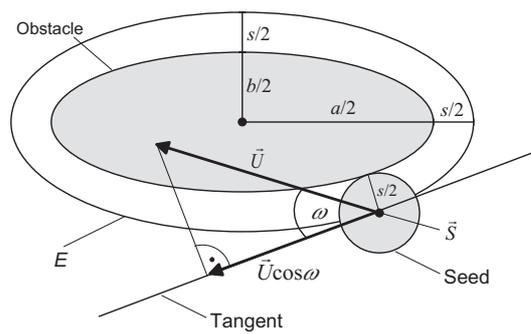
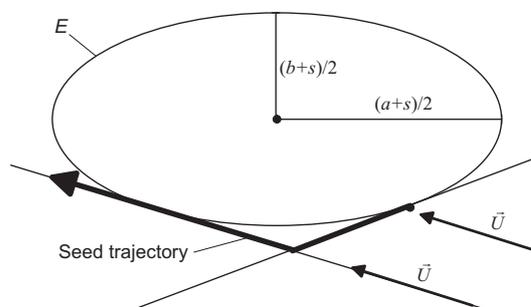
**A****B**

Fig. 2.1. Representation of seed-obstacle interactions in the model. A) The centre, \bar{S} , of a circular seed (diameter s), that is situated at an elliptical obstacle (diameters a and b), lies approximately on an ellipse E with diameters $a+s$ and $b+s$. The wind vector experienced by the seed is calculated as the projection of the ambient wind vector \vec{U} on the tangent on E in \bar{S} . This projection depends on the angle ω between \vec{U} and the tangent. B) The seed moves along this tangent until it reaches the tangent of \vec{U} on E . Thereafter the seed is assumed to have moved 'past' the obstacle and its movement is again determined directly by \vec{U} .

Aggregated model version

The model version described above is not suitable for simulating the dispersal of many seeds over extended periods because the explicit representation of obstacles makes simulations very time-consuming. Thus, I derived an aggregated version of the process-based model that enables large-scale simulations of secondary wind dispersal (see Appendix 1). The aggregated model version was implemented in R 1.8.1 (R Development Core Team 2004) with computer-intensive subroutines coded in C.

The model aggregation is based on the idea that secondary wind dispersal consists of an alternating series of periods in which seeds move between obstacles, and periods of seed retention at obstacles. The final position of a seed is then a function of the sum of individual movement periods within the dispersal period T , and of the wind the seed experiences while moving. In Appendix 1, I derive probability distributions for retention and movement times that can be used in dispersal simulations. I show how empirical distributions of retention time can be calculated under the assumption that obstacles have a circular basal area. For a wide range of wind measurements, U_{ift} and p values, I found these empirical retention time distributions to be well approximated by Gamma distributions. Movement times follow an exponential distribution if (1) seeds moving between obstacles follow a straight line, (2) the spatial distribution of obstacle centres is completely random, and (3) obstacle diameters are substantially smaller than typical distances between obstacles. The parameter of this exponential distribution is the obstacle encounter rate λ , which specifies the mean number of obstacles a seed encounters per unit distance moved ($1/\lambda$ is the mean free path between two obstacles). The obstacle encounter rate can be calculated as

$$\lambda = d(\bar{o} + s) \quad (\text{Eq. 2.12}),$$

where d is the density of obstacle centres and \bar{o} is the mean diameter of obstacles (see Appendix 1).

2.3 Model parameterisation and validation

To validate the model, I conducted a field experiment with seeds of seven species of Proteaceae native to the Cape Floristic Region. The study species cover the range of seed sizes and the main seed morphologies found in wind-dispersed fynbos Proteaceae (Fig. 2.2, Table 2.1, Rebelo 2001): plumed seeds (*Protea repens*, *P. lorifolia*, *P. neriifolia*), winged seeds (*Leucadendron laureolum*, *L. xanthoconus*, *L. salignum*), and parachute seeds (*L. rubrum*, nomenclature follows Rebelo 2001). All study species are serotinous, that is they store their seeds in cones that open after the mother plant has burnt. The high intensity fires in fynbos create a vegetation-free environment in which secondary wind dispersal is promoted (Bond 1988).

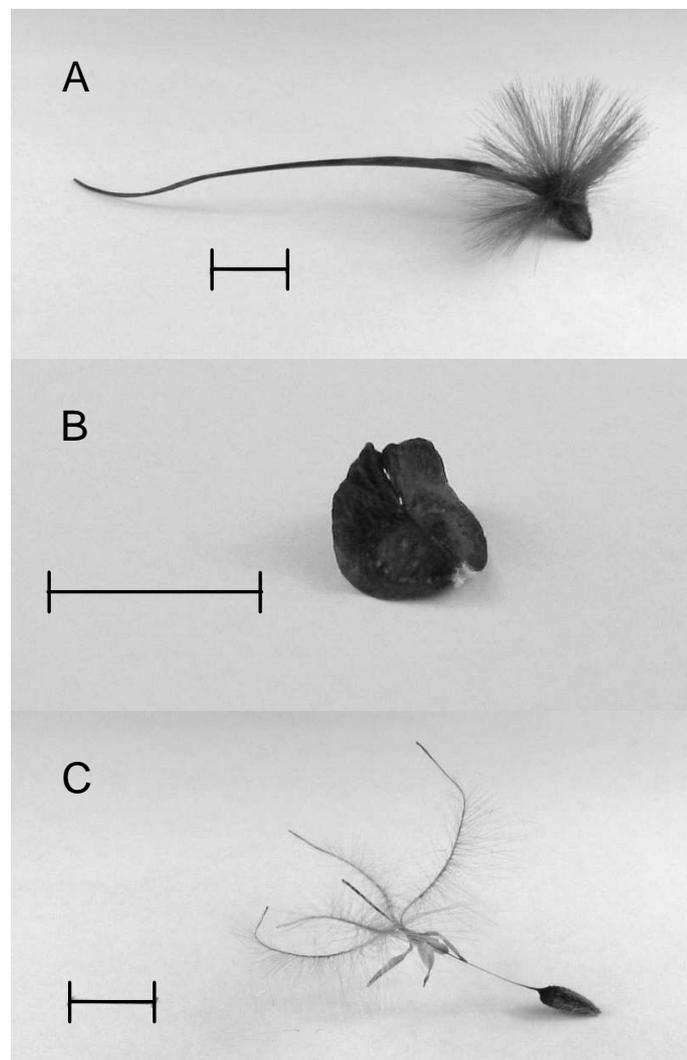


Fig. 2.2 The three basic morphologies of Proteaceae seeds that were used for experimental model validation: A) plumed seed – *Protea repens*, B) winged seed – *Leucadendron salignum*, C) parachute seed – *L. rubrum*. Scale bars mark a length of approximately 1 cm.

Table 2.1 Seed traits of seven species of Proteaceae and summary statistics of their seed movement in the field experiment. The table gives means and standard deviations (in brackets) of quantitative seed trait estimates. h and s , respectively, are the mean vertical projection and the mean horizontal diameter of a seed. Lognormal distributions of lift-off velocity, U_{lift} , are characterized by the mean and the standard deviation (the standard deviations associated with estimates of these two parameters were determined by nonparametric bootstrapping). Experimental results are summarized as the mean (and range) of the proportion of seeds collected at the first trap check after seed release (Fig. 2.3).

Species	Seed type	h (cm)	s (cm)	U_{lift} (m/s)		Proportion trapped (%)
				mean	sd	
<i>Protea repens</i>	plumed	2.1 (0.3)	4.6 (0.8)	2.7 (0.1)	0.9 (0.1)	72.8 (37-100)
<i>P. lorifolia</i>	plumed	0.5 (0.1)	3.1 (0.2)	3.0 (0.1)	1.0 (0.1)	47.4 (0-88)
<i>P. neriifolia</i>	plumed	0.9 (0.2)	3.9 (0.4)	3.7 (0.1)	1.2 (0.1)	32.8 (0-71)
<i>Leucadendron lauroleum</i>	winged	0.3 (0.1)	0.9 (0.1)	4.0 (0.3)	1.8 (0.3)	10.1 (0-32)
<i>L. xanthoconus</i>	winged	0.2 (0.1)	0.5 (0.03)	3.4 (0.2)	1.6 (0.2)	9.4 (0-26)
<i>L. salignum</i>	winged	0.3 (0.1)	0.8 (0.1)	3.1 (0.2)	1.2 (0.1)	13.8 (0-45)
<i>L. rubrum</i>	parachute	1.9 (0.4)	3.1 (0.3)	2.6 (0.4)	1.1 (0.6)	64.8 (9-94)

Field validation experiment

For the validation experiment, a semicircular arena of 25 m radius (Fig. 2.3A) was set up on a sandy, level and obstacle-free section of Noordhoek Beach, Cape Peninsula, South Africa (34°8' S, 18°21' E). The arena was delimited by a seed trap, a 50 cm high strip of 40% shade cloth that was attached to the surface so that seeds moving along the ground could not slip underneath. I repeatedly released batches of 100 seeds at the arena centre and subsequently determined the number of seeds caught in the seed trap. Seeds released at different times were stained with fluorescent powder of different colours (Magruder Color Company, New Jersey, USA). To quantify the direction of seed movement, the trap was divided into four sectors of equal length (Fig. 2.3A). As artificial obstacles I used sand-filled paper bags that had an elliptical basal area (diameters 64 cm and 32.5 cm). These obstacles were introduced into the arena at four different densities (0, 60, 120 and 180 obstacles resulting in densities from 0 to 0.18 obstacles/m²). They were arranged in spatially completely random patterns with their larger diameter parallel to the base line of the arena (i.e. the diameter of the semicircle). The randomized co-ordinates of the obstacles were simulated prior to the experiment. At each

obstacle density, seeds of each study species were released at two different times (Fig. 2.3B). To validate the model, I used data from the trap checks immediately following each of the 56 seed releases (4 obstacle densities x 2 releases x 7 study species). The dispersal period T up to this first check ranged from 22 to 58 minutes. Additionally, I considered data from the second trap check after seed release if the obstacle density had not changed since the release (Fig. 2.3B). This was the case for 28 seed releases (4 obstacle densities x 1 release x 7 species). Dispersal period T up to the second check ranged from 52 to 93 min.

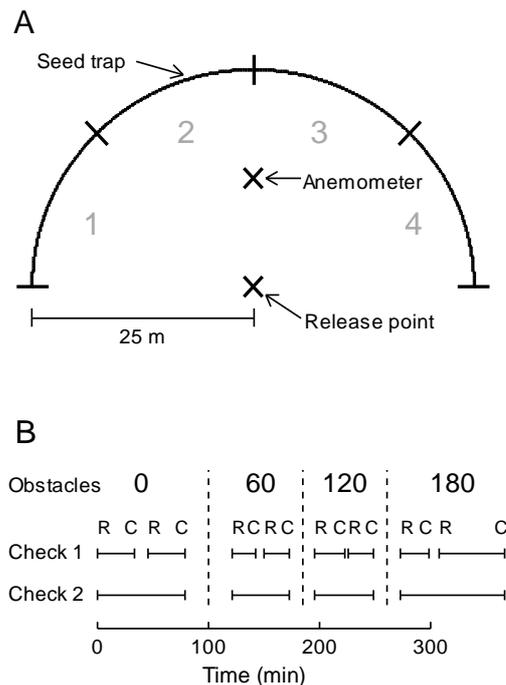


Fig. 2.3. Setup of the field experiment used to validate the seed dispersal model. A) Setup of the experimental arena on a sandy beach. Seeds were released at the release point and the number of seeds collected in different sectors of the semi-circular trap was determined. Wind conditions during the experiment were measured with a sonic anemometer. B) Temporal sequence of seed releases (R) and trap checks (C). At each of the four obstacle densities (0, 60, 120 and 180 obstacles within the experimental arena), seeds of each study species were released at two different times. For model validation I considered all seeds that were found at the first trap check after their release. Seeds found at the second trap check after release were only considered if the obstacle density had not changed since their release.

Wind measurements

During the experiment, time series of horizontal wind velocity components (at reference height $z_{ref} = 145$ cm) were recorded with a triaxial sonic anemometer (Model USA-1, Metek GmbH, Elmshorn, Germany) at a frequency of 10 Hz (therefore $\Delta t = 0.1$ s in the model simulations). Summary statistics of the wind conditions are given in Table 2.2. To determine

the vertical wind velocity profile I took additional cup anemometer measurements (WatchDog 700, Spectrum Technologies, Inc., Illinois, USA) at 33 cm, 47 cm and 103 cm above ground. By fitting Eq. 2.5 to the mean velocities per minute interval with a nonlinear least squares model (R package NLS) I estimated the roughness length as $z_0 = 0.018$ cm. The 95% confidence interval around this estimate is broad (0.005 cm – 0.052 cm) but falls within the range of values reported for a similar beach (Jackson 1996).

Table 2.2 Summary statistics of wind conditions (U_{ref}) during the field experiment at Noordhoek Beach. The table shows the ranges observed for each statistic in the eight periods between seed release and the first trap check (Fig. 2.3B). Wind measurements were taken 145 cm above the ground with a sonic anemometer at a temporal resolution of 0.1 s.

Variable	Mean	Median	Variance	Minimum	Maximum
Wind velocity (m/s)	4.20-7.37	4.18-7.35	1.08-1.72	1.33-3.05	8.69-12.69
Wind direction (radians from E)	1.10-1.53	1.11-1.53	0.03-0.06	0.37-0.53	1.84-2.68

Estimation of seed parameters

The vertical seed projection of a species, h , was calculated by averaging calliper measurements of 100 seeds placed randomly on a smooth board (Table 2.1). To determine horizontal seed extent, I scanned > 50 seeds of each species with a digital scanner, and measured maximum and minimum seed extent with the KS 300 Imaging System 3.0 (Carl Zeiss Vision GmbH, Oberkochen, Germany). The horizontal seed diameter, s , was then calculated as the mean diameter of an ellipse with diameters equal to the maximum and minimum seed extent (Table 2.1).

Lift-off velocities, U_{lift} , were measured with the methodology of Johnson & Fryer (1992) in a wind tunnel of the open jet return circuit type at the Department of Mechanical Engineering, University of Cape Town. In the wind tunnel, seeds were placed on sandpaper (mesh 40, average grain size ca. 400 μm), a surface similar to the surface of sandy fynbos soils. Starting at 2 m/s, I then increased the free stream velocity of the wind tunnel in steps of 1 m/s and recorded the velocity at which each seed started moving ($n=72$ seeds per species). This free stream velocity was translated into U_{lift} , the threshold wind velocity experienced by the seed, by assuming that the velocity profile in the wind tunnel is logarithmic (Eq. 2.5). From the free stream velocity and Pitot tube measurements at four different heights (0.1 cm, 0.6 cm, 1.1 cm, and 2.1 cm), I estimated the roughness length of this velocity profile as $z_0=0.0024$ cm ($R^2=0.98$). To estimate the probability distribution of U_{lift} for each species, I fitted lognormal

density functions to the distributions of measured U_{lift} values (R-function `fitdistr`, Venables & Ripley 2002, Table 2.1).

Model validation

I used the explicit model to simulate the dispersal of 10000 seeds for each of the experimental seed releases. In these simulations, the positions and orientations of obstacles were identical to those in the experiment. The release time of individual seeds was selected randomly within the first minute of the respective dispersal period, and initial seed positions were distributed randomly within a square metre centred at the release point. I compared model predictions to the experimental results both in terms of the overall proportion of seeds trapped, and in terms of the proportion of seeds trapped in each trap sector. The amount of variation in the observed data that is explained by the model was calculated as the generalized coefficient of determination (adjusted R^2 , Nagelkerke 1991). In the calculation of this adjusted R^2 I assumed binomial errors for the overall number of trapped seeds, and multinomial errors for the number of seeds per trap sector. In cases where no seeds were simulated to reach a trap sector, the predicted proportion of trapped seeds was set to 7.5×10^{-5} . This is the per-sector trapping probability of a multinomial distribution for which the probability of trapping none of 10000 seeds is 5%.

2.4 Results

Model validation against experimental data

The proportion of seeds trapped in the field experiment ranged from 0 to 100% per seed batch. Seed distribution was variable in space with seeds being trapped in three of the four trap sectors. Additionally, seed distribution varied in time - in the seed batches undergoing two checks, 0 to 100% of the trapped seeds were found in the second check. Moreover, the mean proportion of seeds trapped up to the first check differed between obstacle densities (ranging from 11.9% at 180 obstacles to 61.7% at 0 obstacles) as well as between species (ranging from 9.4% for *L. xanthoconus* to 72.8% for *P. repens*). Plumed and parachute seeds were markedly more mobile than the smaller winged seeds (Table 2.1).

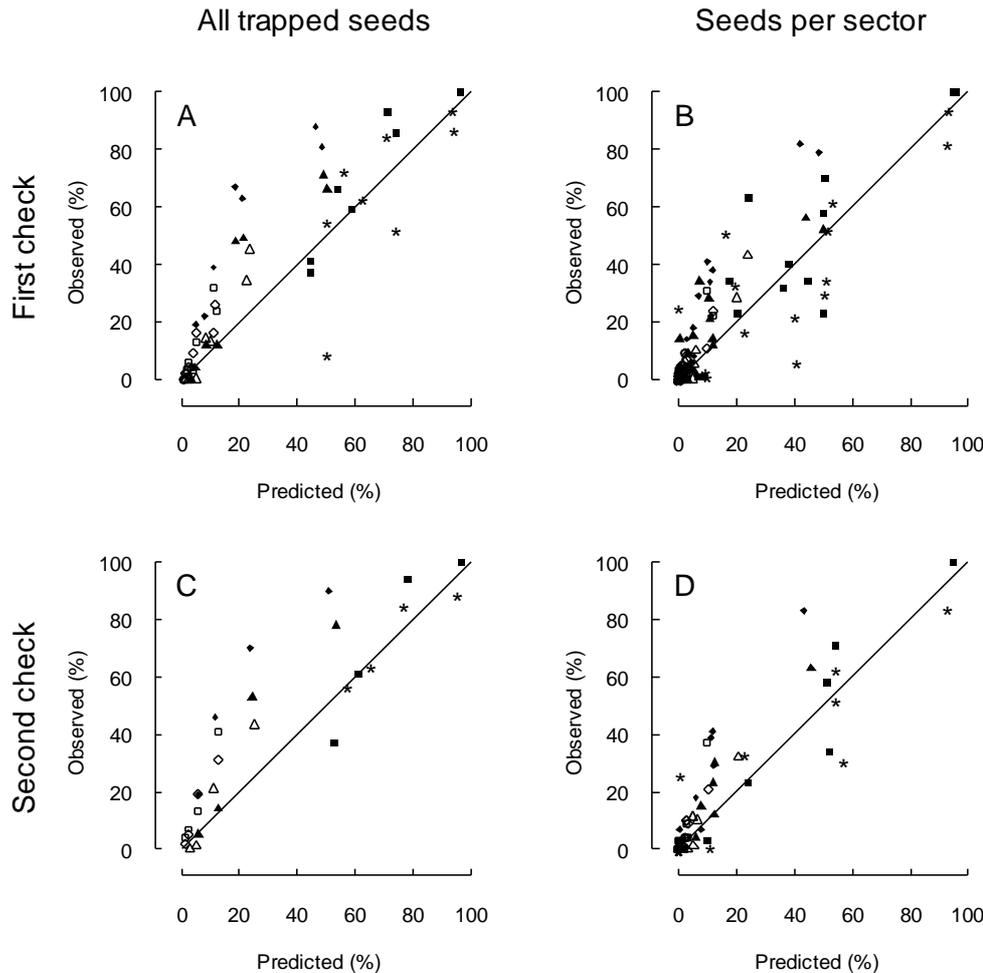


Fig. 2.4. Observed vs. predicted proportions of seeds dispersed over a distance of 25 m in seed release experiments on Noordhoek beach. Figures show the overall proportion of seeds found in the seed trap (left column) and the proportion of seeds found in each trap sector (right column) for the first trap check (top row) and the second trap check (bottom row) after seed release. Symbols represent different species (filled symbols: plumed seeds - square: *Protea repens*, diamond: *P. lorifolia*, triangle: *P. neriifolia*; empty symbols: winged seeds - square: *Leucadendron laureolum*, diamond: *L. xanthoconus*, triangle: *L. salignum*; stars: parachute seeds - *L. rubrum*). Also shown are lines of agreement between predictions and observations.

The explicit version of the process-based model was able to explain most of the variation in the experimental data from independently measured parameters. The model provided a good explanation both of the overall proportion of seeds that covered 25 m up to the first check (Fig. 2.4A, adjusted $R^2=0.77$, $n = 56$ releases) and of the distribution of these seeds to the different trap sectors (Fig. 2.4B, adjusted $R^2=0.69$). The model also performed well at explaining the overall proportion of seeds trapped up to the second check (Fig. 2.4C, adjusted $R^2=0.70$, $n = 28$ releases) and the spatial distribution of these seeds (Fig. 2.4D, adjusted $R^2=0.67$).

