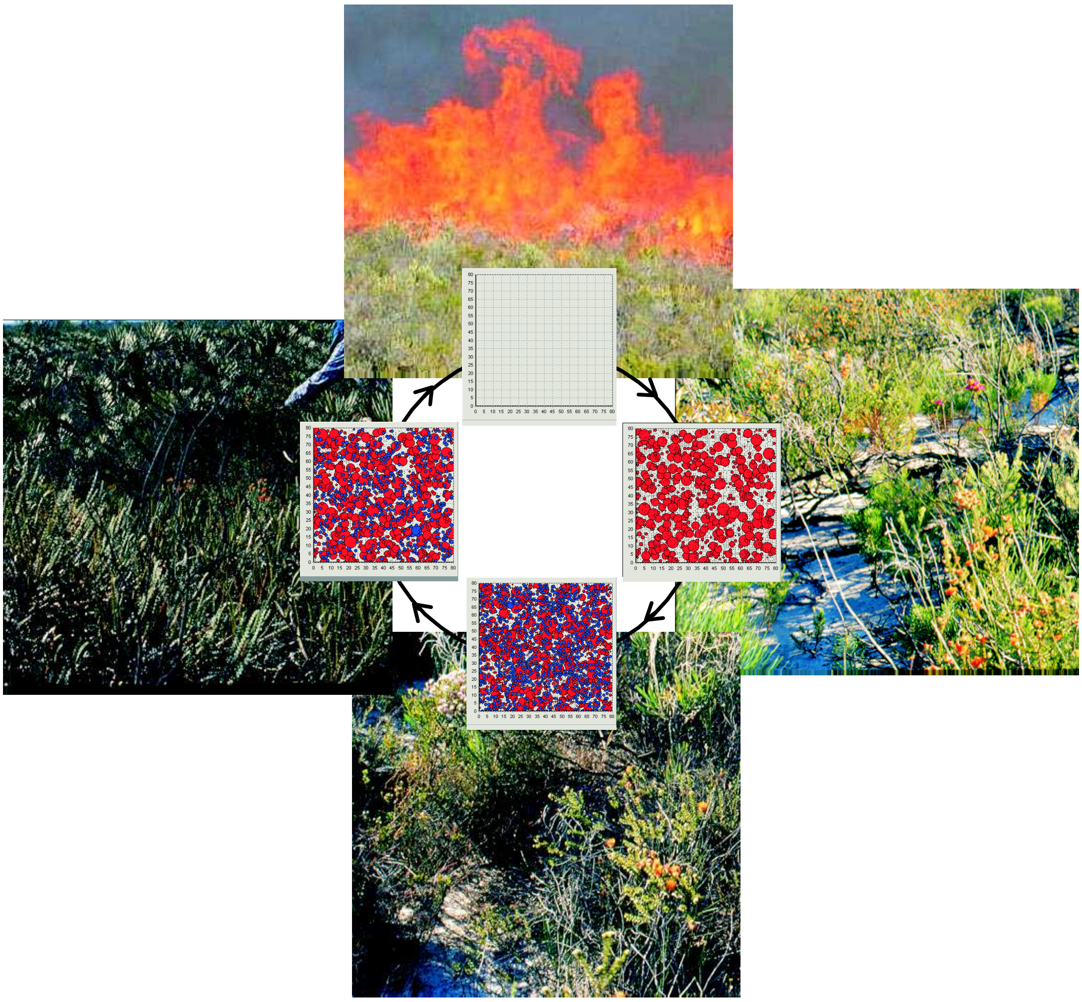
Investigating mechanisms maintaining plant species diversity in fire prone Mediterranean-type vegetation using spatially-explicit simulation models



PhD Thesis
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2010

Investigating mechanisms maintaining plant species diversity in fire prone Mediterranean-type vegetation using spatially-explicit simulation models

DISSERTATION

zur Erlangung des akademischen Grades
"doctor rerum naturalium"
(Dr. rer. nat.)
in der Wissenschaftsdisziplin "Naturschutz und Ökologie"

eingereicht an der
Mathematisch-Naturwissenschaftlichen Fakultät
der Universität Potsdam

von
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Potsdam, Januar 2010

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1 ZUSAMMENFASSUNG

Feuer geprägte, mediterrane Vegetationstypen, wie sie im Mittelmeerraum und Süd-West Australien zu finden sind, gelten als globale „hotspots“ für Pflanzendiversität. Um sicher zu stellen, dass Managementprogramme zum Erhalt dieser hoch diversen Pflanzengesellschaften zielgerichtet beitragen, ist ein profundes Verständnis der wesentlichen Koexistenzmechanismen notwendig. In der aktuellen Literatur werden verschiedene Mechanismen diskutiert. Das Ziel meiner Doktorarbeit ist es, die Bedeutung der Mechanismen für den Erhalt der artenreichen, feuergeprägten Vegetation anhand eines Modells systematisch zu untersuchen. Das von mir dafür entwickelte Modell ist räumlich-explizit, stochastisch und regel- und individuenbasiert. Es ist unter Zuhilfenahme von Daten zu Populationsdynamiken parametrisiert, die über 18 Jahre im Mediterranen Buschland von Eneabba Westaustraliens gesammelt wurden. Anhand von 156 Arten sind sieben für meine Studie relevante Pflanzeneigenschaften identifiziert wurden: *Regenerationsart*, *jährlich maximale Samenproduktion*, *Samengröße*, *maximaler Durchmesser*, *Trockentoleranz*, *Ausbreitungsart* und *Samenbanktyp*. Kombinationen der Eigenschaften bilden funktionelle Pflanzentypen (PFTs), deren jährliche Dynamik über Lebenszyklusprozesse im Modell simuliert wird.