Model bias, the mean difference between model prediction and experimental observation, was -7.7% for the proportion of seeds trapped up to the first check. The model thus tended to underestimate seed dispersal at the maximum likelihood parameter estimates. Since the estimate of the aerodynamic roughness length z_0 was uncertain, I varied this parameter within the 95% confidence interval of the estimate. This parameter variation showed that the model is sensitive to z_0 and that the underestimation of seed dispersal disappears as z_0 becomes smaller (Fig. 2.5). For instance, at $z_0 = 0.012$ cm (a value within the 50% confidence interval of the z_0 estimate), model bias is reduced to -2.2% and the adjusted R^2 is 0.86. Similar results were found when analyzing data from the second check (results not shown).

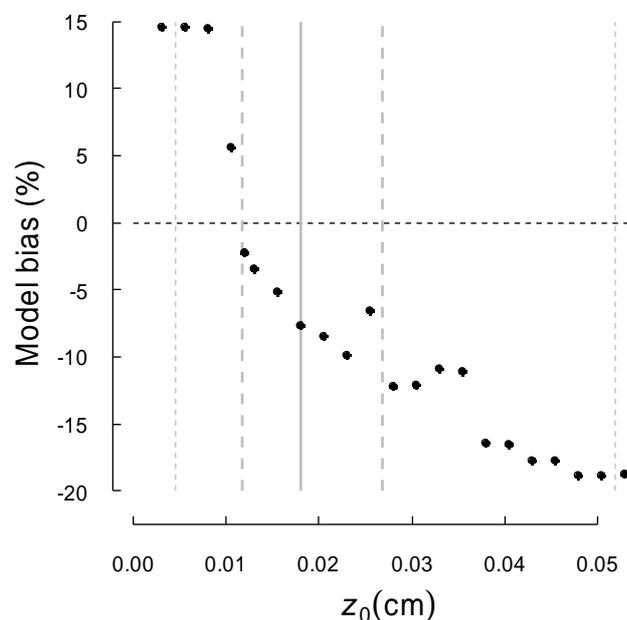


Fig. 2.5. The effect of the aerodynamic roughness length (z_0) on the bias of the explicit model version. Model bias is the mean difference between the proportion of seeds predicted to disperse over 25 m and the respective experimental data (only data from the first trap check were considered). The solid line indicates the maximum likelihood estimate of z_0 . Bold hatched lines show the 50% confidence interval of this estimate and thin hatched lines the 95% confidence interval.

Comparison of explicit and aggregated model version

Predictions of the aggregated and the explicit model showed some deviation if the explicit model was run with the exact distributions and orientations of obstacles used in the beach experiment (Fig. 2.6, $R^2=0.96$, bias=3.7%). This difference may arise because the aggregated model assumes that seeds start at random locations relative to a random obstacle pattern. In

contrast, in simulations of the experimental setting with the explicit model, the initial position of seeds relative to the obstacle pattern varied little. In these simulations, seed trajectories were thus more strongly correlated than in the aggregated model. To introduce variation in the relative location of initial seed positions and obstacles, I generated 100 random obstacle patterns for each obstacle density. These patterns were created by assigning random positions and orientations to individual obstacles. For each obstacle pattern I simulated the dispersal of 100 seeds with the explicit model version. The aggregated model provided an excellent prediction of the proportion of seeds dispersed over 25 m in these simulations (Fig. 2.6, $R^2 > 0.99$, bias = -0.7%).

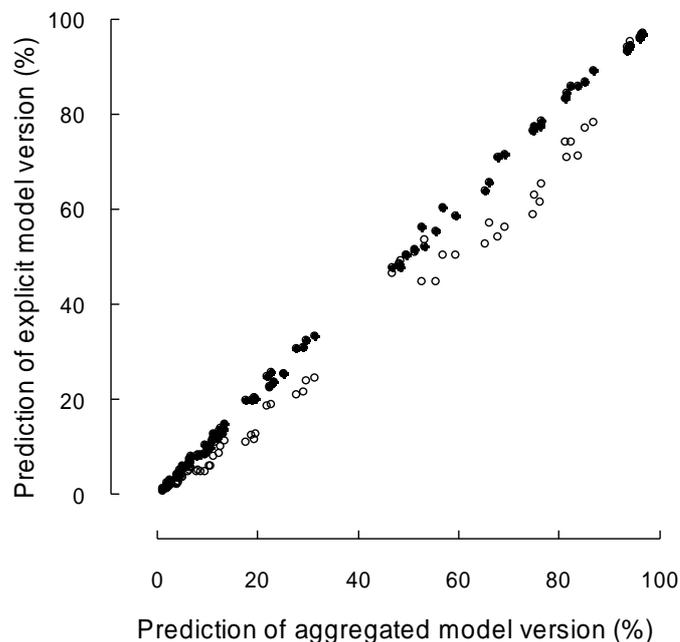


Fig. 2.6 Comparison of explicit and aggregated model version in terms of the proportion of seeds predicted to disperse over 25 m. Empty symbols represent simulations of the explicit model for the configuration of initial seed positions and obstacles in the field experiment ($R^2=0.96$, bias=3.7%, explicit = 1.05 x aggregated + 2%). Filled symbols represent simulations of the explicit model for 100 random configurations of initial seed positions and obstacles ($R^2 > 0.99$, bias = -0.7%, explicit = 0.99 x aggregated - 0.4%).

Sensitivity analysis

To explore the behaviour of the process-based model I performed an extensive sensitivity analysis. The aim of this analysis was to determine the effect of model parameters on typical dispersal distances of seeds released in random locations relative to a random obstacle pattern. Hence, I used the aggregated model version for this analysis. In the sensitivity analysis I independently varied the lift-off velocity U_{lift} , the obstacle encounter rate λ , and the wind

interception parameter p . For each combination of these parameters, I simulated the dispersal of 100 seeds using wind data measured during one hour of the field experiment and calculated the median dispersal distance.

In the absence of obstacles ($\lambda = 0 \text{ cm}^{-1}$), the sensitivity analysis reveals a sigmoidal relation between U_{lift} and dispersal distance (Fig. 2.7A): seeds with high U_{lift} are not dispersed along the surface whereas for low U_{lift} dispersal distance approaches an upper bound. This upper bound reflects the fact that no seed can travel further than the wind it experiences within the dispersal period. Note that in this respect my model differs from that of Greene & Johnson (1997) - the latter predicts an inverse relationship between distance of secondary wind dispersal and wing loading, implying that dispersal distance becomes infinitely large as wing loading (and thus U_{lift} - see Eq. 2.8) approaches 0. My model furthermore reveals an interaction between lift-off velocity and obstacle encounter rate: higher obstacle encounter rates (e.g. $\lambda = 0.1 \text{ cm}^{-1}$) keep all seeds from realizing the maximum dispersal distance and allow substantial dispersal only for seeds with low U_{lift} (Fig. 2.7A).

The sensitivity analysis also demonstrates the importance of the wind interception parameter p . The three curves in Fig. 2.7B show that differences in p can result in different median dispersal distances even if the lift-off velocity measured at reference height (U_{lift}/p) is identical. This is because higher values of p increase seed velocity (Eq. 2.9) thereby decreasing the travel time between obstacles and promoting dispersal distance. U_{lift} and p thus affect secondary wind dispersal independently and cannot be aggregated into a single parameter.

Figure 2.7C shows the joint effect of obstacles and wind interception on the distance of secondary wind dispersal. For $\lambda = 0 \text{ cm}^{-1}$, dispersal distance attains an upper bound that is defined by p and U_{lift} (see Fig. 2.7A and B). At low values of p , dispersal distance decreases steeply with λ , whereas the rate of decrease is less pronounced for larger p . This effect arises because an increase in p reduces the importance of individual obstacles by decreasing the travel time between obstacles and the retention time at obstacles. Finally, for large values of λ (when obstacle encounters are frequent), median dispersal distance is approximately correlated with the inverse of λ (that is with the mean obstacle-free path).

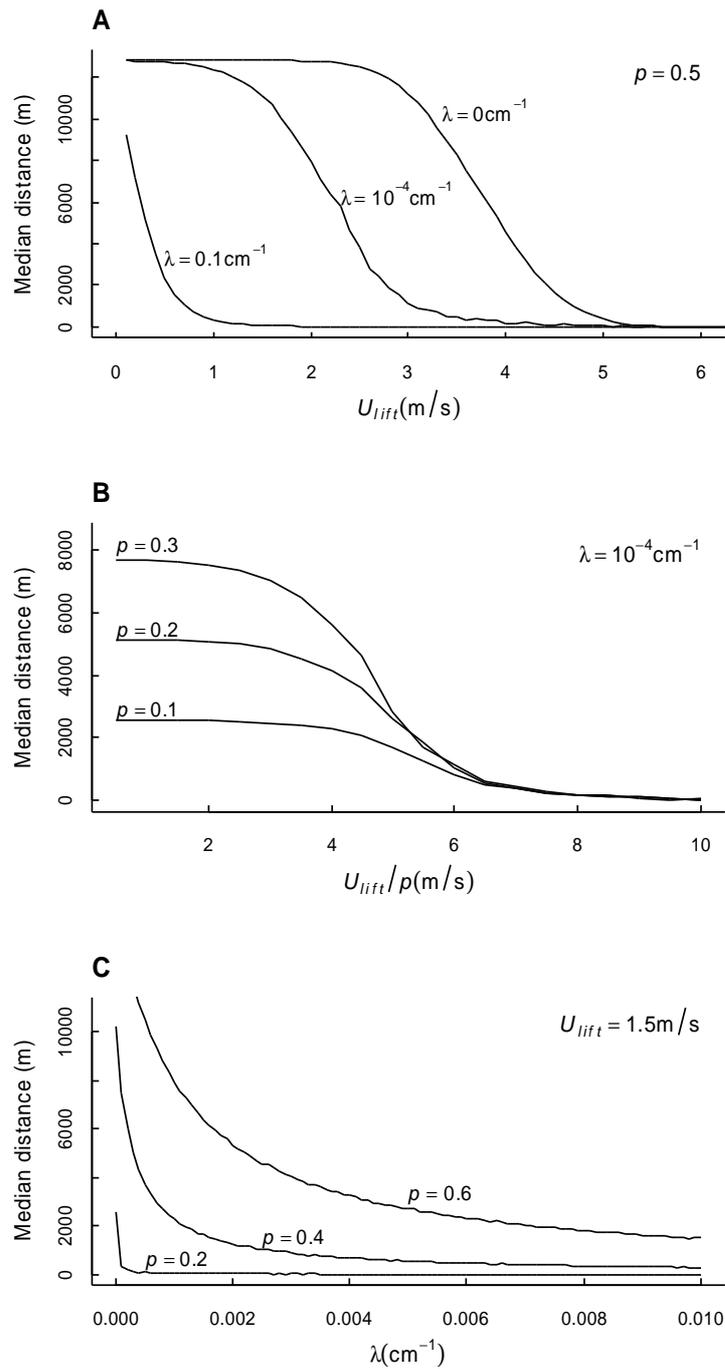


Fig. 2.7 The joint effects of a seed's lift-off velocity (U_{lift}), the wind interception parameter (p) and the obstacle encounter rate (λ) on the median distance of secondary wind dispersal predicted by the aggregated model version. For model simulations I used one hour of wind data measured during the field experiment.

2.5 Discussion

Model evaluation

In the field experiment, I observed large variation in the wind-driven movement of seeds along the ground. The explicit version of the process-based model, when parameterised with independent measurements, explains most of this variation (Fig. 2.4). The aggregated model version seems to be an excellent approximation of the explicit version if initial seed positions vary randomly relative to the obstacle pattern (Fig. 2.6). This condition will be met in most cases where the large-scale simulation of secondary wind dispersal is of interest.

The good agreement between model predictions and experimental data is remarkable since the model makes a number of simplifying assumptions: it (1) ignores turbulence, (2) assumes spatially homogeneous wind conditions away from obstacles, (3) ignores seed momentum, (4) uses a simple rule for seed-obstacle interactions (Fig. 2.1), and (5) describes complex seed morphologies (Fig. 2.2) using three easy to measure parameters (lift-off velocity, vertical seed projection and horizontal seed diameter). Of these assumptions, the omission of turbulence seems particularly important. Turbulence may significantly increase distances of primary seed dispersal by wind (Nathan et al. 2002a, Tackenberg 2003), and it evidently can also affect secondary dispersal by wind. First, turbulent wind fluctuations close to the ground may move seeds smaller than the roughness length z_0 . Second, the turbulence created by obstacles may affect seed retention at obstacles. Finally, turbulent eddies may pick up seeds, thereby terminating secondary seed movement and initiating a new (tertiary) phase of airborne seed dispersal. The importance of turbulence for secondary dispersal by wind will thus increase with decreasing seed size and increasing roughness length. Moreover, it will vary with the size and shape of obstacles.

Although the presented model ignores turbulence, it reasonably described seed movement in the field experiment, in which seed size was varied by more than one order of magnitude (Table 2.1). While the model's slight underestimation of seed movement might be due to the omission of turbulence, it can probably be attributed to the imprecise estimation of roughness length, z_0 (Fig. 2.5). In summary, the model seems to capture the essential processes that determined secondary seed movement in the field experiment. The simplicity of the presented model is in fact one of its advantages: in comparison to a more complex model, it is easier to parameterize and less sensitive to parameter uncertainty (Burnham & Anderson 1998, Clark et al. 2003, Higgins et al. 2003b). Nevertheless, the domain for which the model makes valid predictions is obviously limited. It will be interesting to assess these limits by releasing an

even wider range of seed sizes into environments that have differences in obstacle shape and the amount of turbulence.

The measurement of seed movement in the experimental arena cannot directly validate model predictions with respect to long-distance dispersal. In fact, dispersal models can hardly be validated at large spatial scales, because the empirical quantification of long-distance dispersal requires a prohibitive sampling effort (Chapter 1, Greene & Calogeropoulos 2002, Nathan et al. 2003). Instead, the validation of process-based dispersal models has to focus on aspects of seed movement that are both measurable and relevant for long-distance dispersal, such as (for primary wind dispersal) the proportion of seeds that are uplifted and therefore likely to be dispersed over long distances (Nathan et al. 2002a, Tackenberg 2003). The field experiment similarly quantified the proportion of 'fast' seeds: a seed that travelled the 25 m extent of the experimental arena within 22 min (the minimum time up to the first check, Fig. 2.3B) may disperse over 1.6 km in a 24 h period. The field experiment thus validated model predictions at scales relevant for long-distance dispersal. The experimental validation gives confidence in applying the model to a range of species and environmental settings (Nathan & Muller-Landau 2000).

Long-distance dispersal by secondary seed movement

The distance of secondary wind dispersal depends both on the way in which seeds move along the ground, and on the length of the dispersal period (T) during which seeds can move. While the presented model provides, for a given T , a good description of wind-driven seed movement along the ground (Fig. 2.4), it is not immediately clear which factors influence T .

Secondary wind dispersal can be terminated by the germination of seeds, by their permanent entrapment (e.g. through burial under litter or incorporation into the soil) or by the deterioration of the seed's dispersal structure. Since the factors determining these processes vary substantially between environments (Chambers & MacMahon 1994), it is not surprising that literature estimates of T range from a few hours (Greene & Johnson 1997) to several months (Watkinson 1978). In South African fynbos, rainfall appears to trigger all three causes of termination of secondary wind dispersal (A. Rebelo, P. Holmes, J. Vlok, D. LeMaitre, B. van Wilgen, *personal communication*). Since serotinous Proteaceae release their seeds after the mother plant has burnt, T can be estimated as the time between a fire and the first significant rainfall event. By combining seasonal fire frequencies for fynbos (Brown et al. 1991, Richardson et al. 1994) with seasonal rainfall distributions (Zucchini et al. 1992), one

obtains values of T that range from a few days to one year, with a median of 73 days (Appendix 2).

If T is long, interspecific differences in seed traits can strongly affect the distance of secondary wind dispersal. This is illustrated by model simulations for *L. salignum* and *P. repens*, in which I used long-term wind measurements and parameter values typical of fynbos conditions ($T = 73$ days, $z_0 = 0.1$ cm, $\lambda = 0.098$ cm⁻¹ for *P. repens* and $\lambda = 0.060$ cm⁻¹ for *L. salignum*, see Appendix 2). Although roughness length and obstacle encounter rates were higher than in the beach experiment ($z_0 = 0.018$ cm and $\lambda \approx 0.001$ cm⁻¹ for both species), the maximum of 10000 simulated seed dispersal distances was 59 km for *P. repens*, but only 3 m for *L. salignum*. These results support the notion that secondary wind dispersal is a mechanism by which seeds can move long distances (Bond 1988, Higgins et al. 2003a). They also agree with the empirical finding that serotinous Proteaceae differ substantially in their potential for long-distance dispersal by secondary seed movement (Bond 1988).

It should be noted that these simulations probably overestimate the long-distance dispersal of *P. repens* because they assume that environmental conditions (vertical wind profile and obstacle pattern) are spatially homogeneous. In reality, however, a seed dispersing over several kilometres will enter areas where high obstacle encounter rates and/or low wind interception effectively prevent secondary wind dispersal. Such impermeable areas may be boulder fields, steep slopes, rivers and roads, but the ultimate spatial limit to secondary wind dispersal in fynbos is the dense vegetation characteristic of unburnt patches (Bond 1988). Typical fynbos fires burn areas greater than 1 km² (Horne 1981). Hence, fire extent may well limit the secondary wind dispersal of *P. repens*, whereas it is less likely to do so in *L. salignum*. The finding that large fires promote the spread of good secondary wind dispersers, whereas fire size may be irrelevant for poorer dispersers has important implications for conservation management in fynbos (see Chapter 5).

Seed size and the distance of secondary wind dispersal

Secondary wind dispersal in a given environment is promoted by a decrease in lift-off velocity (U_{lift}), a decrease in the obstacle encounter rate (λ) or an increase in wind interception (p) (Fig. 2.7). λ and p increase with horizontal seed diameter (Eq. 2.12) and vertical seed projection (Eq. 2.7), respectively. Because U_{lift} scales with the square root of wing loading (Eq. 2.8), allometric considerations suggest that U_{lift} increases with the square root of a linear measure of seed size (Johnson & Fryer 1992). For a given seed morphology, a change in seed size should thus affect U_{lift} , p , and λ simultaneously.

The relationship between seed size and the distance of secondary wind dispersal has been discussed by Greene & Johnson (1997) who suggested that dispersal distance is maximized for small seeds because U_{lift} decreases with seed size. Small seeds also have lower obstacle encounter rates which should further promote their dispersal (Fig. 2.7). According to the model, however, there is an overwhelming disadvantage of small seed size: seeds with a vertical projection below the roughness length z_0 will not be moved at all (because for them $p = 0$, Eq. 2.7). Therefore, the distance of secondary wind dispersal is predicted to be maximal for some intermediate seed size.

Turbulence may promote the secondary wind dispersal of small seeds, and thus decrease the difference in dispersal distance between small and intermediate seed sizes. However, seed size did increase dispersability in the field experiment: for example, the seeds of *P. neriifolia* are larger and better dispersed than those of *L. salignum*, although their lift-off velocity is higher (Table 2.1). In addition, Bond (1988) tracked seeds of 6 Proteaceae species (4 of which were not included in this study) and observed that the distance of secondary wind dispersal increased with seed size, and Chambers et al. (1991) showed that for eight species in a disturbed alpine environment, the probability of horizontal seed movement increased with seed size on each of five surface types. Thus, for a range of seed sizes (vertical projection between ca. 1 mm and several cm) and environmental conditions, the secondary dispersal distance does appear to increase with seed size.

The unimodal relationship between dispersal distance and seed size predicted by my model differs from the negative correlation predicted by process-based models for primary wind dispersal (e.g. Greene & Johnson 1996). Such a negative correlation is assumed in many ecological and evolutionary models (Ezoe 1998, Levin et al. 2003), and is often regarded as mediating a competition-colonization trade-off (e.g. Crawley 1997). However, this negative correlation does not seem to hold for animal-dispersed plants (e.g. Coomes & Grubb 2003). The presented model predicts that it also will not hold for wind-dispersed plants if seed movement along the ground is important, and the effect of turbulence is small.

Conclusions

Process-based models present the only realistic option for predicting the dispersal of large groups of species. This is for the simple reason that we cannot hope to empirically measure dispersal distances for large numbers of species. Currently, primary seed dispersal by wind is probably the only dispersal syndrome where process-based models can be applied with any

confidence (Nathan et al. 2002a, Tackenberg 2003). By developing and validating a model for secondary wind dispersal, I expand the domain of process-based seed dispersal models.