Der erste Teil meiner Arbeit präsentiert die Studie zur Bedeutung von „trade-offs“ für den Erhalt der hohen Diversität in artenreichen Systemen. Die Simulationsergebnisse mit 288 virtuellen PFTs zeigen, dass das „trade-offs“-Konzept für die Identifizierung nicht-lebensfähiger Kombinationen von Pflanzeneigenschaften hilfreich sein kann. Allerdings kann der Shannon-Diversitäts-Index der modellierten Pflanzengesellschaft trotz der Anwesenheit von „Supertypen“ hoch sein. Ich schlussfolgere, dass „trade-off“ zwischen zwei Eigenschaften weniger wichtig für die Erklärung der Koexistenz von vielen Arten und hoher Diversität sind, als es durch konzeptionelle Modelle vorhergesagt wird.

Viele Studien zeigen, dass Sameneintrag aus dem regionalen Samenpool essenziell für den Erhalt lokaler Artendiversität ist. Es gibt allerdings noch keine systematischen Studien zur Zusammensetzung des Samenregens artenreichen Systemen. Die Ergebnisse der Simulationsexperimente im zweiten Teil meiner Arbeit machen deutlich, dass ohne Sameneintrag die lokale Pflanzengesellschaft Eneabbas sich in eine Richtung entwickelt, in der nur wenige PFTs koexistieren. Mit steigender Samenimmigrationsrate erreicht die Anzahl an koexistierenden PFTs und die Shannon-Diversität schnell die Werte, die auch im Feld gefunden werden. Der regionale Sameneintrag kann also als Erklärung zur Struktur

lokaler Pflanzengesellschaften dienen. Seine Zusammensetzung sollte jedoch in zukünftigen Studien berücksichtigt werden.

Im dritten Teil meiner Doktorarbeit präsentiere ich Analysen zur Sensibilität der PFTs von Eneabba vorhergesagte Klimaszenarien und der Auswirkungen auf die Samenimmigration. Die Ergebnisse zeigen deutlich, dass Klimaänderungen das Potential haben, die Anzahl an ausgebreiteten Samen der meisten Eneabba PFTs zu verändern. Die Entscheidungsbaum-Analyse veranschaulicht, dass die Reaktion auf Klimaänderung PFT-spezifisch ist. In den Eneabba hängt die Sensitivität der PFTs gegenüber klimatischen Veränderungen von den PFT-spezifischen Eigenschaftskombinationen und vom Klimaszenarium ab, d.h. von der Entwicklung der Regenfallmenge und der Feuerfrequenz. Dieses Ergebnis betont, dass PFT-spezifische Reaktionen und die klimabedingten Änderungen in der Samenimmigration in Studien zum Einfluss von Klimaänderungen auf die zukünftige Artenverteilung berücksichtigt werden sollten.

Die Ergebnisse aus den drei Kapiteln werden in der allgemeinen Diskussion zusammengeführt und analysiert. Das Modell wird diskutiert und Verbesserungen und Vorschläge für weitere Forschung aufgezeigt. Meine Arbeit führt zu folgenden Schlussfolgerungen:

i) Es ist notwendig, empirische Arbeit und Modellierung zu kombinieren, um Koexistenz in artenreichen Systemen zu erklären.

ii) Durch den gewählten Modellansatz kann die Komplexität von Koexistenz erfasst und das Verständnis vertieft werden.

iii) Auf Felddaten basierende Annahmen bezüglich Umweltbedingungen und Lebenzyklus können zur Relativierung der Bedeutsamkeit von Mechanismen führen. So können Trade-offs eine geringere Rolle spielen, als konzeptionelle Modelle nahe legen.

iv) Samenimmigration ist ein Schlüsselprozess für lokale Koexistenz. Deren Änderung aufgrund von Klimawandel sollte für Prognosen zu Artenvorkommen berücksichtigt werden. Feldstudien sollten durchgeführt werden, um die Datenlücken zur Samenregenzusammensetzung zu füllen.

2 SUMMARY

Fire prone Mediterranean-type vegetation systems like those in the Mediterranean Basin and South-Western Australia are global hot spots for plant species diversity. To ensure management programs act to maintain these highly diverse plant communities, it is necessary to get a profound understanding of the crucial mechanisms of coexistence. In the current literature several mechanisms are discussed. The objective of my thesis is to systematically explore the importance of potential mechanisms for maintaining multi-species, fire prone vegetation by modelling. The model I developed is spatially-explicit, stochastic, rule- and individual-based. It is parameterised on data of population dynamics collected over 18 years in the Mediterranean-type shrublands of Eneabba, Western Australia. From 156 woody species of the area seven plant traits have been identified to be relevant for this study: *regeneration mode*, *annual maximum seed production*, *seed size*, *maximum crown diameter*, *drought tolerance*, *dispersal mode* and *seed bank type*. Trait sets are used for the definition of plant functional types (PFTs). The PFT dynamics are simulated annual by iterating life history processes.

In the first part of my thesis I investigate the importance of trade-offs for the maintenance of high diversity in multi-species systems with 288 virtual PFTs. Simulation results show that the trade-off concept can be helpful to identify non-viable combinations of plant traits. However, the Shannon Diversity Index of modelled communities can be high despite of the presence of 'supertypes'. I conclude, that trade-offs between two traits are less important to explain multi-species coexistence and high diversity than it is predicted by more conceptual models.

Several studies show, that seed immigration from the regional seed pool is essential for maintaining local species diversity. However, systematical studies on the seed rain composition to multi-species communities are missing. The results of the simulation experiments, as presented in part two of this thesis, show clearly, that without seed immigration the local species community found in Eneabba drifts towards a state with few coexisting PFTs. With increasing immigration rates the number of simulated coexisting PFTs and Shannon diversity quickly approaches values as also observed in the field. Including the regional seed input in the model is suited to explain more aggregated measures of the local plant community structure such as species richness and diversity. Hence, the seed rain composition should be implemented in future studies.

In the third part of my thesis I test the sensitivity of Eneabba PFTs to four different climate change scenarios, considering their impact on both local and regional processes. The results show that climate change clearly has the potential to alter the number of dispersed seeds for most of the Eneabba PFTs and therefore the source of the ‘immigrants’ at the community level. A classification tree analysis shows that, in general, the response to climate change was PFT-specific. In the Eneabba sand plains sensitivity of a PFT to climate change depends on its specific trait combination and on the scenario of environmental change i.e. development of the amount of rainfall and the fire frequency. This result emphasizes that PFT-specific responses and regional process seed immigration should not be ignored in studies dealing with the impact of climate change on future species distribution.

The results of the three chapters are finally analysed in a general discussion. The model is discussed and improvements and suggestions are made for future research. My work leads to the following conclusions:

i) It is necessary to support modelling with empirical work to explain coexistence in species-rich plant communities.

ii) The chosen modelling approach allows considering the complexity of coexistence and improves the understanding of coexistence mechanisms.

iii) Field research based assumptions in terms of environmental conditions and plant life histories can relativise the importance of more hypothetic coexistence theories in species-rich systems. In consequence, trade-offs can play a lower role than predicted by conceptual models.

iv) Seed immigration is a key process for local coexistence. Its alteration because of climate change should be considered for prognosis of coexistence. Field studies should be carried out to get data on seed rain composition.

3 GENERAL INTRODUCTION

3.1 MOTIVATION

Mediterranean-climate regions occupy less than 5% of the Earth’s surface (Fig. 3.1; Cowling et al. 1996; Montenegro et al. 2004). Nonetheless, this area contains about 20% of the world’s known vascular flora (Cowling et al. 1996; Montenegro et al. 2004). Latest studies assume 46.250 vascular plant taxa, whereas 55% of them are endemic (Syphard et al. 2009). The extraordinary richness of plant species and the high endemic rate made Mediterranean-climate regions to hot spots for species diversity (Myers et al. 2000).

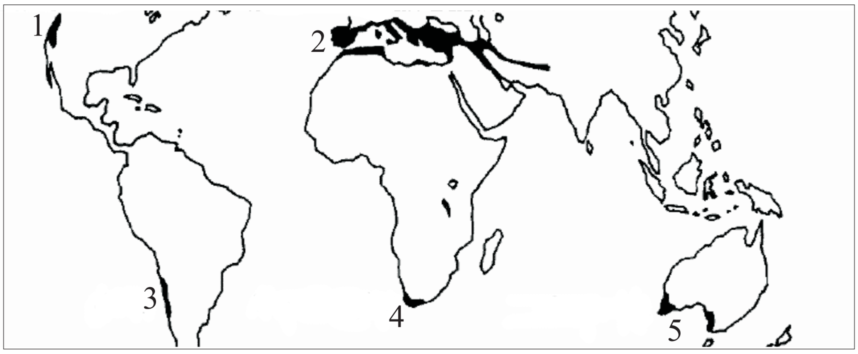

Fig. 3.1 Distribution of the five Mediterranean-climate regions world-wide with the chaparral in California (1), the matorral, maquis and garrigue in the Mediterranean Basin (2), the matorral in Chile (3), the fynbos and renosterveld in South African Cape (4) and the kwongan and mallee in Australia (5). Modified by Cowling et al. (1996).

Humans have a severe impact on the natural ecosystems and the plant species diversity in Mediterranean-climate regions (Montenegro et al. 2004; Vogiatzakis et al. 2006). Human settlements and intensive agriculture have led to a habitat loss of 2.5% between 1950 and 1990 (Millennium Ecosystem Assessment 2005). The increase in both population density and urban area has been estimated to be 13% for the Mediterranean-climate regions from 1990 to 2000. At the same time, area used for agriculture increased by 1% (Underwood et al. 2009). Remaining habitats are managed by fires to avoid uncontrolled ignitions and protect human life and property. Natural reoccurring fires have shaped the evolution of the vegetation in all Mediterranean-type regions except Chile since the Quaternary (Cowling et al. 1996; Montenegro et al. 2004).