3 Can evolutionary age, colonization and persistence ability explain to which extent species fill their potential range?

Abstract

How species traits and environmental conditions affect biogeographical dynamics is poorly understood. Here I test whether estimates of a species' evolutionary age, colonization and persistence ability can explain its 'range filling' (the ratio between realized and potential range size). For 37 species of woody plants (Proteaceae), I estimate range filling using atlas data and bioclimatic models, evolutionary age using molecular phylogenies, persistence ability using field-based estimates of longevity, and colonization ability using process-based seed dispersal models, the arrangement of potential habitat, and data on local abundance. I find phylogenetically independent increases of range filling with colonization and persistence ability, but detect no effect of species age. Thus, colonization and local extinction seem to shape Proteaceae range dynamics on ecological timescales. Although these dynamics cannot be described by the simple metapopulation model of Levins, the results of this study provide a new line of evidence for a metapopulation basis of abundance–range size relationships.

3.1 Introduction

How the range size of a species is determined by the interplay of species traits and environmental conditions has interested biologists for well over a century (Darwin 1859, Schimper 1888). Range size has been postulated to correlate with various properties of species and their environments, but the best documented pattern is the positive relationship between local abundance and range size (Brown et al. 1996, Gaston 2003). However, the mechanisms generating this relationship and other patterns of range size variation are poorly understood (Gaston 2003). A mechanistic understanding of range dynamics has to encompass the three proximate determinants of range size: the amount of potentially suitable habitat, the species' ability to colonize this habitat and the rate at which it goes extinct from already colonized patches (Brown et al. 1996). This interplay of habitat suitability, colonization and local extinction is the central focus of metapopulation ecology (Levins 1969, Hanski 1999). Hence, metapopulation theory provides a framework for understanding biogeographical

dynamics (e.g. Carter & Prince 1981, Hanski 1991, Hanski & Gyllenberg 1997, Holt & Keitt 2000).

The biogeographical analogue of metapopulation occupancy (the proportion of occupied habitat patches) is the ratio between realized and potential range size (the latter is the area a species would occupy if it was not limited by dispersal). This ratio has been termed 'range filling' (Svenning & Skov 2004). Metapopulation theory predicts that range filling (and patch occupancy) increases with colonization ability and decreases with rates of local extinction or patch destruction (Levins 1969, Gyllenberg & Hanski 1997). Moreover, if range filling is low at the time of speciation, it should initially increase with the evolutionary age of a species, albeit this initial expansion phase may be short compared to a species' evolutionary lifespan (Webb & Gaston 2000, Gaston 2003).

One way of testing these predictions is a comparative study of interspecific variation in range filling. Such a comparative test requires quantitative information on realized and potential ranges, on rates of colonization and local extinction, and on evolutionary ages. However, various factors make it difficult to compile this comprehensive information for a larger number of species. Data on global geographic distributions are available only for certain groups of species and estimates of potential range and evolutionary age exist only for a small subset of these species. Colonization rates are difficult to quantify because they critically depend on the frequency of long-distance dispersal events, which is hard to measure (Chapter 1, Nathan et al. 2003). Thus, even extensive dispersal data may not be sufficient for detecting a relationship between dispersal ability and range size (Gaston & Blackburn 2003). Rates of local extinction are difficult to quantify because their empirical estimation requires censuses encompassing long time periods or many populations (Hanski 1999). Besides, in many plant species it is difficult to determine whether a population is extinct or persists in the soil seed bank (Freckleton & Watkinson 2002). Due to these methodological problems, there is so far no study that tests how range filling is affected by interspecific differences in evolutionary age, colonization and local extinction.

In the comparative study presented here, I use the exceptional knowledge available for a group of woody plants to test some biogeographical predictions of metapopulation theory. The 37 study species belong to the Proteaceae family and are endemic to the South African Cape Floristic Region (see Chapter 1). Their global geographic distribution is known in exceptional detail (Rebelo 2001), and bioclimatic models estimate their potential ranges (Midgley et al. 2002a). I assess the age of the study species from molecular phylogenies

(Reeves 2001), use field-based estimates of longevity to classify the species into two persistence types that differ in local extinction probability (Bond & Midgley 2001), and estimate colonization ability from process-based seed dispersal models, data on local abundance, and the distribution of potential habitat (Chapter 2, Rebelo 2001, Midgley et al. 2002a, Tackenberg 2003).

Based on this information, I test whether the range filling of a species increases with evolutionary age, colonization and persistence ability. The results of this test suggest that colonization and local extinction shape the range dynamics of the study species on ecological timescales. Moreover, they provide a new line of evidence for a metapopulation basis of abundance–range size relationships.

3.2 Methods

To relate interspecific variation in range filling to evolutionary age, colonization and persistence ability, I use two complementary model types: the classic metapopulation model of Levins (1969) and standard linear models. The Levins model is process-based and therefore represents a specific hypothesis on the mechanisms determining range filling. Linear models are phenomenological, but have a more flexible structure and allow testing for effects of additional variables (local abundance and dispersal ability). Moreover, established statistical methods can be used to correct linear models for phylogenetic dependence between species.

In the following paragraphs, I first expand the Levins model to a form that can be parameterised with empirical information, and explain how I obtained this information for the study species. I then describe the considered versions of the Levins model and the considered linear models, as well as the statistical methods used to fit and compare these models.

Applying the Levins model to range dynamics

The Levins model describes the dynamics of the proportion of occupied habitat patches, p , a measure of a species' range filling. Changes in p depend on the colonization parameter, k , and the rate m at which local populations go extinct

$$\frac{dp}{dt} = kp(1 - p) - mp.$$

For $k > m$ the Levins model has a non-zero equilibrium

$$p^* = 1 - \frac{m}{k} \quad (\text{Eq. 3.1}).$$

In order to apply the Levins model to range dynamics on macroevolutionary timescales, I make two simplifying assumptions: (1) a species has a potential range of N suitable patches that is constant over evolutionary age t , and (2) at the time of speciation each species occupies one patch, so that $p(t=0) = 1/N$. With this initial condition, the time dependent ('dynamic') solution of the Levins model is:

$$p(t) = \frac{k - m}{k + (kN - k - mN)e^{-(k-m)t}} \quad (\text{Eq. 3.2}).$$

This dynamic version of the Levins model results in a pattern of range transformation that has been postulated by various authors: range size increases after speciation before entering a period of stasis (see Webb & Gaston 2000, Gaston 2003).

The Levins model is time-continuous, whereas processes contributing to colonization and local extinction are typically measured in discrete time intervals. I therefore briefly discuss how the colonization and extinction term of the Levins model can be parameterised from time-discrete data. The extinction term of the Levins model describes an exponential decline with rate m . This rate can be estimated from the probability of local extinction, M , measured over time interval Δt (I choose Δt as the interval between two subsequent dispersal events of a population):

$$m = -\ln(1 - M) / \Delta t \quad (\text{Eq. 3.3}).$$

For small values of p , the colonization term of the Levins model describes an exponential increase with rate k . This rate can therefore be estimated by considering a single occupied patch in an otherwise empty habitat network. If K is the expected number of additional patches that the occupied patch can colonize per dispersal event, the rate k is approximately

$$k = \ln(1 + K) / \Delta t \quad (\text{Eq. 3.4}).$$

Note that Δt cancels out in the equilibrium solution of the Levins model (Eq. 3.1) but is retained in the dynamic solution (Eq. 3.2).

K is modelled as $K = X S D E$, where X is local abundance (in individuals per patch), and S is offspring production (defined as the expected number of reproductive offspring an individual produces per dispersal event). D is dispersal ability (in patches per individual), measured as the expected number of suitable patches reached per offspring produced in a patch. E is the

probability that a population establishes in an empty suitable patch that is reached by one or more offspring. Subsequently I refer to the dimensionless product of local abundance and dispersal ability as the 'colonization ability' C of a species ($C = X D$). Since for the study system there are no species-level estimates of S and E , I combine these two dimensionless parameters into a 'demography parameter' G ($G = S E$). Thus,

$$K = G C \quad (\text{Eq. 3.5}).$$

Study system

The 37 study species belong to three genera (*Aulax*, *Leucadendron* and *Protea*) within the Proteaceae. The Proteaceae are a species-rich family of woody plants that is characteristic of the Cape Floristic Region (CFR), and all study species are endemic to the CFR (Rebelo 2001). Their demography and life history are closely linked to fires, which periodically occur in the CFR (Chapter 1). The study species are serotinous (Rebelo 2001): they store their seeds in cones, which open after fire. Effective seed dispersal and recruitment of serotinous Proteaceae only occurs after fires, and the mortality of adult plants in inter-fire intervals is low (Chapter 1, Bond 1988, Bond & van Wilgen 1996). Therefore, the population dynamics of the study species essentially proceeds in discrete time steps, with step length equal to the return interval of fires (Bond & van Wilgen 1996). Twentieth-century fire data suggest that the mean fire interval is 28.6 years (Polakow & Dunne 1999). However, since there are no data on past fire regimes, I treat the time interval Δt as a free parameter when fitting the dynamic prediction of the Levins model (Eq. 3.2).

The study species can be grouped into two distinct persistence types: sprouters can survive fires as adult plants, whereas adult nonsprouters are killed by fire (Fig. 1.2, Bond & van Wilgen 1996, Bond & Midgley 2001, 2003, Rebelo 2001). Sprouters and nonsprouters show pronounced differences in the extinction risk of local populations and appear to differ in offspring production (Bond & van Wilgen 1996, Bond & Midgley 2001, 2003).

Realized and potential range size

The distribution of Proteaceae in the CFR has been mapped extensively by the Protea Atlas Project (Rebelo 2001). From these data I calculated realized range sizes as the number of 1 min x 1 min (ca. 1.55 km x 1.85 km) grid cells in which a species was recorded (Fig. 3.1). Since all study species are endemic to the CFR, this is a measure of the global range size of these species.

The size and spatial distribution of potential ranges have been estimated using bioclimatic models (Midgley et al. 2002a). These models predict the distribution of suitable habitat (Fig. 3.1) from observed occurrences of a species and from five temperature and water availability-related parameters that are assumed to be critical for plant survival (Midgley et al. 2002a). I calculated the potential range size of each species as the number of suitable cells in the CFR. In accordance with Midgley et al. (2002a), I assume that each suitable cell is a patch that can hold one population.

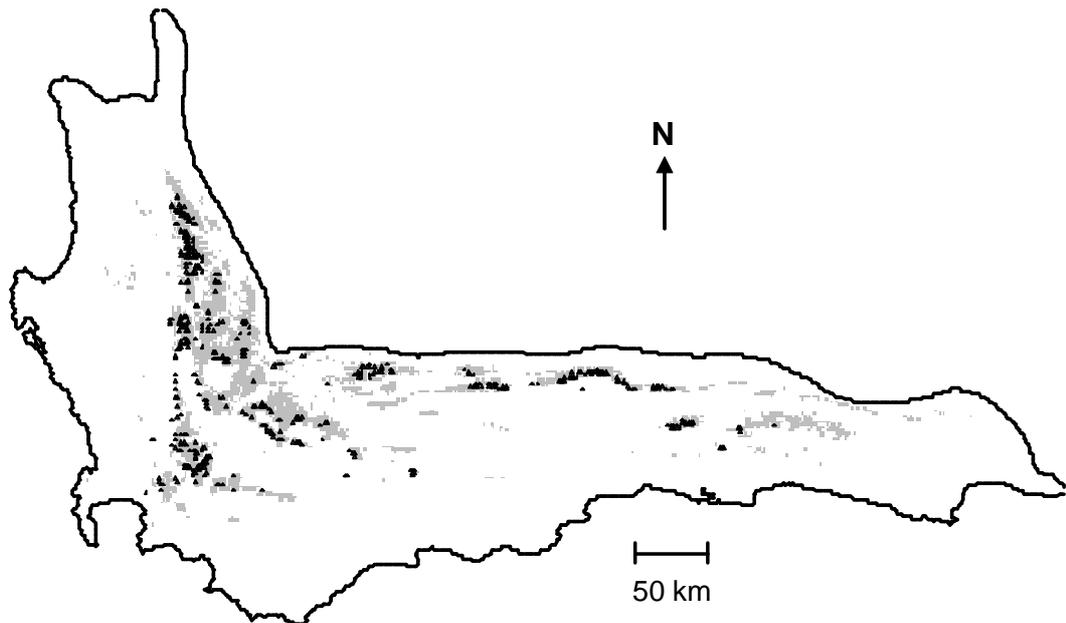


Fig. 3.1 A map of the Cape Floristic Region, South Africa, showing the 1 min x 1min grid cells that are occupied by *Protea scolopendrifolia* (black triangles), and the grid cells that are potentially suitable for this species (grey areas). The realized range is derived from records in the Protea Atlas Database (Rebello 2001), the potentially suitable range from a bioclimatic model (Midgley et al. 2002a).

Local abundance and demography

The Protea Atlas Database (Rebello 2001) contains estimates of the size of 110959 populations of the study species. Population sizes larger than 10 are subdivided into three abundance categories: 'frequent' (11-100 individuals), 'common' (101-10000 individuals) and 'abundant' (>10000 individuals). To estimate the mean local abundance of each species, I assumed an average population size of 55, 5050 and 15000 individuals for these three categories.

In general, the offspring production (S) of sprouters seems to be lower than that of nonsprouters (Bond & Midgley 2003), and the two persistence types may also differ in the probability of population establishment (E). An upper limit of the demography parameter G

(= $S E$) is defined by empirical estimates of S (Bond et al. 1984 report $S \leq 18$, so that $G \leq 18$), but it seems likely that G lies two orders of magnitude lower (a value of $G = 0.18$ implies $E \geq 0.01$). In statistical fits of the Levins model, however, I treat G as a free parameter that may differ between persistence types.

Dispersal

Wind is the predominant vector of long-distance seed movement in serotinous Proteaceae (Chapters 1 and 2, Bond 1988). It transports seeds in a two-phased process: primary seed dispersal through the air is followed by secondary dispersal along the ground surface (Chapter 2, Bond 1988). To estimate dispersal ability, I therefore combined two process-based models for airborne seed movement (Tackenberg 2003) and subsequent movement along the ground surface (Chapter 2). The species-specific parameters contained in these dispersal models describe properties of the mother plant (the distribution of seed release height) and properties of seeds (horizontal seed radius, vertical seed projection and distributions of terminal falling velocity and lift-off velocity). Environmental conditions during dispersal are characterized by the length of the dispersal period, the time series of three-dimensional wind velocities, the aerodynamic roughness length, and by the mean basal radius and mean density of obstacles impeding seed movement along the ground. The methods used to parameterize the dispersal models and estimates of species traits and environmental conditions are given in Appendix 2.

To estimate dispersal ability (D), I used extensive model simulations that incorporated the effect of environmental variability on seed dispersal. For each species, I simulated the dispersal of 10000 seeds in each of 10000 environments (see Appendix 2). In these simulations I assumed that seeds start from random locations within a source cell. For each environment I determined the number of neighbouring cells in which at least one seed was deposited (Fig. 3.2A). Since seed dispersal of serotinous Proteaceae is largely limited by fire extent (Chapter 2, Bond 1988), I only considered seeds deposited within the 24 cells surrounding a source cell (Fig. 3.2A). This is equivalent to a fire extent of ca. 72 km², a typical size of large fynbos fires (Horne 1981). By overlaying the resulting seed shadow to the spatial distribution of potential habitat, I obtained the expected number of suitable cells reached by 10000 seeds starting in a suitable cell (Fig. 3.2B). Averaging these numbers over the 10000 environments and dividing by seed number (10000), yields an estimate of the expected number of suitable cells reached per offspring, D . In this way, I aggregate the spatially explicit information on seed dispersal and habitat configuration into a parameter of the spatially implicit Levins model. Note, however, that some of the spatial information is lost

in the aggregation, since the Levins model assumes that all patches are equally connected to other patches (Hanski 1999).

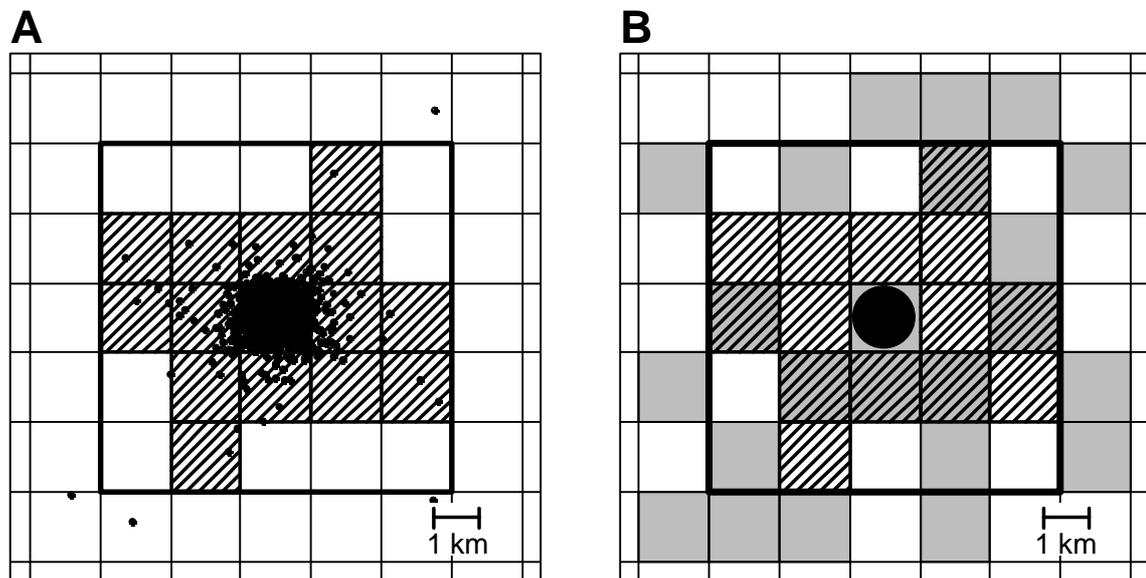


Fig. 3.2 Estimation of a species' dispersal ability D from a process-based seed dispersal model and the spatial distribution of potentially suitable habitat. (A) For each dispersal environment, the dispersal model simulated the post-dispersal locations of 10000 seeds (black dots) starting from the central source cell. The neighbouring cells reached by at least one seed (hatched cells) were determined from this seed shadow. To represent limited fire extent (see text), only the 5x5 cell neighbourhood (delimited by the bold line) was considered. (B) The distribution of reached cells (hatched) was overlaid to the distribution of suitable habitat (grey), yielding the number of suitable cells that can be reached from a given suitable cell (black circle). This procedure was repeated for all suitable cells and all 10000 dispersal environments.

Local extinction and persistence

Nonsprouting Proteaceae form single-aged populations (Bond & van Wilgen 1996) and do not seem to have long-term persistent soil seed banks (Le Maitre & Midgley 1992). Therefore nonsprouters go locally extinct if fire occurs before the onset of reproduction (Bond & van Wilgen 1996). Since most of the nonsprouting study species start reproducing ca. 3 years after a fire, their per-fire probability of local extinction (M) can be roughly estimated from the probability of fire return intervals < 3 years. Twentieth-century fire data (Polakow & Dunne 1999) suggest that the probability of fire return intervals shorter than 3 years is about 0.01, and hence that $M \approx 0.01$ for nonsprouters. Such a simple calculation is not possible for sprouters, but I assume that their local extinction probability is an order of magnitude lower than that of nonsprouters ($M \approx 0.001$). However, since past fire regimes are not known, I consider M to be an unknown parameter in statistical fits of the Levins model.

Species age

To estimate the evolutionary age of the study species, I used 180 equally parsimonious phylogenies that were derived from sequence data for five non-coding regions of the plastid and nuclear genome and from amplified fragment length polymorphism (AFLP) markers (Reeves 2001, G. Reeves *unpublished data*). These phylogenies were converted to chronograms by nonparametric rate smoothing (Sanderson 1997). Species age was then estimated as the length of a species' terminal branch (averaged over these 180 chronograms) (for a discussion of this method see Webb and Gaston 2000). Direct dating of these chronograms is not possible, but a dated phylogeny for the woody plant genus *Phyllica* (Rhamnaceae) indicates that diversification in the CFR began ca. 7-8 million years ago, coincident with severe climatic changes (Richardson et al. 2001). I therefore assumed that the root of all Proteaceae chronograms has an age of 7.5 million years. Note, however, that analyses with linear models are not sensitive to the scaling of evolutionary age.

Statistical models

In statistical fits of the equilibrium Levins model to range filling data, the explanatory variable was colonization ability C , and the estimated parameters were local extinction probability M and demographic parameter G . Fits of the dynamic Levins model additionally included species age t as an explanatory variable, and the time interval between two dispersal events (Δt) as a free parameter. Since sprouters and nonsprouters may differ in M and G , I considered four versions of both the dynamic and the equilibrium model (with and without an effect of persistence type on G and M , respectively, see Table 3.1). These eight versions of the Levins model were fitted with non-linear least squares (R 2.01, R Development Core Team 2004). To account for the fact that range filling is a proportional variable with non-normal error distribution, range filling data and predictions of the Levins model were compared on the arcsine scale (Zar 1999). For comparison of different model versions I used Akaike's An Information Criterion (AIC).

The maximal linear model that I considered predicts arcsine transformed range filling as a function of persistence type (sprouter vs. nonsprouter), and its two-way interactions with colonization ability (C), species age (t), local abundance (X) and dispersal (D). Starting with this maximal model I performed stepwise backward model selection based on AIC (R-function `stepAIC`, Venables & Ripley 2002). The residuals of the selected linear model showed no signs of heteroscedasticity or departure from normality.

The phylogenetic relatedness of species means that they are not completely independent observations for an interspecific comparative analysis (e.g. Paradis & Claude 2002). To control for this phylogenetic dependence, I fitted the selected linear model with generalized estimating equations that consider phylogenetic information (Paradis & Claude 2002, Paradis et al. 2004). I incorporated uncertainty in the phylogenetic estimates by fitting such generalized estimating equations for each of the 180 equally parsimonious phylogenies (Reeves 2001, G. Reeves *unpublished data*).

3.3 Results

The degree to which the study species fill their potential range varies from 0.8% to 45.7% (median: 14%). 45% of the variance in arcsine-transformed range filling is explained by the maximal linear model that includes the effects of colonization ability (C), dispersal ability (D), local abundance (X), species age (t), and the two-way interactions between these variables and persistence type (Table 3.1, Fig. 3.3A).

Table 3.1 Comparison of metapopulation models and linear models for range filling (df: model degrees of freedom; RSS: residual sum of squares; AIC: Akaike's An Information Criterion). Lower AIC values indicate better model performance. The given metapopulation models are the equilibrium predictions of the Levins model with and without an effect of persistence type on demography parameter (G) and local extinction probability (M). The linear models shown are the full model, the model obtained by backward model selection, and the null model (see text for Details).

	Persistence effect		df	RSS*	r^2 *	AIC*
	on G	on M				
<i>Levins models (equilibrium)</i> †						
	yes	yes	5	0.70	0.28	-31.67
	yes	no	4	0.76	0.22	-30.69
	no	yes	4	0.77	0.21	-30.45
	no	no	3	0.79	0.19	-31.35
<i>Linear models</i>						
full model	-	-	11	0.54	0.45	-29.40
selected model	-	-	5	0.56	0.42	-39.88
null model	-	-	2	0.98	0	-25.52

* Model statistics refer to arcsine transformed range filling.

† Statistics for dynamical versions are identical except that df is increased by 1 and AIC is increased by 2.

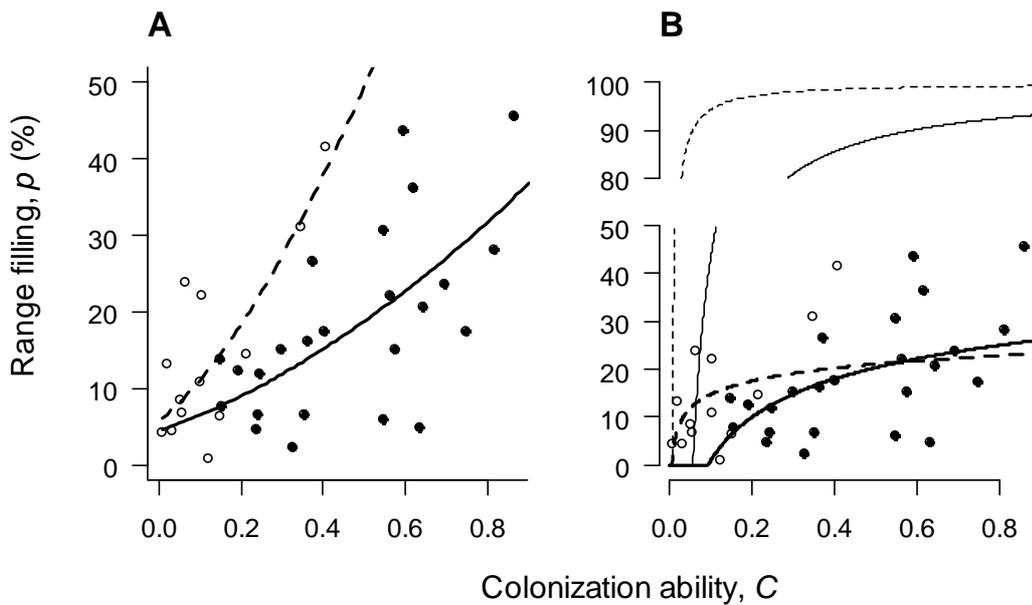


Fig. 3.3 Range filling vs. colonization ability for 37 species of Proteaceae. Range filling (p) is the ratio of realized and potential range size, colonization ability (C) is the dimensionless product of mean local abundance (X) and dispersal ability (D , see Fig. 3.2). Filled points are nonsprouters (low persistence ability); empty points are sprouters (high persistence ability). Solid lines are model predictions for nonsprouters, hatched lines are predictions for sprouters. (A) Predictions of the selected linear model. (B) Predictions of the best Levins model fitted by nonlinear least squares (bold lines), and of a realistically parameterised Levins model (thin lines). Note that the y-axis is scaled differently in the two plots.

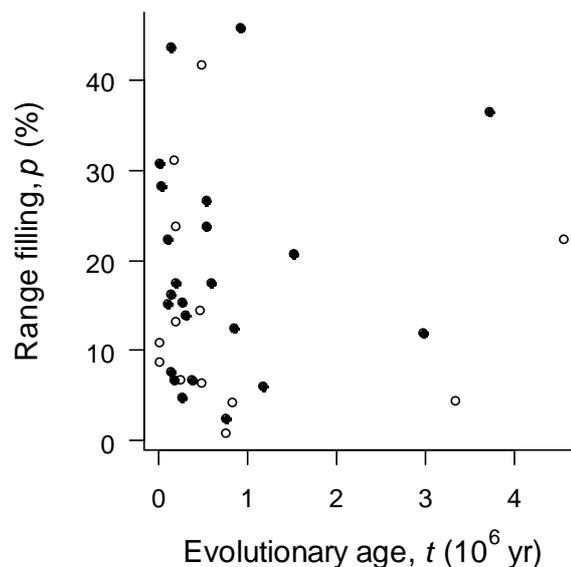


Fig. 3.4 Range filling vs. evolutionary age for 37 species of Proteaceae. Range filling (p) was calculated as the ratio of realized and potential range size, evolutionary age (t) as the mean age estimated from 180 alternative molecular phylogenies (Reeves 2001, G. Reeves *unpublished data*, see Chapter 3.2 for details). Filled points are nonsprouters (low persistence ability); empty points are sprouters (high persistence ability).

Species age (mean values derived from 180 chronograms) showed no obvious relation to range filling (Fig. 3.4). Accordingly, stepwise backward simplification of the maximal model removed species age and its interaction with persistence ability ($P > 0.4$ for main and interaction effect). Model simplification furthermore removed the individual components of colonization ability (local abundance and dispersal ability) and their two-way interactions with persistence type ($P > 0.4$ for all four effects). In contrast, the selected model contains colonization ability itself, and its interaction with persistence type. This model explains 42% of the variance in arcsine-transformed range filling (Table 3.1, Fig. 3.3A).

In analyses controlling for phylogenetic relatedness of species, I found that the interaction between persistence type and colonization ability had a significant effect ($P < 0.05$) on range filling for 174 of the 180 equally parsimonious phylogenies (97%). For 87% of the phylogenies, colonization ability had a positive effect on the range filling of sprouters, and for 75% of the phylogenies it had a positive effect on the range filling of nonsprouters (Table 3.2).

Table 3.2 Results of comparative analyses testing for effects of colonization ability and persistence type on range filling. Comparative analyses were conducted by applying the method of Paradis & Claude (2002) to each of 180 equally parsimonious phylogenies. For the two persistence types (sprouter and nonsprouter) the table reports the number (proportion) of phylogenies for which the estimated colonization effect is positive and negative, respectively.

Persistence type	Colonization effect on range filling	
	Positive	Negative
Sprouter	156 (87%)	24 (13%)
Nonsprouter	135 (75%)	45 (25%)

The effect of persistence type and colonization ability on range filling is also reflected in analyses using the Levins model: amongst the equilibrium versions of the Levins model, the best model (lowest AIC) is the one that allows sprouters and nonsprouters to differ in demographic parameter G and extinction probability M (Table 3.1). The dynamic Levins models that include species age and the additional parameter Δt do not explain more variance than the respective equilibrium models (Table 3.1). The best equilibrium Levins model provides a poorer fit to the range filling data (Fig. 3.3B) than the selected linear model (Fig. 3.3A). Moreover, this Levins model produces parameter estimates that are far from realistic values ($M > 0.999$ and $G > 12000$ for both sprouters and nonsprouters). However, it has to be

noted, that at such high values of G and M , estimates of these two parameters are highly correlated (see Eqs. 3.1, 3.3 and 3.4) and cannot be obtained independent from each other. For this reason, I additionally examined the predictions of the Levins model for realistic parameter values. Fig. 3.3B shows that at realistic extinction probabilities ($M=0.01$ for nonsprouters and $M=0.001$ for sprouters, see Chapter 3.2 - *Local extinction*) the Levins model describes an upper boundary of the observed range filling data if $G = 0.18$ (see Chapter 3.2 - *Local abundance and demography*).

I complemented these analyses of range filling with linear model analyses of range size. In contrast to Webb & Gaston (2000), I found no significant linear effect of evolutionary age on both realized and potential range size (regression of log range size vs. mean age; $P>0.3$ for both range types) and no evidence for a curved relation between range size and age ($P>0.2$ for inclusion of quadratic age terms for both range types). In agreement with many other studies (reviewed by Gaston 2003) I did, however, detect indications of a positive abundance-range size relationship (linear regression of log realized range size vs. log abundance, $F_{1,35}=6.8$, $P=0.01$; estimated slope=0.78). For 73% of the phylogenies, the phylogenetically independent abundance effect was significant ($P<0.05$), and for 57% of the phylogenies this effect was positive.

3.4 Discussion

The studied Proteaceae differ markedly in the degree to which they fill their potential ranges. A substantial proportion of this variation can be explained by the interaction between colonization ability and persistence type (Table 3.1): range filling increases with a species' ability to colonize suitable habitat patches, and this increase is stronger for persistent (sprouter) species that are less prone to local extinction (Fig. 3.3A). For most of the 180 equally parsimonious phylogenies this interaction effect is significant independent of the relatedness between species. However, the estimation of negative colonization effects for some phylogenies (Table 3.2) also demonstrates the importance of incorporating phylogenetic uncertainty into comparative analyses.

Range filling showed no consistent relation to the evolutionary age of a species (Fig. 3.4): the dynamic predictions of the Levins model did not explain more variance than their equilibrium counterparts (Table 3.1). Furthermore, linear models also did not detect a significant effect of evolutionary age on range filling (although they are more flexible than the Levins model and do not assume a specific range filling at speciation or long-term constancy of potential range

sizes). Thus, the extent to which the study species fill their potential ranges does not seem to be limited by initial post-speciation spread processes. Moreover, evolutionary age did not have a significant effect on either realized or potential range size. In summary, the studied Proteaceae neither provide evidence for the 'age and area' hypothesis (Willis 1922), nor do they show signs of range transitions that could be related to taxon cycles (Ricklefs & Bermingham 2002) or similar dynamics (Webb & Gaston 2000). Instead, the presented results suggest that the range dynamics of the study species is determined on ecological rather than macroevolutionary timescales.

The usefulness of metapopulation models for describing plant dynamics at ecological timescales has been the subject of vigorous debate (e.g. Freckleton & Watkinson 2002, 2003, Ehrlén & Eriksson 2003). It has been criticized that many studies claiming the existence of plant metapopulations failed to demonstrate that potential habitat is patchily distributed, that local populations go extinct, and that empty patches are (re-)colonized (Freckleton & Watkinson 2002). In contrast, there is good evidence that the studied Proteaceae have metapopulation dynamics. Bioclimatic models for these species identify habitat that is suitable but unoccupied, and predict that this habitat is patchily distributed (Midgley et al. 2002a, Fig. 3.1). I showed that range filling increases with a species' ability to colonize these patches (Fig. 3.3). Moreover, the study species go locally extinct (Bond & van Wilgen 1996) and range filling is higher for species with lower rates of local extinction (Fig. 3.3). Hence, the biogeographical dynamics of the study species seems to be shaped by the metapopulation processes of patch colonization, extinction and recolonization.

Metapopulation processes also seem to contribute to the positive relationship between abundance and range size of the study species. The linear model analysis detected a positive correlation between range filling and local abundance (results not shown). Such a correlation is predicted by the metapopulation explanation of abundance-range size relationships (Hanski 1991), but not by the alternative niche-based explanation (Brown 1995). Further evidence for the metapopulation explanation comes from the fact that linear model simplification retained colonization ability but removed abundance. Hence, the metapopulation process of colonization is a better predictor of range filling than abundance on its own. On the whole, these analyses of range filling provide a new line of evidence for a metapopulation basis of abundance-range size relationships.

Despite good evidence for metapopulation dynamics in the study species, statistical fits of the Levins model produced unrealistic parameter estimates. At realistic parameter values, the

Levins model predicts non-zero range filling for all study species, but strongly overestimates the range filling of species with high colonization ability (Fig. 3.3B). This discrepancy may in part arise from the imprecise estimation of the considered variables: estimates of seed dispersal, local abundance, realized and potential ranges do involve uncertainty (e.g. Higgins et al. 2003b, Thuiller et al. 2004). However, the discrepancy may also arise because the metapopulation dynamics of the study species are not well described by the simple Levins model.

Of the large number of processes ignored by the Levins model (Hanski 1999, Higgins & Cain 2002), two seem particularly relevant for the range dynamics of Proteaceae. Firstly, the entire geographic range of a species is likely to comprise not just one but several metapopulations with largely uncoupled dynamics (Holt & Keitt 2000). Range filling in such a 'population of metapopulations', will be lower than in a single large metapopulation, especially if some of the component patch networks are small and therefore have a high probability of stochastic metapopulation extinction (e.g. Hanski et al. 1996). Secondly, the distribution of suitable patches is unlikely to remain static for extensive periods of time (as I have assumed so far). In the past centuries the Cape Floristic Region has undergone severe land transformation (Rouget et al. 2003) that resulted in the destruction of habitat for Proteaceae (Midgley et al. 2003, Latimer et al. 2004). Such patch destruction is expected to decrease the patch occupancy of single-species metapopulations (e.g. Hanski et al. 1996). Moreover, the potential ranges of the study species are predicted to shift as a consequence of climate change (Midgley et al. 2002a, 2003). If such directed patch turnover has already occurred in the recent past, it will have decreased range filling (Higgins et al. 2003b). Thus, habitat destruction and climate-induced range shifts are likely to have lowered the range filling of the studied Proteaceae below the levels predicted by the realistically parameterised Levins model (Fig. 3.3B). Due to its simplicity, the Levins model provides a good starting point for the development of process-based models that incorporate these effects.

Finally, the results of this study highlight the importance of colonization for the future survival of the studied Proteaceae. I showed that their range filling increases with the ability to colonize suitable habitat patches (as various authors have hypothesized for other plant species, e.g. Honnay et al. 2002, Svenning & Skov 2004). This suggests that conservation measures should target the determinants of colonization ability: local abundance, seed dispersal, and the arrangement of suitable habitat. In part, this can be achieved by improving habitat quality and optimising reserve design (Cowling et al. 2003). To promote the

colonization ability of the study species, it will furthermore be important to remove dispersal barriers created by farmland, roads, and small fires (Chapter 2, Bond 1988). The maintenance of colonization ability may become even more important under future environmental change: if land transformation and climate change cause increased extinction of populations (Midgley et al. 2002a, Latimer et al. 2004), the importance of colonization will increase relative to the importance of *in situ* persistence (Higgins et al. 2003b). The species most vulnerable to increased rates of environmental change will be those that currently compensate low colonization ability by high persistence ability.

4 Long-distance dispersal need not save species threatened by climate driven range shifts

Abstract

In this study, I assess how climate change and migration ability will influence the range sizes of 26 plant species in the year 2050. These forecasts were made by combining process-based models for seed dispersal and migration, and are based on an existing bioclimatic scenario. For most of the species examined, the range size forecasts were robust, despite substantial uncertainty in predicted migration rates. Although model simulations predict some long-distance dispersal for all study species and use assumptions that upwardly bias estimates of migration ability, the median forecasts suggest that nine of the studied species will lose more than half their current range and that two of these species have a future range size of zero. These findings imply that climate change-integrated conservation strategies should not exclusively rely on the intrinsic migration ability of plants, and that even optimal reserve designs will not be sufficient to protect plant diversity from climate change.

4.1 Introduction

Future climate change may cause many species to disappear from parts, or all, of their current ranges (Parmesan & Yohe 2003, Thomas et al. 2004, Thuiller et al. 2005). Simultaneously, new areas may become climatically suitable and might be colonized by migration (Fig. 4.1). The fate of species facing climate change will thus critically depend on their ability to migrate to their future potential ranges (Thomas et al. 2004, Thuiller et al. 2005). Moreover, the migration ability of plant species will have important consequences for the response of the terrestrial biosphere to global change (Pitelka et al. 1997). Despite the importance of migration ability for projections of species loss and climate-vegetation feedbacks, global models of these processes use only simplistic descriptions of migration (Pitelka et al. 1997, Cramer et al. 2001, Clark et al. 2003, Thomas et al. 2004, Thuiller et al. 2005). Here I show that forecasts of plant migration can be improved by combining advances in process-based models of long distance seed dispersal (Chapter 2, Nathan et al. 2002a, Tackenberg 2003) and population-level migration (Clark et al. 2001a). Specifically, I predict the migration rates and future range sizes that plant species can realize by means of wind-driven seed dispersal.

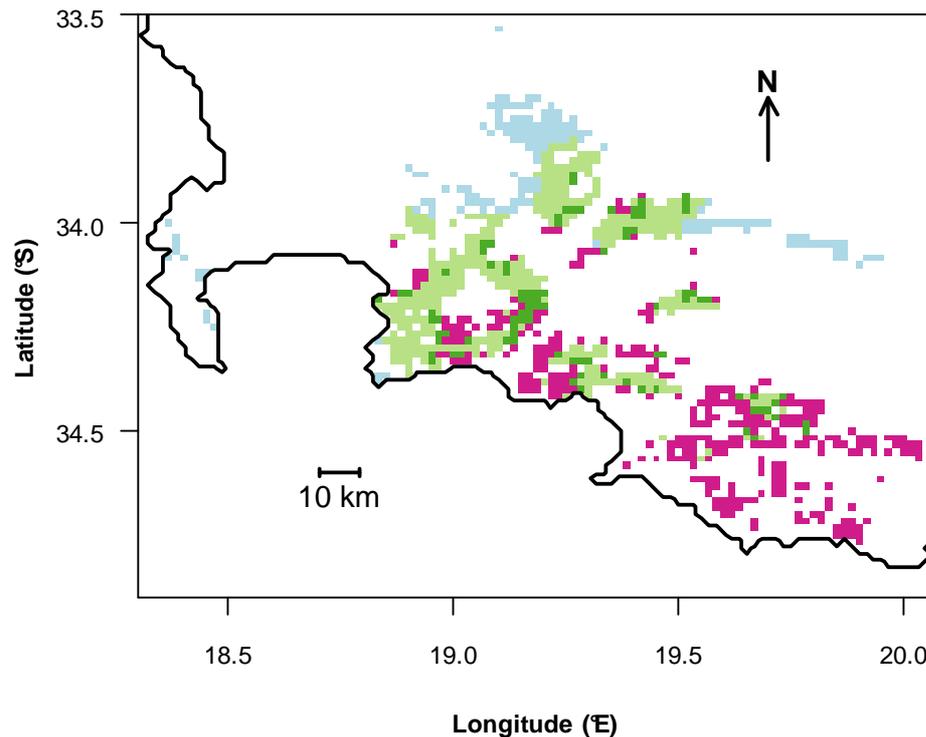


Fig. 4.1 Effects of climate change and migration ability on the future range size of a plant species. The map shows range shift predictions for *Protea longifolia*, a species endemic to the Cape Floristic Region (Rebello 2001, Midgley et al. 2002a). Purple areas are parts of the current range from which *P. longifolia* is predicted to go extinct by 2050 and dark green areas are parts where the species is predicted to persist. For a typical migration simulation, the map furthermore shows parts of the potential range in 2050 that *P. longifolia* can reach within 50 years (light green) and parts it cannot reach (blue).