As characteristical for Mediterranean-type climate mild and rainy winter months support an intensive vegetation growth. They are followed by a long summer drought producing high amounts of dry and flammable biomass (Montenegro et al. 2004). Mediterranean-climate plants are well adapted to these environmental conditions. The vegetation is dominated by drought resistant, evergreen, woody, sclerophyllous shrubs and post-fire persistence traits, such as fire-triggered germination of seeds and resprouting (i.e. the ability to regrow from protected buds after fire), are common (Cowling et al. 1996; Cowling and Lamont 1987; Enright et al. 1998a; Pausas 1999; Montenegro et al. 2004). However, change of the fire regime can lead to the extinction of even well adapted species (Syphard et al. 2009). Resistance, the regeneration capacity and the reproductive ability are limited (Syphard et al. 2009). Altering the natural fire regime towards shorter fire-intervals can lead to extinction of native plant species, can support the invasion of alien plants and can change the plant species succession (Montenegro et al. 2004; Millennium Ecosystem Assessment 2005; Underwood et al. 2009). Likewise, longer inter-fire periods lead to fuel accumulation with increased probabilities for ignitions and fires of uncommon intensity, able to kill fire-resistant species (Syphard et al. 2009).

Human activities threaten about 17% of all Mediterranean-climate vascular plant taxa (Vogiatzakis et al. 2006). This rate is especially high in Western Australia, where the area of native bush converted to wheat cultivation is estimated to be 1 million acres per year by 1980 (Underwood et al. 2009). In the time span between the European settlements in the early 1800s and 1994, about 54 of the about 7465 native vascular plant species of Western Australia may have become extinct (Greuter 1994). Additionally, not less than 1451 species are vulnerable by habitat fragmentation, diseases, invasive weeds, and rising saline groundwater (Cowling et al. 1996; Hopper and Gioia 2004; Lamont et al. 2007; Underwood et al. 2009).

Furthermore, besides the direct anthropogenic influence on Mediterranean-climate vegetation, climate change is expected to drastically influence these plant communities (Sala et al. 2000; Vogiatzakis et al. 2006; Underwood et al. 2009). Following the Millennium Ecosystem Assessment (2005), climate change will be the largest forthcoming threat to biodiversity across most biomes. Precipitation, a key driver of vegetation dynamics is especially expected to change. Shifts in fire regimes are expected due to increased drought and fuel accumulation (Mouillot et al. 2002; Vogiatzakis et al. 2006; Underwood et al. 2009). Species are expected to shift their ranges as a result of climatic change and some of the species will become extinct (Vogiatzakis et al. 2006; Fitzpatrick et al. 2008; Underwood et al. 2009).

Sala et al. (2000) estimate that alterations in biodiversity caused by land use, biotic exchange and climate change will be proportionally the highest in Mediterranean-climate regions, followed by grasslands and other biomes until 2100. In the light of rapid global change and increasing anthropogenic influence, Mediterranean-climate regions are of high global conservation concern (Vogiatzakis et al. 2006; Syphard et al. 2009). However, projections are sensitive to many widely acknowledged uncertainties, including migration rates of species and the magnitude and direction of future climate change (Fitzpatrick et al. 2008) and it is still not sufficiently understood why so many species are able to coexist. There are many studies with focus on a few processes, factors and species by field studies (Cowling et al. 1987; Lamont et al. 1993; Richardson et al. 1995) and frequently by using modelling approaches (Enright et al. 1998a, b; Groeneveld et al. 2002; Miller and Chesson 2009; Reyes and Casal 2008). However, studies covering the complexity of real multi-species communities are still rare, partly because of the lack of data. Thus, to understand plant species diversity in Mediterranean-climate regions and evaluate the resilience of their vegetation against climatic change, it is necessary to evaluate the importance of mechanisms explaining local multi-species coexistence.

3.2 POTENTIAL COEXISTENCE MECHANISMS

It is widely accepted that fire as an extrinsic factor (non-equilibrium theory) is a major driver for coexistence in Mediterranean-climate regions (Richardson et al. 1995; Cowling et al. 1996; Bellingham 2000; Bell 2001). Inferior competitors can avoid exclusion by colonizing empty space cleared by fire in the commonly dense Mediterranean-climate vegetation. Due to the recurrent fire, plants have evolved special life history traits for survival (Enright et al. 1998a, b; Lamont et al. 2007). Adaptations include fire tolerance connected with vegetative regrowth after a fire (resprouters), and soil and canopy seed storage (Enright et al. 1998a, b, 2007). The germination of most seeds is only trigged by heat or chemically by smoke (Lamont and Connell 1996). Thus, most studies analysing coexistence in Mediterranean-climate regions focus on regeneration niches created by fire and deal with species specific differences in plant history traits (Lamont et al. 1993; Richardson et al. 1995; Bellingham 2000; Bell 2001).

Trade-offs between plants’ abilities associated with recurrent fire seem to be important. Species can be roughly divided into resprouters (plants that survive fire) and non-sprouters (plants that are killed by fire). Due to resource limitation, plants that invest in belowground storage biomass and survive fire tend to produce less seeds than non-sprouters (Bellingham 2000).

Beside fire, fluctuations in rainfall offer further niches for coexistence. Species produce either a few, large seeds or many, small seeds (Lamont and Groom 1998). Seedlings from large seeds seem to be more robust against drought than seedlings from small seeds, which have a numerical advantage in good years. Fluctuating rainfall conditions could lead to similar overall reproductive success of small seeded and large seeded species, and therefore facilitates coexistence (Lamont and Groom 1998; Bell 2001).

Although many potential trade-offs among species are proposed in niche coexistence models (Stearns 1992; Cornelissen et al. 2003), it is difficult to find empirical evidence of trade-offs especially in multi-species communities (Richardson et al. 1995; Chave 2004; Clark et al. 2004). Modelling studies contradict the low-dimensional trade-off concept, i.e. between only two plant traits, when more realistic assumptions such as biotic and abiotic heterogeneity and whole plant life histories are considered (Jeltsch et al. 1996, 1998; Howard and Goldberg 2001; Moles and Westoby 2006). Therefore, further studies considering low-dimensional trade-offs are needed to evaluate their potential as explanatory factor of the high species diversity in fire-prone Mediterranean-climate communities.