4.2 Methods

To generate range size forecasts I follow a three-step protocol that describes processes operating at the level of individuals, populations and species, respectively (Appendix 3). Step 1 of the protocol uses the dispersal parameters of a species and parameters describing a range of dispersal environments to simulate dispersal distances of individual seeds. In step 2, the resulting distribution of dispersal distances is combined with data on the population dynamics of species ('demographic parameters') to simulate population-level migration rates (Clark et al. 2001a). In step 3, I use the obtained distribution of migration rates, data on the current location of populations and a scenario for the future location of climatically suitable areas to simulate the future range size of a species (Fig. 4.1). All parameters describing the dispersal and demography of species, as well as the parameters describing dispersal environments are empirically based (see Appendices 2 and 3).

The simulation design I used (Fig. A3.1) considers two major sources of uncertainty in migration forecasts (Clark et al. 2003, Higgins et al. 2003b): parameter uncertainty (arising from incomplete knowledge of species parameters) and inherent uncertainty (caused by stochasticity in the migration process). While parameter uncertainty can be reduced by collection of additional data on species parameters, inherent uncertainty is irreducible. I included parameter uncertainty by repeatedly simulating the protocol described above with species parameters sampled from their empirically derived distributions. Inherent uncertainty was incorporated in these simulations as stochasticity in dispersal environments, in the dispersal of individual seeds, the migration of populations and the expansion of species. To implement this extensive simulation design I simulated, for each species, the dispersal of 10^8 seeds in 10^4 dispersal environments, and generated 5×10^5 population-level migration rates as well as 100 range size forecasts.

The forecasts are based on several assumptions that simplify model structure: (1) dispersal is not limited by areas impermeable to seed movement, (2) all sites encountered during migration are suitable for establishment (i.e. effects of habitat fragmentation or limiting environmental factors are ignored), (3) migrating populations are large, and (4) migration is not limited by Allee effects (e.g. through pollination failure). These assumptions cause an upward bias in predicted migration rates (Kot et al. 1996, Collingham & Huntley 2000, Clark et al. 2001a, Higgins et al. 2003c). Consequently, the forecasts presented here can be interpreted as upper limits of migration abilities.

The plant species to which I apply the forecast protocol are endemic to one of the world's 'biodiversity hotspots', the South African Cape Floristic Region (CFR) (Myers et al. 2000). The CFR harbours an exceptional richness of vascular plants and is predicted to undergo substantial aridification within the next decades (Schulze & Perks 2000). For this study I selected 26 species of nonsprouting Proteaceae (see Chapter 1) that belong to three genera (*Aulax*, *Leucadendron*, *Protea*). Several factors make these species well-suited to study plant migration in response to climate change: (1) their current distribution is known in exceptional detail (the Protea Atlas Database holds 69293 records of the study species, Rebelo 2001); (2)

bioclimatic models¹ predict their potential ranges in 2050 under the climate change scenario HadCM2n (Fig. 4.1, Midgley et al. 2002a); (3) transplant experiments with two of the study species confirm that climate limits recruitment as predicted by these bioclimatic models (Agenbag et al. 2004); (4) the time lag between climate change and consequent population extinction is likely to be short, since the study species have non-overlapping generations that are linked only by recruitment from seeds (Chapter 1, Bond et al. 1995, Rebelo 2001); (5) seeds of the study species are predominantly wind-dispersed (Chapter 1, Bond 1988, Rebelo 2001) and wind dispersal is well described by process-based models (Chapter 2, Nathan et al. 2002a, Tackenberg 2003).

To predict wind dispersal, I combine two of these models that simulate airborne seed movement (Tackenberg 2003) and subsequent movement along the ground surface (Chapter 2). The species-specific parameters contained in these dispersal models (Table A3.1) describe, amongst others, distributions of seed release height and terminal seed falling velocity (Tackenberg 2003). Dispersal environments (Table A2.2) are represented by parameters such as aerodynamic roughness length and high-resolution time series of wind vectors (Tackenberg 2003).

The demographic parameters considered in the migration model are generation time and net reproductive rate (Table A3.2, Clark et al. 2001a). The empirical determination of these parameters is facilitated by the fire-dependent life cycle of the study species (Chapter 1, Bond et al. 1995). Their generation time is equal to the return interval of stand replacing fires (Bond et al. 1995), which can be estimated from long-term fire records. Net reproductive rate can be estimated as the ratio between densities of post-fire recruits and pre-fire adults, since generations do not overlap and interfire mortality of established plants is low (Bond et al. 1995). I used recruit:adult ratios collected in 509 populations of 25 species (Schutte-Vlok, Bond & Cowling, *unpublished data*) to parameterize the migration simulations.

¹ Bioclimatic projections for the study species are comparatively benign (Midgley et al. 2002a): complete range dislocations are expected for only three of the 26 species (12%). In comparison, complete range dislocations are predicted for one third of the total of 330 Proteaceae species for which bioclimatic projections have been made (Midgley et al. 2002a).

4.3 Results

Population-level migration rates generated by the model simulations differ largely between species (Fig. 4.2): median predictions range from 0.2 to 19140 m/yr. Thus, differences in demographic and dispersal parameters can cause large variation in migration rates even within an apparently homogenous group of predominantly wind-dispersed species. For all species there is substantial uncertainty in the predicted migration rates (Fig. 4.2). In most species, a large part of this uncertainty is inherent and hence irreducible². This suggests that there is limited potential for improving migration rate forecasts by collection of additional data on species parameters (Clark et al. 2003, Higgins et al. 2003b).

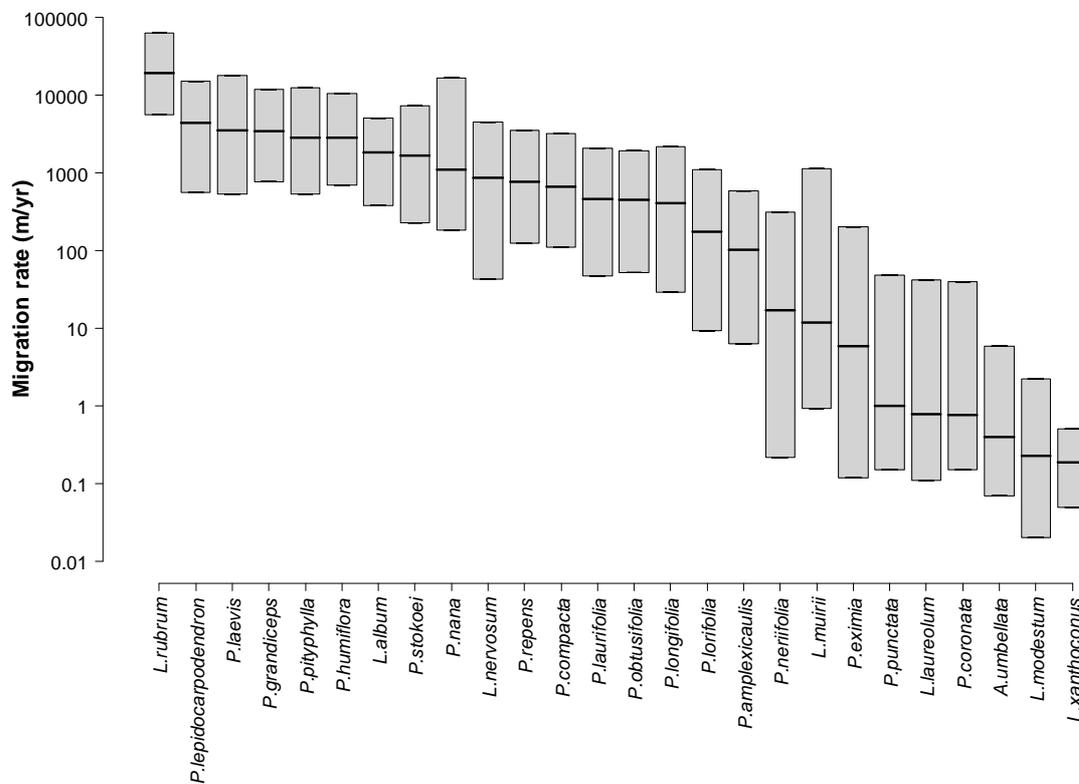


Fig. 4.2 Predicted rates of wind-driven migration for 26 species of South African Proteaceae. Horizontal lines show the median predicted migration rates of a population, and boxes span the range between the 5% and the 95% quantile of migration rate simulations that incorporate parameter and inherent uncertainty. Note that migration rates are plotted on a log scale.

² To quantify the effect of inherent uncertainty, I repeated the migration simulations with species parameters held constant at the respective point estimates (see Appendix 3). For individual species, the resulting 90% confidence intervals comprised 18% to 85% of the respective confidence intervals generated by parameter uncertainty and inherent uncertainty. For 21 of the 26 study species this ratio of confidence interval widths was greater 50%.

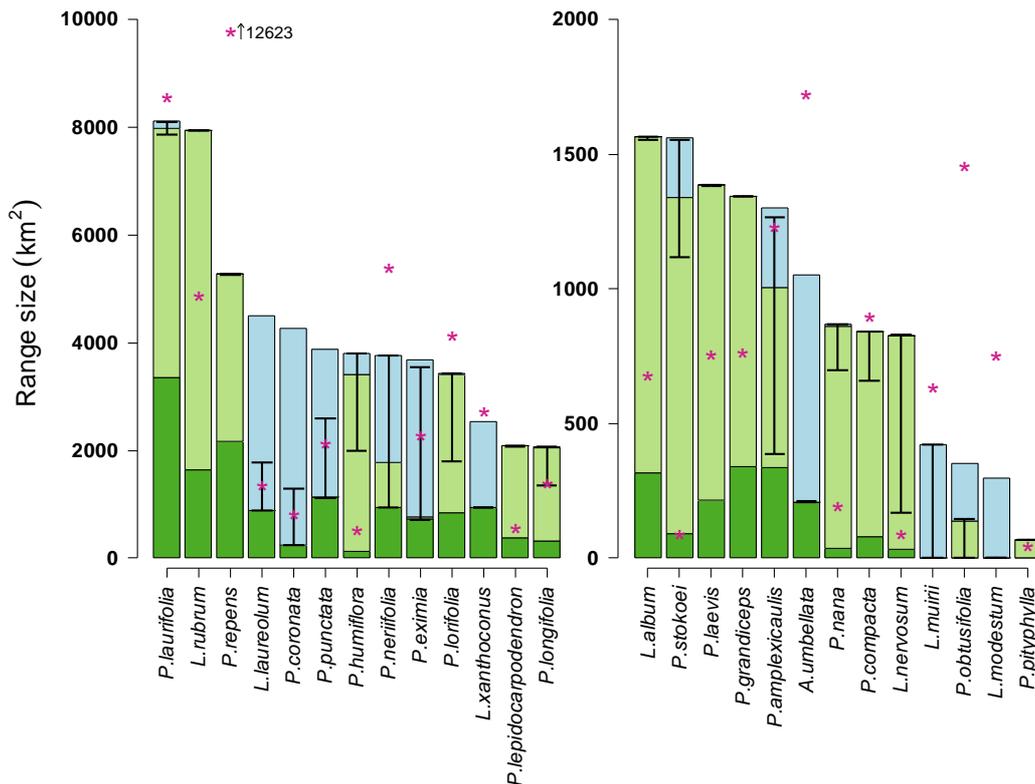


Fig. 4.3 Climate driven changes in range size predicted for 26 species of South African Proteaceae. Overall bar size represents the potential range in 2050 under a bioclimatic scenario (Midgley et al. 2002a). Dark green bars show the proportion of this range already occupied by a species, light green bars the median predicted proportion a species can reach by wind-driven migration within 50 years, and blue bars the median predicted proportion that cannot be reached. Dark and light green bars together indicate median range size forecasts. Whiskers span the range between the 5% and the 95% quantile of range size forecasts that are generated by simulations incorporating parameter and inherent uncertainty. Stars indicate current range size.

The study species do not only differ in migration rates but also in the ability to cover their future potential range. For 11 species, the median forecast range fills more than 95% of the potential range in 2050 (Fig. 4.3). This suggests that these species possess effectively unlimited migration ability as assumed by some dynamic global vegetation models (Pitelka et al. 1997). However, this result has to be treated with caution because the model assumptions upwardly bias migration forecasts. Despite this upward bias, the median forecasts suggest that migration ability limits the future range size of the remaining 15 species. Eight of these are predicted to reach less than 5% of the newly available potential range, which means that they will be largely restricted to those parts of their current range where they can persist over the next 50 years. The limited migration ability of these species will make them particularly vulnerable to climate change. For several species the uncertainty in range size forecasts is remarkably low (Fig. 4.3), despite the large uncertainty in migration rate forecasts (Fig. 4.2).

This is because these species either cover most of their future potential range in most simulation runs or because they mostly fail to reach any new sites. Thus, for a given bioclimatic scenario, future range sizes may be relatively predictable even if migration rate forecasts are uncertain³.

When comparing median range size forecasts to current range sizes, I predict that range size will decline for 15 of the 26 study species and that nine species will have future range sizes that are less than 50% of their current range sizes (Fig. 4.3). Species experiencing such severe range reductions may be 'committed to extinction' (*sensu* Thomas et al. 2004) even though the quantitative link between range reduction and extinction risk is unclear (e.g. Thuiller et al 2004). This lack of clarity appears irrelevant for the two study species that have forecast range sizes of zero – for them extinction seems inevitable.

The predicted range reductions are little affected by parameter and inherent uncertainty. For 10 species the 95% quantile of the forecasts of future range size falls below the current range size (Fig. 4.3). That is, these species experience range losses in $\geq 95\%$ of all simulations. Similarly, five species undergo severe ($>50\%$) range reductions in $\geq 95\%$ of all simulations. One species (*Leucadendron modestum*) has a forecast range size of zero in 98% of all simulations.

4.4 Discussion

The finding that predominantly wind-dispersed species can have limited potential for wind-driven migration is noteworthy with respect to current research on long-distance seed dispersal by wind. Recent studies suggest that wind can transport seeds over long distances even in species lacking apparent adaptations for wind dispersal (Nathan et al. 2002a, Higgins et al. 2003a). The dispersal simulations do not contradict these earlier results, in that the model predicts some long-distance dispersal for all study species (the maximum of the 10^8 seed dispersal distances simulated per species was always greater than 1 km). Yet, these long-distance dispersal events are often too infrequent to generate rapid range expansion in a few generations. This means that even plant species with the potential for occasional long-distance

³ Note that bioclimatic projections are based on models that have their own sets of uncertainty (e.g. Thuiller et al. 2004).

dispersal by wind may migrate too slowly to keep track with climate driven shifts in potential ranges.

The results of this study have important implications for the formulation of climate change-integrated conservation strategies. It has been suggested that such strategies should focus on the establishment of 'migration corridors', networks of conservation areas that facilitate the migration of species to their future potential ranges (Hannah et al. 2002, Cowling et al. 2003, Araujo et al. 2004, Williams et al. *in press*). At best, such corridors will provide conditions similar to the ones assumed in this study: continuous stretches of suitable habitat without barriers to dispersal. The protocol presented here can be used to identify the species with high migration potential for which migration corridors will be crucial. However, the results of this study also suggest that a number of plant species will migrate too slowly, even in migration corridors. These species might only be conserved in nature by assisted introduction to their future potential ranges (Huntley 1991). The practical and ethical challenges of such assisted introductions need to be brought into the forefront of the conservation-climate change debate.

5 General Discussion and Outlook

This final chapter has three parts. First, I summarize the basic methodological and ecological findings of this thesis. I then discuss the implications of these results for the conservation of Cape Proteaceae. Finally, I suggest some directions for further research.

5.1 Ecological and methodological findings

Methodological findings

The studies presented in the previous chapters span a wide range of scales and hierarchical levels: from the movement of individual seeds at short temporal and small spatial scales (Chapter 2) to the biogeographical dynamics of species at large timescales (Chapters 3 and 4).

The upscaling of ecological models is a complex enterprise (Levin 1992). I therefore proceeded in a stepwise manner: In Chapter 2, I developed a process-based model that describes wind-driven seed movement along the ground surface at a high spatial and temporal resolution. This model was tested in a field experiment in which I released seeds that cover the range of seed sizes and seed morphologies typical for serotinous Proteaceae. The experiment successfully validated the model at scales relevant for long-distance dispersal. In Chapter 3, I therefore combined this model with a model for primary seed dispersal by wind, data on local abundance, and a bioclimatic model to calculate the colonization ability of Proteaceae. This colonization variable explained a significant part of the variation in range filling, which suggests that the combined dispersal models predict long-distance dispersal at a scale relevant for biogeographical processes. Hence, in Chapter 4, I used these dispersal predictions together with data on population growth rates and bioclimatic range shift predictions to forecast the future range of Proteaceae species.

The use of process-based models enabled me to incorporate the uncertainty that arises at various hierarchical levels in a transparent way (Fig. A3.1). Similar to Clark et al. (2003), I found that forecasts of population-level migration rates involve a large amount of inherent uncertainty (Fig. 4.2). However, when taking these forecasts one step further and comparing migration rate forecasts to predictions of bioclimatic range shifts, I obtained a different result: forecasts of future range size (Fig. 4.3) are less uncertain than predicted migration rates. Thus, informative forecasts on the future distribution of plant species can be made despite the uncertainty inherent in migration rate forecasts.

The results of this thesis suggest that process-based models can help to understand and predict the spatial dynamics of plants at various scales. I hope that the presented models for seed dispersal, colonization and range dynamics will be useful additions to the toolbox of ecologists.

Ecological findings

Model simulations suggest that the joint action of primary and secondary wind dispersal may occasionally disperse the seeds of all study species over more than 1 km (Chapter 4). This agrees with simulations of primary wind dispersal which found that even species with traits unfavourable for airborne seed movement may occasionally be dispersed over long distances (Nathan et al. 2002a, Higgins et al. 2003a, Tackenberg et al. 2003). However, the *amount* of long-distance dispersal differs strongly between the Proteaceae species studied here (Chapter 2, Table A2.1). Again, this is in accordance with other studies that demonstrated pronounced interspecific differences in the quantity of long-distance seed dispersal (Nathan et al. 2002a, Tackenberg et al. 2003). These results have implications for the ecological and evolutionary view of seed dispersal. Models for the evolution of dispersal distance typically assume that dispersal kernels are completely determined by species traits (e.g. Ezoe 1998, Hovestadt et al. 2001, Rousset & Gandon 2002). In contrast, parts of the ecological literature tend to downplay the importance of species traits for long-distance dispersal, while emphasizing the importance of chance events (Pitelka et al. 1997). Truth is likely to lie in between these extremes points of view: species-traits affect the probability that rare environmental conditions lead to long-distance seed dispersal.

Interspecific differences are also manifest in the predicted ability of the study species to colonize suitable habitat patches (Fig. 3.3) and in their migration ability (Fig. 4.2). The predicted colonization ability, together with a measure of persistence ability, explains variation in the biogeographical range filling of Proteaceae (Fig. 3.3). This suggests that the study species have metapopulation-like range dynamics characterized by the colonization of habitat patches and the local extinction of populations. In contrast, range filling is not influenced by a measure of the study species' evolutionary age (Fig. 3.4). This might indicate that occupation of the potential range proceeds at a faster pace than speciation. The forecast migration rates of many study species are nevertheless lower than the rapid rates at which their potential ranges are predicted to be shifted by climate change (Chapter 4). The future range size of these species is thus likely to be limited by their migration ability (Fig. 4.3). In summary, the findings of this thesis suggest that colonization and migration limit the large-

scale distribution of Proteaceae. This lends support to the revived appreciation of long-distance dispersal as an important determinant of biogeographical distributions (Muñoz et al. 2004, de Queiroz 2005).

5.2 Implications for conservation

Colonization and migration are predicted to be important for the future viability of Proteaceae in the face of habitat destruction and climate change (Chapters 3 and 4). In the following, I discuss how conservation strategies could target the determinants of colonization and migration: offspring production, generation time, long-distance seed dispersal, and the spatial arrangement of suitable habitat. In particular, I propose a simple conceptual model (Fig. 5.1) that describes how the viability of the study species depends on fire regime - the standard tool of conservation management in fynbos.

A decrease in generation time increases the number of generations per unit time, thereby increasing colonization and migration rates (Clark et al. 2001a). Since the generation time of the study species is determined by fire interval (Fig. 5.1A; Chapters 3 and 4), a shortening of fire intervals could promote colonization and migration. However, fire interval also affects reproductive rates (Fig. 5.1A): if fire intervals are very short, populations cannot produce canopy seed banks (Fig. 1.1). As fire interval increases, seed reserves will build up until they reach a saturation level. Finally, if fire intervals are too long, seed reserves may collapse due to the senescence of populations (Bond 1980). Thus, since fire interval simultaneously affects generation time and reproductive rate, its effect on the viability of serotinous Proteaceae is unlikely to be monotonous (Fig. 5.1A).

Long-distance seed dispersal can be promoted by removing dispersal barriers. As discussed in Chapter 2, an increase in fire size will promote the long-distance dispersal of at least some serotinous Proteaceae (Fig. 5.1B). However, large fires also carry a risk for Proteaceae with metapopulation-like dynamics: large fires will synchronize the dynamics of local populations (Fig. 5.1B), which may decrease metapopulation viability (e.g. Johst & Drechsler 2003). Due to the opposing effects of fire size on long-distance dispersal and population asynchrony, one might therefore expect a unimodal relationship between the metapopulation viability of Proteaceae and fire size (Fig. 5.1B).

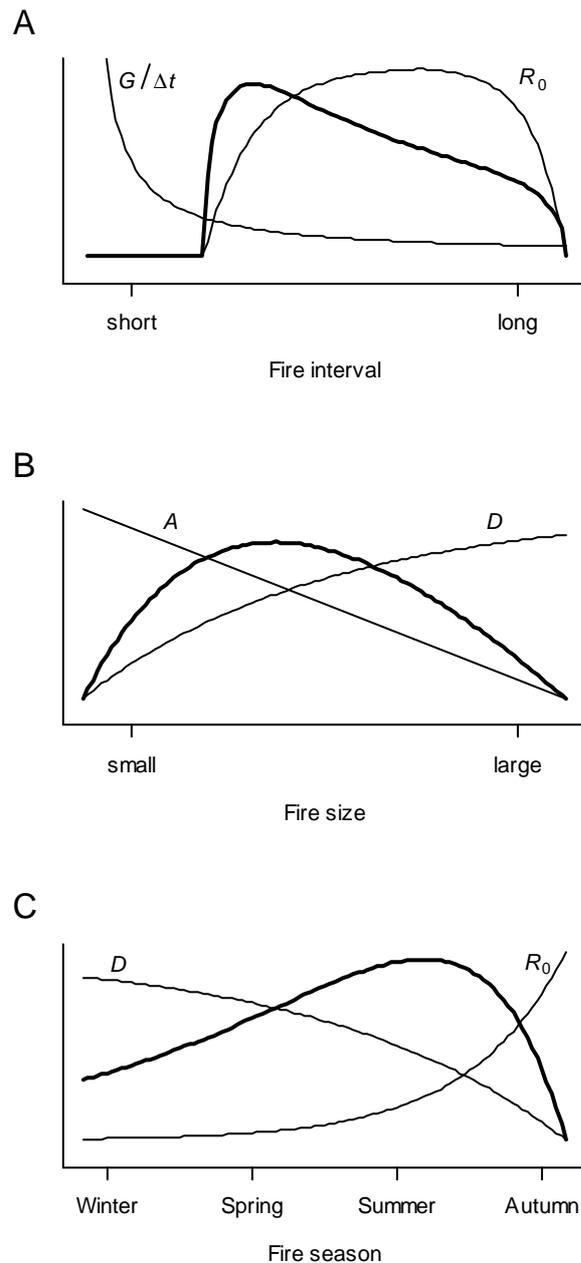


Fig. 5.1. A conceptual model for the effect of fire regime on the viability of serotinous Proteaceae that face habitat destruction and climate change (see text for details). The model considers three aspects of fire regime: the interval, size and season of fires. Each of these aspects has opposing effects on two demographic quantities (thin curves) that positively affect the viability of species. The bold curves indicate the qualitative response of viability to changes in these quantities. A) Effects of fire interval on reproductive rate (R_0) and the number of generations per unit time ($G/\Delta t$) B) Effects of fire size on the scale of long-distance dispersal (D) and the asynchrony in local population dynamics (A). C) Effects of fire season on reproductive rate (R_0) and the scale of long-distance dispersal (D).

The scale of dispersal also depends on the length of the period between fire and the first effective rainfall (see Chapter 2). This period will, on average, be longest for fires occurring

in late winter. Thus, long-distance seed dispersal could be promoted by burning in the right season (Fig. 5.1C). However, fire season simultaneously affects reproductive rates (Fig. 5.1C): it has been shown that local recruitment decreases with the time between fire and rainfall (Bond 1984). This may in part result from increased dispersal (Bond et al. 1984), but it also seems due to rodent predation (Bond 1984) and seed decay (Musil et al. 1998).

Clearly, colonization and migration ability of Proteaceae can also be promoted by measures other than fire management. For instance, the offspring production of sparse populations can be enhanced by increasing population density. This may be achieved by the clearing of alien plants that invade the habitat of certain Proteaceae species (Latimer et al. 2004). Moreover, the reproductive output of Proteaceae populations could be increased by decreasing levels of wildflower harvesting (Maze & Bond 1996). In fact, colonization and migration may be more sensitive to wildflower harvesting than local recruitment. This is because the frequency of long-distance dispersal events is expected to increase monotonously with offspring production (Clark et al. 2001a), whereas local recruitment may reach saturation or may even decline as offspring production increases. Thus, the relatively high levels of wildflower harvesting that seem sustainable at the local scale (85% inflorescence removal for *Protea neriifolia*, Maze & Bond 1996), may lower colonization and migration rates to critical levels if applied at large scales. All measures targeting population size and offspring production should acknowledge that the relationship between these quantities is not necessarily monotonous: the reproduction of some Proteaceae species shows overcompensating density dependence, so that high levels of recruitment in one generation result in low recruitment in the next generation (Bond et al. 1995).

The spatial arrangement of suitable habitat affects colonization and migration ability. The viability of species may therefore be increased by conservation planning that optimizes the amount of suitable habitat and its spatial arrangement. To facilitate migration in response to climate change, the Cape Action Plan for the Environment (CAPE) explicitly considers the protection of upland-lowland and macroclimatic gradients (Cowling et al. 2003). More specifically, efforts have been made at optimizing reserve design with the aim of creating corridors for the future migration of Proteaceae (Williams et al. *in press*, see Chapter 4).

In summary, the colonization and migration of Proteaceae can be enhanced by improving local habitat quality, and optimizing fire management and reserve design. The use of these conventional conservation tools may be optimized by means of simulation models that are more detailed than the ones presented in this thesis. However, even under optimal conditions

some Proteaceae species may migrate too slowly to escape climate-driven extinction (Chapter 4). It seems thus necessary to develop novel conservation strategies. One of these strategies would be the assisted introduction of species to their future potential ranges (Chapter 4). Such introductions might be feasible for the Cape Proteaceae that are endangered by climate change. Still, with more than 6000 plant species endemic to the Cape Floristic Region (CFR), it appears difficult to identify and translocate all the species that are critically endangered by climate change. Given these prospects, it seems appropriate that a program is currently underway that aims at storing parts of the CFR's genetic richness in a 'DNA bank' (Savolainen & Reeves 2004). An effective measure to preserve the Cape Flora in the wild would be to reduce rates of anthropogenic climate change (Thomas et al. 2004).

5.3 Directions for further research

Here, I will sketch some directions for further research that go beyond the research perspectives proposed in the previous chapters.

Functional ecology of seed dispersal

Comparative analyses of process-based dispersal simulations can be used to address a number of questions on the functional ecology of seed dispersal: (1) To what extent is the proportion of seeds dispersed over a certain distance controlled by species traits as compared to environmental conditions? (2) Does the amount of control exerted by species traits differ between short- and long-distance dispersal? (3) Which species traits are important for determining different properties of the dispersal kernel (such as the median and the 99% quantile of dispersal distance)? (4) How flexible are dispersal kernels, e.g. how strong is the interspecific correlation between different properties of the dispersal kernel? Various authors have recently used process-based seed dispersal models to examine aspects of these questions (e.g. Nathan et al. 2001, 2002a, Tackenberg 2003, Tackenberg et al. 2003, Higgins et al. 2003a, Soons et al. 2004). However, these studies typically used either a limited set of species or a limited set of environmental conditions. Results of the extensive full-factorial simulation design used in Chapter 3 (37 Proteaceae species x 10000 environmental conditions, see Appendix 2) can be used to approach the above questions in a more comprehensive fashion.

Process-based models can also help to unravel the genetic basis of seed dispersal. They identify phenotypic determinants of seed dispersal, the basis of which can then be examined in (quantitative) genetic studies. The current knowledge on the genetic determination of dispersal-relevant traits is still limited: Imbert (2001) measured the narrow-sense heritability

of the proportion of *Crepis sancta* achenes that have a pappus and are presumably well-dispersed. In a more detailed analysis, Liljegren et al. (2000, 2004) elucidated the molecular regulatory networks underlying pod opening in *Arabidopsis thaliana*. By combining such genetic and molecular biological information with organism-level dispersal models, it may ultimately be possible to construct process-based models that describe how a plant's genotype affects seed dispersal. These models would for instance be useful for better understanding the evolutionary dynamics of seed dispersal (see next paragraph).

Evolution of seed dispersal

A number of models have recently been developed to describe the evolution of dispersal distance as a function of life history, population dynamics, and environmental factors (Ezoe 1998, Savill & Hogeweg 1998, Hovestadt et al. 2001, Murrell et al. 2002, Rousset & Gandon 2002, Muller-Landau et al. 2003). So far, the predictions of these models are largely untested. The sprouter-nonsprouter dichotomy in serotinous Proteaceae offers an opportunity for testing some of these predictions by means of comparative analyses: molecular phylogenies suggest that sprouting species have repeatedly evolved from nonsprouting ancestors (Reeves 2001, G. Reeves *unpublished data*), and the two strategies differ in life history and population dynamics (see Chapter 1). Evolutionary models predict that these differences should lead to increased long-distance seed dispersal in nonsprouters. First, by spreading its offspring over a larger area, a nonsprouter plant reduces the probability that all offspring are killed by a fire before they have become reproductively mature (Wheelan 1995). A nonsprouter genotype with such a spatial risk-spreading strategy should have lower variance in reproductive success, which may increase its geometric mean growth rate and thereby its long-term fitness (Venable & Brown 1988). Second, higher rates of population extinction should select for increased dispersal ability in nonsprouters (Comins et al. 1980, Gandon & Michalakis 2001). As a result of both selective pressures, the seeds of nonsprouters should have a higher probability of long-distance dispersal than the seeds of sprouters - given that long-distance seed dispersal has a heritable component and carries some costs. This prediction can be tested with a comparative analysis of the simulation results presented in Chapter 3. If data were available on the reproductive success of individual species, it could furthermore be tested whether long-distance dispersal indeed has reproductive costs.

Macroevolutionary dynamics

Quantitative descriptions of long-distance seed dispersal could serve to test models on the macroevolutionary dynamics of plants, and the serotinous Proteaceae may be a suitable

system for such tests. Cowling & Lamont (1998) proposed a simple model for the macroevolutionary dynamics of Proteaceae: they suggested that speciation occurs through the geographical isolation of populations, so that speciation rates are higher in lineages with non-overlapping generations (nonsprouters) and limited gene flow through seed and pollen dispersal. A simple test for the effect of seed dispersal on speciation would be to compare speciation rates (estimated from molecular phylogenies) between lineages with poorly-dispersed (winged) seeds and lineages with well-dispersed (plumed or parachute) seeds (see Chapter 2). More sophisticated analyses could be conducted with the help of statistical methods that reconstruct ancestral character states (Harvey & Pagel 1991): such analyses could not only be used to test how the scale of seed dispersal affects speciation, they would also be useful for estimating effects of persistence type and the scale of pollen dispersal (the latter would require quantitative data on interspecific variation in pollen dispersal distance). Finally, such analyses could serve to assess how the shape of the seed dispersal kernel influences speciation: species with exponentially bounded kernels spread as continuous fronts, whereas species with fat-tailed kernels form outlying populations that remain isolated until they eventually coalesce with the spreading front (e.g. Clark et al. 1998). Therefore, lineages with fat-tailed seed dispersal kernels may be more likely to form isolated populations, and may consequently have higher speciation rates.

Extending the domain of models for demographic processes

Process-based models for seed dispersal and population spread have proven useful for predicting the wind-driven migration of plant species in response to climate change (Chapter 4). These and similar models could also be applied profitably to forecast the invasion of alien plant species (Hastings et al. 2005) and the spread of genetically modified crops (Klein et al. 2003).

At present, the application of process-based models for seed dispersal is limited by their restricted domain: models exist only for seed movement by wind and to some extent for seed movement by animals (see Chapters 1 and 2). This limited domain could be extended by developing a model for seed dispersal by water (*nautochory*), a process similar to secondary seed dispersal by wind. It may also be feasible to model some aspects of seed dispersal by human activities (*hemerochory*): for instance, dispersal through motor vehicles could be predicted by combining measures of seed retention on vehicles with information on traffic flow. Furthermore, it will be necessary to formulate models for the joint action of several

dispersal processes (a first step towards this goal has been taken by the integration of primary and secondary wind dispersal in Chapters 3 and 4).

A promising direction is the combination of process-based dispersal models that describe immigration and emigration with process-based models for the two other demographic processes: birth and death. Recently developed models use a description of fundamental metabolic processes to predict - amongst others - rates of individual mortality and population growth (Brown et al. 2004). Moreover, models are now available that describe the local dynamics of plant populations from a representation of physiological processes (Reineking et al. *in press*). These models might for instance be useful for deriving process-based rather than phenomenological descriptions of bioclimatic potential ranges.

Generic process-based models for demographic processes offer the possibility to forecast the effects of environmental change for large numbers of species (see Chapter 4). This requires that measurements of the relevant traits are available for many species. Some of these traits are already included in large functional trait databases that are currently being established (Bonn et al. 2000, Knevel et al. 2003, Poschlod et al. 2003, Kühn et al. 2004). Ideally, the establishment of these trait databases should go hand in hand with the development of process-based demographic models. This will guarantee that the databases provide the optimal empirical basis for forecasting the demographic response of species to environmental change. To maximize the value of trait databases for conservation, it will furthermore be important to ensure that they cover the geographical regions and the species that are most affected by environmental changes.

Conclusions

The results of this thesis add to a functional understanding of seed dispersal and biogeography, help to predict the future range dynamics of plants, and may prove useful for other areas of ecology, evolutionary and conservation biology. In a broader context, models of demographic processes that are based on first principles of biology, chemistry and physics hold promise for the future development of ecology (Brown et al. 2004). Clearly, the applicability of these generic models will be limited: they inevitably ignore much of the individuality that is the 'most striking, intrinsic and inspiring characteristic' of populations and communities (Simberloff 1980). Still, to protect this diversity in the face of environmental change, it is important to make ecological forecasts (Clark et al. 2001b), and generic demographic models may prove to be essential for this task.

Summary

Seed dispersal affects the rate at which plant populations colonize unoccupied habitat, and the speed at which plant species migrate. In this thesis, I aim (1) to better understand seed dispersal processes, (2) to investigate the consequences of dispersal for the geographical range dynamics of plants, and (3) to forecast the future range size of plant species under climate change. To this end, I developed process-based models for seed dispersal, colonization and range dynamics. These models were parameterised with empirical data for serotinous Proteaceae endemic to the Cape Floristic Region (South Africa). The study species are woody plants with a canopy seed bank and predominantly wind-dispersed seeds.

To better understand the seed dispersal of these species, I formulated a process-based model for secondary seed dispersal by wind (the wind-driven movement of seeds along the ground surface). This model was successfully validated in a field experiment in which I released seeds of 7 species that cover the range of seed sizes and seed morphologies typical of the studied Proteaceae. The model predicts a unimodal relationship between dispersal distance and seed size. This indicates that the ecological consequences of secondary seed dispersal by wind are qualitatively different from those of airborne seed movement.

To investigate the consequences of seed dispersal for large-scale range dynamics, I derived a model of habitat colonization that links seed dispersal models to data on local abundance and habitat arrangement. This model was used to estimate the colonization ability of 37 Proteaceae species. I found that the extent to which these species fill their potential ranges increases with colonization ability, decreases with the extinction probability of local populations, and is not related to a species' evolutionary age. This suggests that colonization and local extinction shape the range dynamics of the study species on ecological timescales.

To forecast how climate change and migration ability will influence the range sizes of 26 Proteaceae species in the year 2050, I combined process-based models for seed dispersal and migration with an existing bioclimatic scenario. Model simulations indicate that informative forecasts of future range size can be made despite the substantial uncertainty inherent in forecasts of population-level migration rates. Although the simulations predict some long-distance dispersal for all study species and use assumptions that upwardly bias migration estimates, they forecast that several species will experience severe range losses or go extinct. This suggests that climate change-integrated conservation strategies should not exclusively rely on the intrinsic migration ability of plants. I nevertheless identify conservation measures by which colonization and migration rates of Proteaceae may be enhanced.

The results of this thesis add to a functional understanding of seed dispersal and biogeography, help to predict the future range dynamics of plants, and may prove useful for other areas of ecology, evolutionary and conservation biology.

Zusammenfassung

Die Ausbreitung von Diasporen beeinflusst die Rate, mit der Pflanzenpopulationen unbesiedeltes Habitat kolonisieren, und die Geschwindigkeit, mit der Pflanzenarten wandern. Ziel der vorliegenden Arbeit ist es, (1) Ausbreitungsprozesse von Diasporen besser zu verstehen, (2) die Konsequenzen von Ausbreitung für die Arealodynamik von Pflanzen zu untersuchen und (3) die zukünftige Arealgröße von Pflanzenarten unter Klimawandel vorherzusagen. Zu diesem Zweck entwickelte ich prozessbasierte Modelle für Diasporenausbreitung, Habitatkolonisierung und Arealodynamik. Parametrisiert wurden diese Modelle mit empirischen Daten für serotine Proteaceen-Arten - endemische Gehölzpflanzen der südafrikanischen Capensis-Region, die eine Kronensamenbank haben und deren Diasporen vorwiegend windausgebreitet sind.

Zum besseren Verständnis der Diasporenausbreitung dieser Arten entwickelte ich ein prozessbasiertes Modell für Chamaechorie (die windgetriebene Diasporenbewegung entlang der Bodenoberfläche). Erfolgreich validiert wurde dieses Modell in einem Freilandexperiment mit 7 Arten, deren Diasporen die für die untersuchten Proteaceen typische Variationsbreite in Diasporengröße und -morphologie abdecken. Das Modell sagt eine unimodale Beziehung zwischen Ausbreitungsdistanz und Diasporengröße vorher. Damit zeigt es, dass Chamaechorie sich in ihren ökologischen Konsequenzen qualitativ von der windgetriebenen Diasporenausbreitung durch die Luft unterscheidet.

Zur Untersuchung der Auswirkungen von Diasporenausbreitung auf die Arealodynamik von Proteaceen formulierte ich ein Modell für Habitatkolonisierung, das Ausbreitungsmodelle mit Daten zur Populationsgröße und Habitatverteilung verknüpft. Mit diesem Modell schätzte ich die Kolonisierungsfähigkeit von 37 Proteaceen-Arten. Der Anteil des potentiellen Areals, den diese Arten ausfüllen, steigt mit der Kolonisierungsfähigkeit, sinkt mit der Aussterbewahrscheinlichkeit lokaler Populationen und zeigt keine Beziehung zum evolutionären Alter der Arten. Demnach scheinen Kolonisierung und lokales Aussterben die Arealodynamik der untersuchten Arten auf ökologischen Zeitskalen zu prägen.

Zur Vorhersage der Effekte von Klimawandel und Wanderungsfähigkeit auf die Arealgrößen von 26 Proteaceen-Arten im Jahr 2050 entwickelte ich ein prozessbasiertes Modell, das Modelle für Diasporenausbreitung und Populationswanderung mit einem existierenden bioklimatischen Szenario kombiniert. Die Modellsimulationen zeigen, dass - trotz erheblicher Unsicherheit in den vorhergesagten Wanderungsraten von Populationen - informative Vorhersagen über zukünftige Arealgrößen möglich sind. Das Modell simuliert für alle Arten Fernausbreitung und trifft Annahmen, die Wanderungsraten überschätzen. Trotzdem sagt es vorher, dass mehrere Arten starke Arealverluste erleiden oder gar aussterben werden. Dieses Ergebnis legt nahe, dass Strategien zum Naturschutz unter Klimawandel nicht ausschließlich

auf das intrinsische Wanderungsvermögen von Pflanzen setzen sollten. Ich zeige dennoch Schutzmassnahmen auf, mit denen Kolonisierungs- und Wanderungsraten von Proteaceen erhöht werden können.

Die Ergebnisse dieser Arbeit tragen zum funktionellen Verständnis von Diasporenausbreitung und Biogeographie bei, helfen die zukünftige Arealdynamik von Pflanzen vorherzusagen und könnten sich als nützlich für andere Gebiete der Ökologie, Evolutions- und Naturschutzbiologie erweisen.