Further stabilising and equalising processes may prevent extinction of weaker competitors and facilitate local coexistence (Cowling et al. 1996). These include local intrinsic processes such as intraspecific competition (Perry et al. 2008), and weighted lottery competition (Lavorel and Lebreton 1992; Lamont and Wittkowski 1995), as well as regional processes (Cowling et al. 1996). Seed immigration may be one regional process crucial to local coexistence (Lamont et al. 1993; Richardson et al. 1995). The same applies in other biomes and is the focus of many field studies (Turnbull et al. 1999; Mouquet et al. 2004), and therefore integrated in many modelling studies (Hanski 1999; Loreau and Mouquet 1999; Pulliam 2000). However, these studies have not analysed the magnitude and composition of seed rain systematically. It is hypothesised that small changes in the seed rain will have a large impact on the community compositions and coexistence (Chesson 2000; Levine and Murrell 2003; Brooker et al. 2007). But studies systematically testing this hypothesis are missing. The importance of such studies is evident, since seed rain is expected to play a major role in plant species and communities response to climate change (Chesson 2000; Hovenden et al. 2007; Duguy and Vallejo 2008).

3.3 ASSESSING COEXISTENCE MECHANISMS WITH MODELS

To sustain plant species diversity in Mediterranean-climate regions and to assess the effects of climatic change it is essential to understand which mechanisms drive coexistence. This complex issue necessitates considering intrinsic and extrinsic factors. Simulation models can overcome the problem by consideration of whole life histories. Thus, models rather than experimental studies have been used to identify drivers of coexistence in fire-prone Mediterranean-climate systems. They focus on various aspects (e.g. variation in fire-regime: Burgman and Lamont 1992, Groeneveld et al. 2002; life history traits: Enright et al. 1998a, b, Bellingham 2000, Groeneveld et al. 2002, Miller and Chesson 2009; lottery competition: Chesson and Warner 1981, Laurie and Cowling 1995; special life history processes: Reyes and Casal 2008, Miller and Chesson 2009). However, none of the models known to the author considered the high number of species in Mediterranean-climate landscapes with realistic environmental conditions. Thus, the next step for evaluating the relevance of mechanisms for multi-species coexistence in fire-prone Mediterranean-climate is to develop a spatially-explicit model with rules based on expert knowledge and processes and traits derived from real assemblages.

To develop such a model is a challenging task in face of the high number of species (Díaz et al. 2002). A promising way for answering ecological questions is the classification of plant species as plant functional types (PFTs; Díaz et al. 2002; Cornelissen et al. 2003; Jeltsch et al. 2008). PFTs or plant strategic types can be defined as groups of plant species sharing similar responses to environmental factors (Cornelissen et al. 2003). The similarities of species' responses are based on their similar set of key functional traits (Cornelissen et al. 2003). In fire prone, Mediterranean-climate systems a high number of species can be grouped into a limited number of different functional groups defined by potentially important traits. Groups can be described by species reacting in a similar way to disturbance (e.g. non-sprouters vs. resprouters) or sharing seed storage mechanisms (canopy seed bank vs. soil seed bank) (Bell 2001; Enright et al. 1998a, b). Morphological and physiological attributes can also be considered in the design of functional groups (e.g. drought tolerance based on leaf size and plant allometry). These groups can be closely related to interactions between plants (Lavorel et al. 1999; Bell 2001). The PFT approach can be implemented in a model simulating life histories of plants and realistic traits, especially in models simulating coexistence of high number of different plants explicitly (Jeltsch et al. 2008).

Many studies show the potential of spatially-explicit, individual-based simulation models to identify the major processes mediating coexistence between two or a few species or PFTs (Silvertown et al. 1992; Czárán 1997; Jeltsch et al. 1998; Grimm 1999; Jeltsch and Moloney 2002; Wiegand et al. 2003; Breckling et al. 2006). Processes important for coexistence, such as seed dispersal, spatial aggregation and neighbourhood interactions between individuals can be considered in detail. Space can be presented explicitly as a grid or a field, and plants can be distributed individually in space (i.e. assigned specific coordinates in space). The individual-based approach allows simulating life history processes such as reproduction and growth of each plant and improves the structural realism. Biological information and expert knowledge can be directly incorporated as rules into the model. Additionally, environmental and demographical stochasticity can also be implemented. A multitude of results can be measured from such modelling approach, e.g. abundances, age class distributions, mean times to extinctions, spatial configuration and aggregation patterns. Output properties such as ‘numbers of individuals per trait categorical’ can be compared with corresponding empirical data and the influence of mechanism can be evaluated.

Few attempts have been made to apply this simulation technique to entire realistic communities (Franklin et al. 2001; Mouillot et al. 2001). One reason for this can be that comprehensive expert knowledge is necessary to develop a complex model and data sets to evaluate the impacts of mechanism orientated on realistic assemblages.