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Appendix 1 - Aggregation of the process-based model for secondary seed dispersal by wind

The aggregated model version describes secondary wind dispersal as a process alternating between periods of seed movement between obstacles and periods of seed retention at obstacles. Probability distributions are used to describe the length of movement periods (M) and retention periods (R). In the following I derive distributions of M and R , and show how they can be used to efficiently simulate secondary wind dispersal. In deriving distributions of movement and retention periods, I assume that obstacles have a circular basal area and are arranged randomly. Note, however, that for arbitrary obstacle shapes and patterns, empirical density functions of M and R can be generated by means of simulations.

Distribution of movement times

For a seed with lift-off velocity U_{lift} , I consider only those intervals in which the wind velocity is high enough to move the seed in the absence of obstacles. T_{pot} , the total time in which seed movement is possible, is the sum of these intervals, and \vec{U}_{pot} , the set of wind vectors considered, is

$$\vec{U}_{pot} = \left\{ \vec{U}(t) \mid |\vec{U}(t)| \geq U_{lift} \right\}.$$

The duration of an individual movement period, m , can be approximated by

$$m \approx \frac{l}{\bar{v}} \quad (\text{Eq. A1.1}),$$

where \bar{v} is the average speed of seed movement (approximated as the mean of $|\vec{U}_{pot}|$) and l is the free path between two consecutively encountered obstacles. To derive a parametric distribution of l , I assume that (i) while moving between two obstacles the seed follows a straight line, (ii) obstacles have circular basal areas with diameter o , (iii) l is typically much larger than o , and (iv) the obstacle centres have a completely spatially random distribution with density d . Under these assumptions, the number of obstacles a seed encounters per unit distance is described by a Poisson process. l is thus equivalent to the waiting time between two successive events of a Poisson process which follows an exponential distribution. The rate of this exponential, λ , is the obstacle encounter rate, that is the expected number of obstacles a seed encounters while moving along a line of unit length. A seed with diameter s can interfere with those obstacles that have centres less than $(o + s)/2$ away from either side of the seed centre's trajectory. If $p(o)$ is the PDF of o , the obstacle encounter rate is

$$\lambda = d \int_0^{\infty} (o + s) p(o) do = d(\bar{o} + s),$$

where \bar{o} is the mean diameter of obstacles.

Distribution of retention times

Imagine seeds positioned randomly relative to a circular obstacle. Those seeds that encounter the obstacle at time t_0 are deposited along the windward half of the obstacle perimeter. I describe the location of a seed on this semicircle by the angle ω between the obstacle tangent in that location and the wind direction $\alpha(t_0)$ ($0 \leq \omega \leq \pi$, compare Fig. 2.1A). The cumulative density function (CDF) of initial seed locations at the obstacle is then

$$O(\omega) = \frac{1}{2} - \frac{1}{2} \cos(\omega) \quad \text{for } 0 \leq \omega \leq \pi \quad (\text{Eq. A1.2}).$$

According to Eq. 2.10, a seed situated at an obstacle is moved if

$$\left| \vec{U}_{pot}(t_0 + t) \right| \geq \frac{U_{lift}}{|\cos(\omega + \alpha(t_0) - \alpha(t_0 + t))|} = \frac{U_{lift}}{|\cos(\omega - \Delta\alpha(t, t_0))|},$$

where $\Delta\alpha(t, t_0) = \alpha(t_0 + t) - \alpha(t_0)$ is the change in wind direction between t_0 and $t_0 + t$. It follows, that in any time step, a seed is retained by the obstacle if its location ω fulfils $\omega_{min} < \omega < \omega_{max}$ with

$$\omega_{min}(t, t_0) = \Delta\alpha(t, t_0) + \frac{\pi}{2} - \arcsin\left(\frac{U_{lift}}{|\vec{U}_{pot}(t_0 + t)|}\right) \quad \text{and}$$

$$\omega_{max}(t, t_0) = \Delta\alpha(t, t_0) + \frac{\pi}{2} + \arcsin\left(\frac{U_{lift}}{|\vec{U}_{pot}(t_0 + t)|}\right).$$

From time series of $\omega_{min}(t, t_0)$ and $\omega_{max}(t, t_0)$ one can calculate $\theta_{min}(t, t_0)$ and $\theta_{max}(t, t_0)$, the lower and the upper limit of the locations of those seeds deposited in t_0 that are still retained at $t_0 + t$. θ_{min} is the cumulative maximum of ω_{min} , and θ_{max} is the cumulative minimum of ω_{max} . With Eq. A1.2 one can calculate the probability that a seed deposited at an obstacle at time t_0 is still retained after a period of length t

$$P_{t_0}(r \geq t) = O(\theta_{max}(t, t_0)) - O(\theta_{min}(t, t_0)).$$

The empirical CDF of retention time is thus

$$P_{t_0}(r < t) = 1 - P_{t_0}(r \geq t).$$

I estimate a CDF of R that is representative of U_{lift} and \vec{U}_{pot} by averaging these empirical CDFs for a larger number of start times t_0 (I used 100 equally spaced start times). In the presented simulations, this average CDF was typically fitted very well by a Gamma distribution (fitting was done by nonlinear least squares, R package NLS). I used this parametric description to simulate r if $T_{pot} > 10$ s. Otherwise, r was simulated directly from the average CDF.

Simulating secondary wind dispersal

Let $T_{sum}(k)$ be the time elapsed after k pairs of movement and retention periods, and let $T_{move}(k)$ be the sum of these movement periods:

$$T_{sum}(k+1) = T_{sum}(k) + m + r \quad (\text{Eq. A1.3}), \text{ and}$$

$$T_{move}(k+1) = T_{move}(k) + m \quad (\text{Eq. A1.4}),$$

where m and r are random numbers drawn from M and R , $T_{sum}(0) = 0$, $T_{move}(0) = 0$. The number of complete pairs of movement and retention periods the seed undergoes in the period T_{pot} is:

$$n = \max\{k \mid T_{sum}(k) < T_{pot}\}$$

and the total movement time T_M is calculated as

$$T_M = T_{move}(n) + \frac{m}{m+r} (T_{pot} - T_{sum}(n)).$$

To simulate seed position after secondary wind dispersal, I assume that \vec{U}_{pot} has a bivariate normal distribution $\vec{U}_{pot} = N^2(\vec{\mu}, \vec{\sigma})$, and that temporal autocorrelation in \vec{U}_{pot} can be ignored. $\vec{\mu}$ and $\vec{\sigma}$ are vectors describing the means and standard deviations of the x - and y -components of \vec{U}_{pot} . A seed's post-dispersal location can then be simulated by taking the sum of $T_M / \Delta t$ samples from $N^2(\vec{\mu}, \vec{\sigma})$:

$$\vec{S} = \Delta t \sum_{T_M / \Delta t} N^2(\vec{\mu}, \vec{\sigma}) = N^2(T_M \vec{\mu}, \sqrt{\Delta t T_M} \vec{\sigma}).$$

Implementation of the aggregated model version

While the model aggregation developed above markedly increases simulation speed, simulations can still be time-consuming if U_{lift} varies between seeds and if the expected number of obstacle encounters, $E(n) = T_{pot} / [E(M) + E(R)]$, is large. To increase simulation efficiency, I use two approximations. The first approximation is that seeds with variable U_{lift}

are divided into discrete categories and the mid values of these categories are used for model simulation (for the presented simulations I set category width to 10 cm/s).

The second approximation efficiently estimates T_{sum} and T_M by considering the sums of Δk movement and retention periods, $m^*(\Delta k)$ and $r^*(\Delta k)$, rather than the individual periods.

From Eqs. A1.3 and A1.4 it follows that

$$T_{sum}(k + \Delta k) = T_{sum}(k) + m^*(\Delta k) + r^*(\Delta k) \text{ and}$$

$$T_{move}(k + \Delta k) = T_{move}(k) + m^*(\Delta k).$$

Under the parametric descriptions of seed movement and seed retention derived above, $m^*(\Delta k)$ and $r^*(\Delta k)$ are themselves described by parametric distributions. Eq. A1.1 leads to $m^*(\Delta k) = l^*(\Delta k) / \bar{v}$, where $l^*(\Delta k)$ is the movement distance between Δk obstacles. If obstacle encounters are described by a Poisson process, then $l^*(\Delta k)$ follows a Gamma distribution with rate λ and shape parameter Δk . Moreover, if retention period, r , is Gamma distributed with rate a and shape b , then $m^*(\Delta k)$ follows a Gamma distribution with rate a and shape Δkb .

To efficiently simulate n for a large number of seeds, I use the following algorithm: Initially, k is set to 0. k is then increased by 2^i for $i = i_{max}, i_{max}-1, \dots, 0$ if $T_{sum}(k + 2^i) < T_{pot}$ for all seeds (i_{max} is calculated as the smallest integer greater $\log_2 E(n)$). Subsequently, k is increased for each seed by a constant c as long as $T_{sum}(k + c) < T_{pot}$. k_{final} , the final value of k , is then used to approximate the total movement time of each seed as

$$T_M = T_{move}(k_{final}) + \frac{m^*(c)}{m^*(c) + r^*(c)} (T_{pot} - T_{sum}(k_{final})).$$

Appendix 2 - Simulation of seed dispersal by wind and estimates of parameters relevant for the range dynamics of serotinous Proteaceae

This appendix describes the design used to simulate seed dispersal by wind for serotinous Proteaceae and the methods used to obtain parameters describing dispersal-relevant species traits and dispersal environments. For the 37 species studied in Chapter 3, Table A2.1 gives dispersal traits and predicted dispersal abilities, and summarizes the available information on persistence type, local abundance, evolutionary age, realized and potential range size.

Simulation design

The two-phased wind dispersal of Proteaceae seeds (Bond 1988) was simulated by combining a process-based model for airborne seed dispersal (Tackenberg 2003) with a process-based model for seed movement along the ground (Chapter 2). Environmental conditions considered in both models are the vertical wind velocity profile (described by a logarithmic profile with aerodynamic roughness length, z_0) and high-resolution time series of wind vectors. The model for seed movement along the ground furthermore describes the effects of obstacles to seed movement (characterized by mean density and mean basal radius of obstacles) and the effect of processes terminating seed movement (characterized by the length of the dispersal period). Dispersal parameters considered for airborne movement describe distributions of seed release height and terminal seed falling velocity (Tackenberg 2003); parameters affecting seed dispersal along the ground are vertical seed projection, horizontal seed radius and the distribution of seed lift-off velocity (Chapter 2). All dispersal simulations assumed that topography is level. To incorporate variation in dispersal environments, I generated 10000 random sets of dispersal parameters. In each dispersal environment I simulated the dispersal distances of 10^4 seeds that are released at random times during the first day of the dispersal period.

Species-specific dispersal parameters

Species parameters relevant for the dispersal models (Table A2.1) describe properties of the mother plant (the distribution of seed release height) and properties of seeds (horizontal seed radius, vertical seed projection and distributions of terminal falling velocity and lift-off velocity) (Tackenberg 2003, Chapter 2). All seed parameters used in Chapters 3 and 4 were determined for 50 filled (presumably fertile) seeds per species. Note that seed parameters

reported in Table 2.1 are based on measurements of both fertile and infertile seeds. I measured terminal seed falling velocities with a laser-triggered system (Askew et al. 1997). Lift-off velocity was measured in a low-speed wind tunnel at the University of Cape Town (see Chapter 2). To describe between-seed variation in terminal velocity and lift-off velocity I fitted lognormal distributions to the respective data for each species. Vertical seed projection was measured with a digital calliper and horizontal seed radius with a digital scanner and the KS 300 Imaging System 3.0 (Carl Zeiss Vision GmbH, Oberkochen, Germany) (see Chapter 2). Seed release height was modelled with a triangular distribution with constant minimum h_{min} and maximum h_{max} . h_{max} was taken to be the maximum plant height given in Rebelo (2001), and h_{min} was determined as the minimum seed release height measured for ≥ 5 individuals per species. The modal release height, h_{mode} , was taken as $0.7 h_{max}$.

Dispersal environments

Environmental conditions during dispersal are characterized by the length of the dispersal period, the time series of three-dimensional wind velocities, the aerodynamic roughness length, and by the mean basal radius and mean density of obstacles impeding seed movement along the ground (Table A2.2, Tackenberg 2003, Chapter 2). Dispersal period was estimated as the time between a fire (which stimulates seed release) and the first rainfall event sufficient for germination (assumed to be >25 mm rain within two days, Chapter 2). Fire dates were drawn from a joint empirical frequency distribution of area burnt per month in four regions within the CFR (Brown et al. 1991, Richardson et al. 1994). Rainfall sequences of 1000 years were generated with a rainfall model (Zucchini et al. 1992) for 12 locations distributed across the CFR. For each fire date I randomly selected a year from these rainfall sequences and determined the dispersal period as the number of days until the next rainfall event sufficient for germination. Time series of 10 Hz three-dimensional wind velocity components were measured with triaxial sonic anemometers (USA-1, METEK GmbH, Elmshorn, Germany) at two sites (Grootbos: $34^{\circ}35'S$, $19^{\circ}20'E$; Jonaskop: $33^{\circ}56'S$, $19^{\circ}31'E$) for a total of 206 days. For a dispersal period of x days, I selected wind data by sampling x times with replacement from the daily wind data sets recorded in the respective season. Season was defined as the months that include the dispersal period plus the preceding and the following month. I ordered the sampled wind data according to the month of recording. Roughness length values were sampled from data compiled by Garratt (1992) for open soil and sparse vegetation. Mean densities and mean basal radii of obstacles were sampled from empirical data for eight types of obstacle patterns (F. Schurr, *unpublished data*).

Table A2.1 Range sizes (realized and potential), range filling, persistence type (S: sprouter, N: nonsprouter), mean local abundance, dispersal-relevant traits, simulated dispersal ability, and evolutionary age for 37 species of Proteaceae.

Species	Range size (min x min cells)		Range filling, p (%)	Persist ence	Abundance, X (ind./cell)*	Seed release height (cm)‡			Terminal velocity (m/s)§		Lift-off velocity (m/s)§		Vertical seed projection (cm)	Horizontal seed radius (cm)	Dispersal ability D (10^4 cells/ind.)	Species age, t (10^6 yr)¶
	realized*	potential†				h_{mode}	h_{min}	h_{max}	mean	sd	mean	sd				
<i>Aulax pallasia</i>	326	3046	11	S	408	210	39	300	2.4	0.3	2.6	0.7	0.8	0.7	2.5	0.02
<i>A. umbellata</i>	525	1712	31	N	2473	175	7	250	2.8	0.3	3.4	0.9	0.6	0.5	2.2	0.02
<i>Leucadendron laureolum</i>	423	2788	15	N	2778	140	15	200	2.6	0.3	4.8	3.0	0.3	0.4	2.1	0.27
<i>L. rubrum</i>	1461	7094	21	N	1591	175	9	250	1.1	0.2	2.0	0.5	2.1	1.6	4.1	1.53
<i>L. salignum</i>	5617	13484	42	S	1855	140	24	200	2.5	0.3	4.9	3.1	0.3	0.4	2.2	0.5
<i>L. xanthoconus</i>	851	1862	46	N	4029	140	108	200	3.6	0.3	5.5	2.0	0.2	0.3	2.1	0.92
<i>Protea acaulos</i>	837	3525	24	S	817	2	1	4	2.8	0.3	4.1	1.9	0.7	0.8	0.8	0.19
<i>P. amplexicaulis</i>	362	2628	14	N	1019	28	0	40	2.5	0.3	3.6	1.2	1.1	1.0	1.5	0.3
<i>P. angustata</i>	33	792	4	S	81	24	1	35	3.3	0.6	6.6	3.3	0.8	0.7	0.9	0.84
<i>P. aspera</i>	206	2411	9	S	772	5	0	7	2.9	0.3	3.6	1.3	0.7	1.6	0.7	0.02
<i>P. coronata</i>	263	5540	5	N	2624	350	82	500	3.3	0.4	6.6	2.6	0.9	0.8	2.4	0.27
<i>P. compacta</i>	278	987	28	N	2761	245	16	350	3.4	0.6	4.6	2.4	1.0	1.7	2.9	0.03
<i>P. eximia</i>	688	4550	15	N	1419	175	45	250	3.2	0.5	4.6	2.1	0.6	1.4	2.1	0.1
<i>P. grandiceps</i>	210	3198	7	N	927	140	19	200	2.1	0.3	2.7	1.2	1.2	0.8	2.6	0.19
<i>P. humiflora</i>	159	6881	2	N	1133	70	0	100	1.9	0.2	2.5	1.1	1.1	1.0	2.9	0.76
<i>P. inopina</i>	4	92	4	S	568	70	27	100	4.6	0.2	7.3	2.6	1.0	2.3	0.5	3.35
<i>P. intonsa</i>	90	1423	6	S	817	21	0	30	1.8	0.2	1.7	0.4	1.0	0.7	1.8	0.48
<i>P. laevis</i>	240	1937	12	N	1059	4	3	6	2.5	0.5	3.8	2.3	0.9	1.0	1.8	0.86
<i>P. lanceolata</i>	126	1908	7	N	1401	280	25	400	3.4	0.5	6.1	3.6	0.7	0.6	2.5	0.39
<i>P. laurifolia</i>	2592	7137	36	N	1747	560	80	800	2.7	0.4	3.9	2.0	0.8	2.1	3.5	3.74

Table A2.1 (cont.)

Species	Range size (min x min cells)		Range filling, p (%)	Persist ence	Abundance, X (ind./cell)*	Seed release height (cm)‡			Terminal velocity (m/s)§		Lift-off velocity (m/s)§		Vertical seed projection (cm)	Horizontal seed radius (cm)	Dispersal ability D (10^{-4} cells/ind.)	Species age, t (10^6 yr)¶
	realized*	potential†				h_{mode}	h_{min}	h_{max}	mean	sd	mean	sd				
<i>P. lepidocarpodendron</i>	184	1060	17	N	2508	210	8	300	3.1	0.6	4.9	3.4	1.1	2.1	3	0.59
<i>P. longifolia</i>	425	1597	27	N	1613	105	22	150	3.6	0.4	4.6	2.6	0.8	2.3	2.3	0.54
<i>P. lorea</i>	30	3956	1	S	1349	7	2	10	2.3	0.1	3.0	0.8	1.1	2.6	0.9	0.76
<i>P. lorifolia</i>	1284	7341	17	N	1325	350	1	500	2.6	0.3	4.4	2.5	0.6	1.7	3	0.21
<i>P. magnifica</i>	378	3207	12	N	1531	175	0	250	4.8	0.3	5.6	2.1	0.8	2.0	1.6	2.99
<i>P. nana</i>	63	1067	6	N	2156	91	50	130	1.6	0.3	1.9	0.6	0.9	0.9	2.5	1.18
<i>P. nerifolia</i>	1609	7242	22	N	2218	210	11	300	2.8	0.4	4.1	2.0	0.6	2.2	2.5	0.1
<i>P. nitida</i>	2560	8244	31	S	1329	700	100	1000	3.4	0.3	6.8	2.5	1.2	1.2	2.6	0.19
<i>P. obtusifolia</i>	435	1837	24	N	2160	280	24	400	2.7	0.4	2.8	1.1	0.8	2.0	3.2	0.54
<i>P. pityphylla</i>	19	413	5	N	1021	70	20	100	1.7	0.3	2.2	1.0	0.8	0.6	2.3	0.27
<i>P. punctata</i>	635	3918	16	N	1661	280	30	400	3.0	0.4	5.6	2.4	0.7	0.9	2.2	0.15
<i>P. repens</i>	3835	8783	44	N	1822	315	24	450	2.4	0.3	4.4	1.9	2.0	2.5	3.3	0.15
<i>P. scabra</i>	459	2069	22	S	1105	3	1	4	3.0	0.7	5.3	2.5	1.1	1.0	1	4.57
<i>P. scorzonerifolia</i>	96	1441	7	S	625	7	2	10	2.9	0.5	4.3	2.0	0.7	2.3	0.9	0.24
<i>P. speciosa</i>	320	2429	13	S	107	84	14	120	2.6	0.5	3.3	0.9	1.2	2.4	1.8	0.21
<i>P. scolopendrifolia</i>	456	3165	14	S	968	7	0	10	2.9	0.3	4.0	2.5	0.9	1.3	2.2	0.47
<i>P. stokoei</i>	30	398	8	N	613	140	43	200	2.5	0.4	4.2	2.4	1.0	2.4	2.5	0.15

* from the Protea Atlas Database (Rebelo 2001)

† from Midgley et al. 2002a

‡ described by triangular distributions

§ described by lognormal distributions

¶ mean age estimated from 180 equally parsimonious phylogenies (Reeves 2001, G. Reeves *unpublished data*);

age of root assumed to be 7.5×10^6 yr

Table A2.2 Environmental parameters used for seed dispersal simulations. The table reports medians and ranges (in brackets) of 10000 sets of environmental parameters that describe variation between dispersal environments. No statistics are displayed for the time series of wind velocities because this parameter is high-dimensional.