3.4 STUDY SIDE – ENEABBA

The basis of this thesis and subject of more than 18 years of ecological research is the shrubland of the Eneabba Plains (278 km north of Perth) (Fig. 3.2; Lamont et al. 2007). It is part of the fire-structured ‘kwongan’ of the Southwest Botanical Province in Western Australia and covers about 700 km² (Bell 2001). Fires have been present in the landscape history for at least the past 5000 years (Bell 2001). The area was settled by Europeans around 1870 and opened up for agriculture in the 1950s. Intentional burning is a common management tool to protect human life and property. Over the last 30 years the fire interval has averaged 13 years (Enright et al. 2005; Miller et al. 2007). The rainy season in Eneabba occurs in the winter and lasts from May to September. Almost 80% of the average yearly rainfall of about 500 mm is restricted to this period (Fig. 3.3, www.bom.gov.au). November until February are the hottest months with maximum temperatures of >45°C (Fig. 3.3, www.bom.gov.au). The plains are characterised by unconsolidated, acidic and nutrient-poor sands. The sand lays 60-500 cm thick in low dune and swale series, over clay or laterite layers (Groeneveld et al. 2002). On areas with deeper sand small trees with sizes of 4–8 m height can be found. Elsewhere a dense shrubland (> 70% plant cover) of less than 2 m height is common (Groeneveld et al. 2002). The vegetation is composed of species belonging to the family of *Proteaceae* and *Myrtaceae* including many endemic species such as *Banksia hookeriana* and *B. elegans* (Lamont et al. 1993; Groeneveld et al. 2002).

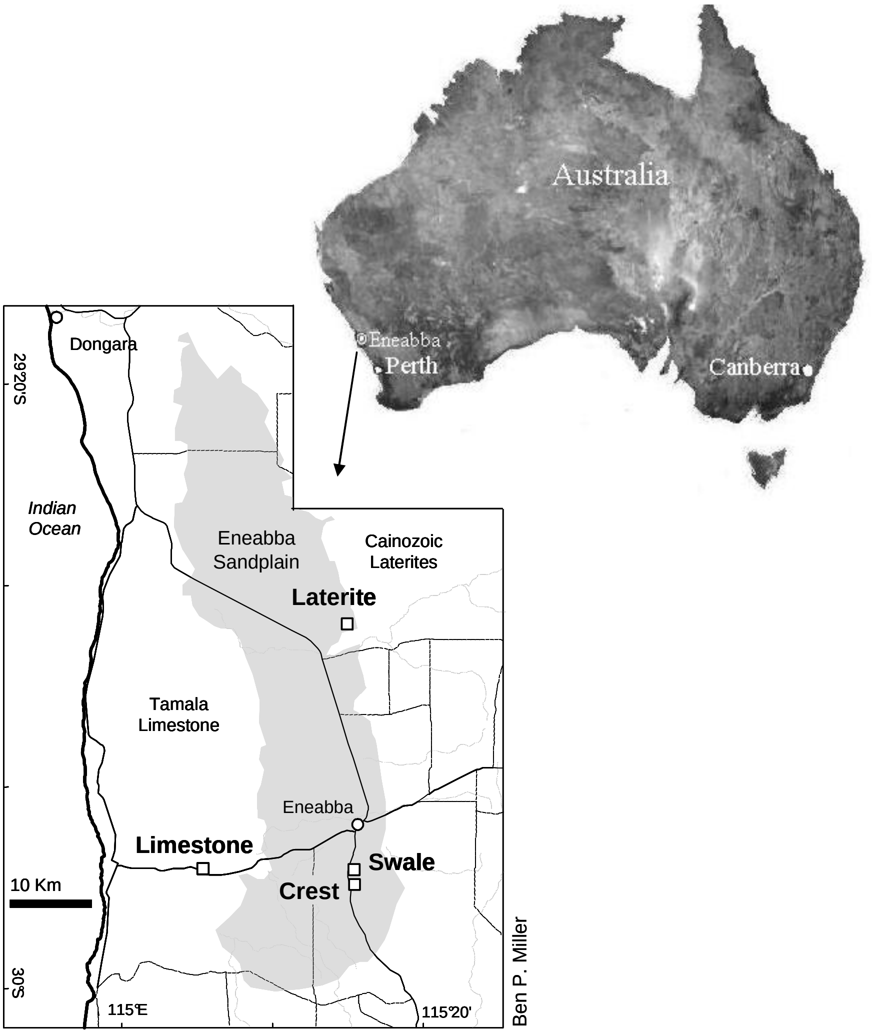

Fig. 3.2 Map of the fire-structured heathlands at the Eneabba Sandplain in Western Australia (courtesy of Ben P. Miller). The data of four study sites - Limestone, Laterite, Crest and Swale – were used as basis of the model.

Information on 156 species were derived from four 40 m by 40 m, sites (‘limestone’, ‘swale’, ’crest’ and ‘laterite’) near the town of Eneabba, and were used together with expert knowledge to identify potentially important plant traits for survival in fire-prone Mediterranean climate.

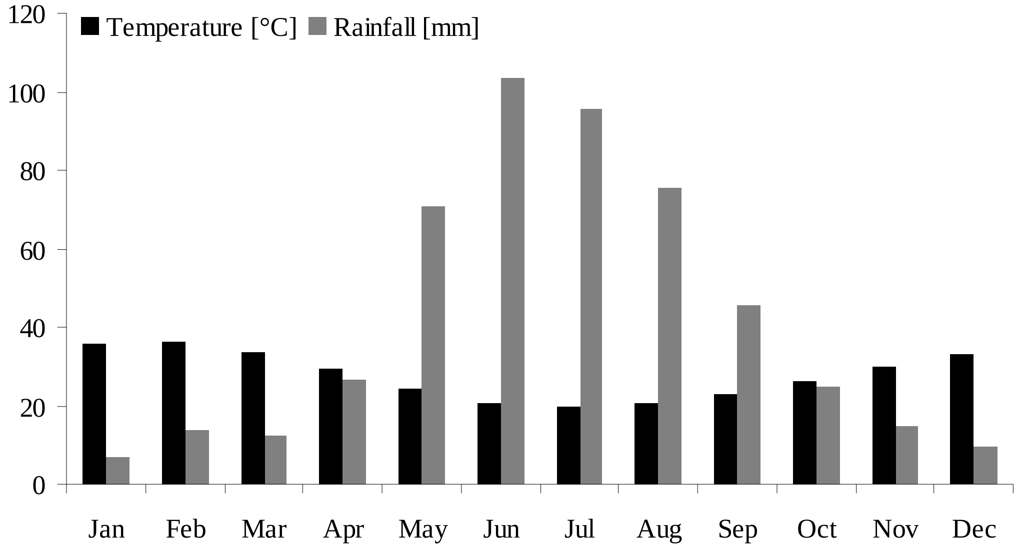

Fig. 3.3 Monthly average maximum temperature (1964-2009) and average rainfall (1972-2009) of the Eneabba weather station (29.82°S, 115.27 °E, www.bom.gov.au).

3.5 OBJECTIVES OF THE THESIS

The main objectives of this thesis are to understand local multi-species coexistence in fire-prone, Mediterranean-climate regions and to evaluate the importance of potential mechanisms promoting coexistence. The aims were:

i) Develop a spatially-explicit, individual-based model.
ii) Evaluate the influence of potential coexistence mechanisms, low-dimensional trade-offs and seed immigration.
iii) Assess the effect of climate change on realistic multi-species communities under consideration of seed immigration change.

Simulating the PFT communities shall allow systematic evaluation of single mechanisms, to improve the understanding of the coexistence of multi-species communities. In detail, I utilize the spatially-explicit modelling approach to evaluate the importance of trade-offs and seed immigration. It is proposed that low-dimensional trade-offs, such as colonisation vs. competition, explain the coexistence of high number of species (Stearns 1992; Rosenzweig 1995; Gordon 2000; Turnbull et al. 1999; Jakobsson and Eriksson 2000; Cornelissen et al. 2003). Their importance however is questioned in multi-species communities under consideration of realistic environments and life histories (Clark et al. 2004, 2007; Chave 2004; Bampfylde et al. 2005). Low-dimensional trade-offs could be part of a spectrum of life history traits, including plant size, longevity, juvenile survival rate and time to maturity (Moles and Westoby 2006). Viewing low-dimensional trade-offs as independent sets could not be sufficient for the explanation of multi-species coexistence.

The importance of the regional process of seed immigration for local species coexistence has been frequently identified (Turnbull et al. 1999; Zobel et al. 2000; Foster 2001; Coomes and Grubb 2003; Kisdi and Geritz 2003; Mouquet et al. 2004; Hiltunen et al. 2006). Although the composition of seed rain drastically influences communities, systematic studies are missing. They are however necessary for the understanding of the local multi-species coexistence. Through systematic variation of seed rain I assess the effect on the local community of the process of seed immigration.

In the third study I highlight the effect of the expected alteration of seed rain by climate change on communities. The composition of local communities is influenced by composition of the regional species pool, but this interaction may change as environmental conditions change (Levine and Murrell 2003; Davis 2005; Kuparinen et al. 2009), and this process has been neglected in the most climate change studies. Using a spatially-explicit model I focus on the alteration of seed immigration to get an impression how climate change predictions could affect local communities of the highly biodiverse Mediterranean-type fire-adapted vegetation.

3.6 STRUCTURE OF THE THESIS

In this thesis I present results from a simulation model that I developed and used to systematically explore the importance of possible coexistence mechanisms, and to improve our understanding of the effects of climate change on multi-species communities. The underlying data and expert knowledge is provided by Australian and New Zealand partners, Prof. Neal Enright, Prof. Byron B. Lamont, Dr. Ben P. Miller, and Dr. George L.W. Perry. The results are presented in the chapters 4–6, which are submitted or published as independent papers in international scientific journals in cooperation with co-authors. Hence, especially the model description and the introduction of the research area recur throughout the chapters. The chapters can be read independently and are connected by intersections. In Chapter 4, I investigate the importance of low-dimensional trade-offs to explain community structure and plant species richness. In Chapter 5, I assess the importance of seed immigration from the regional seed pool as a coexistence mechanism for species-rich local communities. In Chapter 6, the sensitivity of plant functional types and communities to climate change is analysed, considering the effects on local and regional dynamics. The thesis is concluded with a general discussion and future research implications.