Parameter	
Aerodynamic roughness length, z_0 (cm)	1.0 (0.1-3.9)
Length of dispersal period (d)	73 (1-362)
Mean basal obstacle radius (cm)	2.6 (2.4-3.3)
Mean obstacle density (m^{-2})	108 (59-127)

Appendix 3 - Simulating population-level migration rates and future range sizes of serotinous Proteaceae

Fig. A3.1 depicts the three-step protocol to forecast plant migration and the simulation design used to quantify the effect of parameter and inherent uncertainty. To quantify effects of inherent uncertainty, I used the same simulation design but held species parameters constant at their point estimates (cf. Clark et al. 2003). All simulations and statistical analyses were carried out in R 1.8.1 (R Development Core Team 2004) with computer-intensive subroutines coded in C. In the following, I first explain how I implemented the individual steps of the protocol. Subsequently, I describe how the distributions of species parameters and environmental conditions used in the simulations were obtained from empirical data for the 26 Proteaceae species studied in Chapter 4.

Step 1: Simulating dispersal distance

To simulate seed dispersal of Proteaceae, I used the simulation design described in Appendix 2. However, in simulations incorporating the effect of parameter uncertainty I first selected 100 sets of dispersal parameters, and then selected 100 dispersal environments for each set of dispersal parameters (Fig. A3.1). I used these 100 dispersal environments to represent a range of dispersal environments to which populations of the study species could be exposed during migration. In each dispersal environment I simulated the dispersal distances of 10^4 seeds that are released at random times during the first day of the dispersal period. For each set of dispersal parameters these dispersal simulations were then combined into one composite distribution that represents dispersal distances in a variety of environments (Fig. A3.1). The method applied in Step 2 simulates migration rates from marginal distributions of dispersal distance in one direction (Clark et al. 2001a). Each composite dispersal distribution was therefore transformed into a marginal distribution by first assigning a random dispersal direction to each dispersal distance and then projecting the obtained two-dimensional coordinates to a randomly orientated axis.

Step 2: Simulating population-level migration rate

I used the furthest-forward method (Clark et al. 2001a) to simulate population-level migration rates from marginal distributions of dispersal distance and from demographic parameters. To this end I first derived $p(x)$, an empirical probability density function of the distance a population can move in one generation (following equations 1-4 in Clark et al. 2001a). $p(x)$ can be calculated from the composite dispersal distribution, the net reproductive rate (R_0), and

from the size and density of a population. I assume that each population consists of 10000 individuals spaced at 0.1 m.

The distance over which a population migrates within the forecast period (50 years) was simulated as the sum of n random samples from $p(x)$. n is the number of dispersal events a population experiences within 50 years. To obtain random values of n , I generated random sequences of dispersal events by drawing intervals between successive events from the distribution of generation time (see *Species parameters*). The simulated migration distance was then divided by 50 years to calculate the migration rate.

In summary, the demographic parameters affecting migration rates are R_0 and the distribution of generation time. I incorporated uncertainty in estimates of these parameters by combining each of the 100 composite dispersal distributions with a different set of demographic parameters (Fig. A3.1). For each of these 100 combinations I simulated 5000 migration rates to include inherent uncertainty (Fig. A3.1).

Step 3: Simulating future range size

I simulated future range sizes of a species using the distributions of population-level migration rates, data on the species' current distribution and a scenario for the location of its potential range in 2050. Potential ranges of the study species are predicted at a resolution of 1 min x 1 min, i.e. each cell covers approximately 1.5 km x 1.8 km (Midgley et al. 2002a). I determined the current distribution of a species by assuming that each cell, for which the Protea Atlas Database (Rebelo 2001) holds at least one record, contains a population of 10000 individuals (compare Step 2 above). This is an optimistic estimate of actual population densities, especially for rarer species and for populations at range margins (Rebelo 2001).

For each of the 100 distributions of population-level migration rates I simulated one future range size (Fig. A3.1). These simulations incorporated inherent uncertainty by assigning a randomly sampled migration rate to each current population. A species' future range size was then calculated as the sum of all cells that are climatically suitable in 2050 and can be reached within 50 years by at least one population.

Species parameters

The species parameters relevant for the dispersal models and the methods used to estimate these parameters are described in Appendix 2. I used the maximum likelihood estimates of seed parameters as the point estimates for each species (Table A3.1). Distributions of seed parameters about these point estimates (Table A3.1) were generated by nonparametric

bootstrapping. The modal release height, h_{mode} , was assumed to follow a uniform random distribution ranging from $0.6 h_{max}$ to $0.8 h_{max}$ and the point estimate was taken as $0.7 h_{max}$ (Table A3.1).

The demographic parameters considered are mean net reproductive rate and the distribution of generation time (Table A3.2). I estimated mean net reproductive rate, R_0 , from recruit:adult ratios (Bond et al. 1984) determined in 509 populations of 25 wind-dispersed *Aulax*, *Leucadendron* or *Protea* species with non-overlapping generations (Schutte-Vlok, Bond & Cowling, *unpublished data*). Since recruit:adult ratios differed significantly between the three genera studied (Kruskal-Wallis rank sum test, $\chi^2_{2df} = 11.2$, $P < 0.01$), I used the genus means as point estimates of R_0 . Distributions of R_0 for each genus were generated by nonparametric bootstrapping. The distribution of generation time was sampled from six Weibull distributions of fire return intervals parameterized for different regions within the CFR (LeMaitre 1998, Polakow & Dunne 1999). Point estimates of parameters describing the distribution of generation time were determined as the parameters of the Weibull distribution that minimizes the summed Kullback-Leibler distance to these six distributions.

Dispersal environments

The estimation of parameters describing dispersal environments and the protocol used to obtain distributions of these parameters are described in Appendix 2 (see Table A2.2).

Table A3.1 Dispersal parameters of 26 Proteaceae species endemic to the Cape Floristic Region. The table reports point estimates and ranges (in brackets) of 100 sets of dispersal parameters representing parameter uncertainty.

Species	Seed release height (cm)*			Terminal velocity (m/s)†		Lift-off velocity (m/s) †		Vertical seed projection (cm)	Horizontal seed radius (cm)
	mode	min	Max	mean	sd	mean	sd		
<i>Aulax umbellata</i>	175 (150-200)	7	250	2.8 (2.6-2.9)	0.3 (0.3-0.4)	3.4 (3.2-3.9)	0.9 (0.7-1.2)	0.6 (0.6-0.7)	0.5 (0.5-0.5)
<i>Leucadendron album</i>	140 (121-159)	25	200	2.5 (2.4-2.6)	0.3 (0.3-0.4)	2.3 (2-2.6)	0.8 (0.6-0.9)	1.1 (1.1-1.2)	0.7 (0.6-0.7)
<i>L. laureolum</i>	140 (120-160)	15	200	2.6 (2.5-2.7)	0.3 (0.2-0.4)	4.8 (3.8-5.6)	3 (2.3-3.9)	0.3 (0.3-0.3)	0.4 (0.4-0.5)
<i>L. modestum</i>	42 (36-48)	11	60	2.5 (2.4-2.6)	0.2 (0.1-0.2)	3.7 (3.3-4.5)	1.8 (1.3-2.3)	0.2 (0.2-0.2)	0.3 (0.3-0.3)
<i>L. muirii</i>	140 (121-160)	2	200	1.9 (1.8-2.1)	0.3 (0.2-0.4)	3.7 (2.9-4.3)	2.2 (1.5-2.7)	0.2 (0.2-0.2)	0.3 (0.3-0.4)
<i>L. nervosum</i>	105 (90-120)	81	150	2.9 (2.8-3.1)	0.4 (0.3-0.5)	5 (4.3-5.7)	2.6 (1.9-3.2)	1.1 (1.1-1.2)	0.4 (0.4-0.5)
<i>L. rubrum</i>	175 (150-200)	9	250	1.1 (1-1.2)	0.2 (0.1-0.3)	2 (1.8-2.2)	0.5 (0.3-0.7)	2.1 (2-2.2)	1.6 (1.5-1.6)
<i>L. xanthoconus</i>	140 (120-159)	108	200	3.6 (3.5-3.7)	0.3 (0.2-0.3)	5.5 (4.8-6.1)	2 (1.5-2.5)	0.2 (0.2-0.2)	0.3 (0.3-0.3)
<i>Protea amplexicaulis</i>	28 (24-32)	0	40	2.5 (2.4-2.6)	0.3 (0.2-0.4)	3.6 (3.3-4)	1.2 (0.9-1.5)	1.1 (1-1.2)	1 (0.9-1)
<i>P. coronata</i>	350 (300-400)	82	500	3.3 (3.2-3.4)	0.4 (0.3-0.5)	6.6 (6-7.2)	2.6 (1.9-3.3)	0.9 (0.9-1)	0.8 (0.7-0.8)
<i>P. compacta</i>	245 (211-279)	16	350	3.4 (3.2-3.6)	0.6 (0.4-0.7)	4.6 (3.7-5.5)	2.4 (1.6-3.6)	1 (0.9-1)	1.7 (1.4-1.9)
<i>P. eximia</i>	175 (150-199)	45	250	3.2 (3-3.3)	0.5 (0.3-0.6)	4.6 (4-5.6)	2.1 (1.6-3)	0.6 (0.5-0.6)	1.4 (1.1-1.6)
<i>P. grandiceps</i>	140 (120-159)	19	200	2.1 (2.1-2.2)	0.3 (0.2-0.4)	2.7 (2.3-3.2)	1.2 (0.6-1.8)	1.2 (1.2-1.3)	0.8 (0.8-0.9)
<i>P. humiflora</i>	70 (60-80)	0	100	1.9 (1.9-2)	0.2 (0.2-0.3)	2.5 (2.2-2.9)	1.1 (0.8-1.6)	1.1 (1-1.2)	1 (1-1.1)
<i>P. laevis</i>	4 (4-5)	3	6	2.5 (2.3-2.6)	0.5 (0.4-0.6)	3.8 (3-4.9)	2.3 (1.2-3.7)	0.9 (0.8-1)	1 (0.9-1)
<i>P. laurifolia</i>	560 (481-638)	80	800	2.7 (2.5-2.8)	0.4 (0.3-0.5)	3.9 (3.2-5.3)	2 (1.4-3.8)	0.8 (0.7-0.8)	2.1 (2-2.3)
<i>P. lepidocarpo-dendron</i>	210 (181-239)	8	300	3.1 (2.9-3.3)	0.6 (0.5-0.7)	4.9 (3.8-6.1)	3.4 (2.4-4.6)	1.1 (1-1.2)	2.1 (1.8-2.2)
<i>P. longifolia</i>	105 (91-120)	22	150	3.6 (3.4-3.7)	0.4 (0.3-0.4)	4.6 (3.6-5.6)	2.6 (1.6-3.7)	0.8 (0.8-0.9)	2.3 (2.3-2.4)
<i>P. lorifolia</i>	350 (303-398)	1	500	2.6 (2.6-2.7)	0.3 (0.2-0.4)	4.4 (3.7-5.1)	2.5 (1.7-3.2)	0.6 (0.5-0.6)	1.7 (1.7-1.8)
<i>P. nana</i>	91 (79-104)	50	130	1.6 (1.5-1.7)	0.3 (0.2-0.3)	1.9 (1.7-2.2)	0.6 (0.4-0.9)	0.9 (0.8-1)	0.9 (0.8-0.9)
<i>P. nerifolia</i>	210 (180-239)	11	300	2.8 (2.6-3)	0.4 (0.3-0.6)	4.1 (3.3-4.8)	2 (1.5-2.6)	0.6 (0.5-0.6)	2.2 (2-2.3)
<i>P. obtusifolia</i>	280 (241-320)	24	400	2.7 (2.6-2.9)	0.4 (0.3-0.5)	2.8 (2.4-3.2)	1.1 (0.8-1.6)	0.8 (0.7-0.9)	2 (1.9-2)
<i>P. pityphylla</i>	70 (60-80)	20	100	1.7 (1.6-1.8)	0.3 (0.2-0.4)	2.2 (1.9-2.6)	1 (0.6-1.3)	0.8 (0.7-0.9)	0.6 (0.6-0.6)
<i>P. punctata</i>	280 (241-320)	30	400	3 (2.8-3.1)	0.4 (0.3-0.4)	5.6 (5-6.5)	2.4 (1.8-2.9)	0.7 (0.6-0.8)	0.9 (0.8-1)
<i>P. repens</i>	315 (271-359)	24	450	2.4 (2.3-2.5)	0.3 (0.2-0.4)	4.4 (3.9-5)	1.9 (1.3-2.7)	2 (1.6-2.5)	2.5 (2.3-2.6)
<i>P. stokoei</i>	140 (121-160)	43	200	2.5 (2.3-2.6)	0.4 (0.3-0.5)	4.2 (3.5-5)	2.4 (1.6-3.5)	1 (0.9-1.2)	2.4 (2.4-2.4)

* described by triangular distributions with varying mode; minimum and maximum were not varied

† described by lognormal distributions

Table A3.2. Demographic parameters of three genera of Proteaceae from the Cape Floristic Region. The table reports point estimates and ranges (in brackets) of 100 sets of demographic parameters representing parameter uncertainty. Generation time is equal to fire interval and does thus not differ between genera.

Genus	Mean net reproductive rate, R_0	Generation time (yr)*	
		mean	sd
<i>Aulax</i>	5.0 (1.7-12.0)		
<i>Leucadendron</i>	13.1 (7.8-21.1)	17.8 (10.4-28.6)	11.4 (4.7-15.5)
<i>Protea</i>	7.2 (5.2-9.6)		

* described by Weibull distributions (Le Maitre 1998, Polakow & Dunne 1999)

Fig. A3.1 (on following page). The three-step protocol to forecast plant migration and the simulation design used to quantify effects of parameter and inherent uncertainty. The individual steps of the protocol generate 1) distributions of dispersal distance, 2) distributions of population-level migration rate and 3) distributions of future range size. Parameter uncertainty was included by using 100 randomly sampled sets of dispersal parameters (Table A3.1) in Step 1 and 100 randomly sampled sets of demographic parameters (Table A3.2) in Step 2. To incorporate inherent uncertainty in Step 1 I combined each set of dispersal parameters with a different set of 100 dispersal environments (Table A2.2) and simulated the dispersal of 10^4 seeds in each environment. In the remaining two steps I included inherent uncertainty by simulating, for each set of species parameters, 5000 population-level migration rates (Step 2) and one future range size (Step 3). For each species I thus simulated the dispersal of 10^8 seeds (=100 sets of dispersal parameters x 100 dispersal environments x 10^4 seeds) and generated 5×10^5 migration rates (= 100 sets of species parameters x 5000 migration rates) as well as 100 range size forecasts.

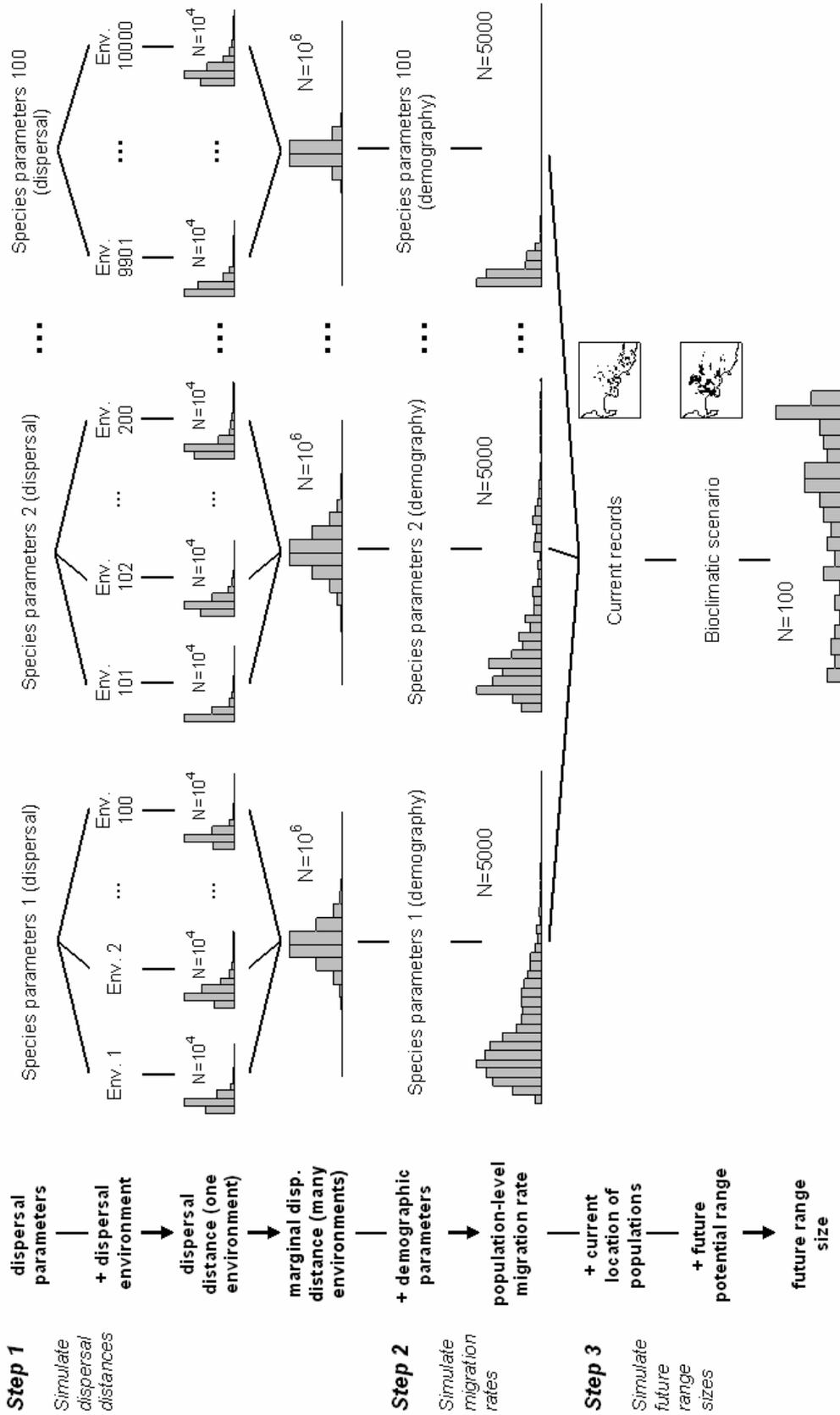


Fig. A3.1 (caption on previous page)

List of figures

Fig. 1.1	Examples of Gaussian, exponential and fat-tailed seed dispersal kernels	3
Fig. 1.2	The life cycle of serotinous Proteaceae in response to a typical fire cycle	12
Fig. 2.1	Representation of seed-obstacle interactions in the seed dispersal model	21
Fig. 2.2	Morphologies of Proteaceae seeds used for experimental model validation	23
Fig. 2.3.	Setup of the field experiment used to validate the seed dispersal model	25
Fig. 2.4	Experimentally observed vs. predicted proportion of seeds dispersed over 25 m	28
Fig. 2.5	Effect of aerodynamic roughness length on the bias of the seed dispersal model	29
Fig. 2.6	Comparison of explicit and aggregated version of the seed dispersal model	30
Fig. 2.7	Sensitivity analysis of the seed dispersal model	32
Fig. 3.1	Realized and potential range of <i>Protea scolopendrifolia</i>	43
Fig. 3.2	Estimation of a species' dispersal ability	45
Fig. 3.3	Range filling vs. colonization ability for 37 species of Proteaceae	48
Fig. 3.4	Range filling vs. evolutionary age for 37 species of Proteaceae	48
Fig. 4.1	Effects of climate change and migration ability on the future range size of <i>Protea longifolia</i>	55
Fig. 4.2	Predicted migration rates for 26 species of South African Proteaceae	58
Fig. 4.3	Climate driven changes in range size predicted for 26 species of South African Proteaceae	59
Fig. 5.1	Effects of fire regime on the viability of serotinous Proteaceae that face habitat destruction and climate change	65
Fig. A3.1	The three-step protocol to forecast plant migration and the simulation design used to quantify effects of parameter and inherent uncertainty	104

List of tables

Table 1.1	Definitions of terms relevant for seed dispersal and the spatial dynamics of plant species	2
Table 2.1	Seed traits of seven Proteaceae species and summary statistics of seed movement in the field experiment	24
Table 2.2	Summary statistics of wind conditions during the field experiment	26
Table 3.1	Performance of metapopulation models and linear models for range filling	47
Table 3.2	Results of comparative analyses testing for effects of colonization ability and persistence type on range filling	49
Table A2.1	Range sizes, range filling, local abundance, species traits, simulated dispersal ability, and evolutionary age for 37 species of Proteaceae	96
Table A2.2	Environmental parameters used for seed dispersal simulations	98
Table A3.1	Dispersal-relevant traits of 26 Proteaceae species	102
Table A3.2	Demographic parameters of three genera of Proteaceae	103