4 HOW IMPORTANT ARE TRADE-OFFS IN EXPLAINING COMMUNITY STRUCTURE AND PLANT RICHNESS? [1]

4.1 ABSTRACT

Mathematical models suggest that life history trade-offs can explain species diversity and community structure. In the absence of trade-offs, communities would be dominated by single, jack-of-all-trade, species. However, it has proven difficult to find strong empirical evidence for such trade-offs in species rich ecosystems. We developed a spatially-explicit, rule-based and individual-based stochastic model to explore the importance of trade-offs. This model simulates community dynamics of 288 virtual plant functional types (PFTs), which are described by seven life history traits. These include trait combinations that fit into the trade-off concept, as well as 'super-types', which are not constrained by energy or resource limitation, and 'loser-types', which do not exploit resources efficiently. The model is parameterised using data from a species rich, fire-prone Mediterranean-type shrubland in South-Western Australia. Simulation results show that the trade-off concept can be helpful to identify non-viable combinations of life history traits. However, species diversity can be high despite the presence of 'super-types'. Furthermore, the exclusion of such super-types does not necessarily lead to a strong increase in PFT richness and diversity, and thus to changes of community structure. We conclude that low-dimensional trade-offs do not provide simple explanations for multi-species coexistence as expected from many conceptual models.

4.2 INTRODUCTION

A dominant perspective in theoretical and empirical plant ecology is that trade-offs, such as those between competitiveness and colonisation ability, are largely responsible for the maintenance of plant species diversity at the local scale (e.g. Stearns 1992; Tilman 1994; Cornelissen et al. 2003). This view is based on the fact that there is a finite amount of energy and resources available for plants, and, due to the costs involved in development and maintenance of life history traits, the competitiveness of plants is constrained by certain inevitable trade-offs (e.g. Crawley 1997). In the absence of trade-offs, communities would be dominated by highly competitive 'jack-of-all-trade' super-species combining all advantageous life history traits (Rosenzweig 1995; Gordon 2000).

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[1] submitted by Theoretical Ecology as Esther A., Groeneveld J., Enright N.J., Miller B.P., Lamont B.B., Perry G.L.W., Tietjen, B., Jeltsch F. - How important are trade-offs to explain community structure and plant richness?

The number of suggested trade-offs is large (Stearns 1992; Cornelissen et al. 2003), with Stearns (1992) noting at least 45 readily-defined trade-offs between life history traits. The most commonly considered trade-offs include those between reproduction and current and future survival, reproduction and growth, and number and quality of offspring. Successful establishment of seedlings may, for example, be associated with seed size (Lamont and Groom 1998). Large seeds provide more resources for growth, enhancing the survival probability of young seedlings and their protection from environmental hazards such as drought or shading, and biotic hazards such as herbivory. Large-seeded species generally have lower seed production than small-seeded species (Turnbull et al. 1999; Jakobsson and Eriksson 2000), so that the former has a quality advantage while the latter has a quantity advantage. Ultimately, it is often assumed that these trade-off combinations, ‘less but large seeds’ and ‘more but small seeds’, lead to the same reproductive success (Tilman 1994; Cornelissen et al. 2003; Moles and Westoby 2006). However, seed size vs. seed number and other trade-offs evolve as part of a spectrum of life history traits, including plant size, longevity, juvenile survival rate and time to maturity (Moles and Westoby 2006), and must not be viewed simply as independent sets of alternative conditions. In fire-prone ecosystems one potential trade-off is related to the two main strategies for regeneration that have evolved in response to fire: resprouting (individuals survive fire, re-growing from protected buds above or below ground) and reseeding (individuals are killed by fire, but accumulate a seed bank with seed germination cued to fire) (Bell et al. 1984). Thus, seeders (or non-sprouters) generally produce and store a larger number of viable seeds, leading to a larger number of seedlings after fire (Groom and Lamont 1996).

Although there are many potential low dimensional trade-offs among species in plant communities, their relevance for explaining species diversity in real communities has been questioned (Clark et al. 2007) and a number of empirical studies, especially in species-rich communities, have often failed to identify trade-offs as a significant explanatory factor for coexistence (Clark et al. 2004; Chave 2004). Rather, the perceived importance of trade-offs is mostly based on the findings of elegant but simplistic mathematical models, e.g. ordinary differential equation models (ODEs). In principle, these models can explain the coexistence of an infinite number of species so long as their life history attributes match a certain life history trade-off, e.g. between dispersal and competitive abilities (Tilman 1994; Clark et al. 2007).

In marked contrast to trade-off theories, Hubbell (1997) presented a neutral model of species diversity. In his theory, species are seen as functionally equivalent, lacking niche differences, with a slow drift to extinction offset by speciation (Hubbell 1997). Clearly, the neutral theory and classical ODE trade-off models are opposite extremes along a range of theoretical approaches that try to explain species coexistence, often for a specific system (e.g. savannas: Jeltsch et al. 1996, 1998; Higgins et al. 2000; fire-prone shrubland: Groeneveld et al. 2002, Esther et al. 2008; forests: Tilman 1994, Bampfylde et al. 2005). While some of these models either explicitly or implicitly include certain trade-offs, it remains unclear how crucial these trade-offs are for species coexistence, since other mechanisms that may mediate coexistence, such as seed immigration or density regulation, are typically included in such models as well. This, together with the empirical uncertainty concerning the role of trade-offs in multi-species systems, clearly poses the need to clarify the importance of trade-offs for mediating coexistence in high biodiversity ecosystems.

Here, we explore the necessity of trade-offs for the maintenance of species richness. For this we use a spatially-explicit, rule- and individual-based, stochastic simulation model. Discrete trait categories define the details of the PFT-specific life history processes. The chosen PFTs include trait category sets that fit into the trade-off concept (e.g. few large seeds vs. many small seeds) as well as ‘super-types’ that are not constrained by energy or resource limitation (jack-of-all-trade, Rosenzweig 1995), and ‘loser-types’ that do not exploit resources efficiently. With this approach we address the importance of trade-offs in explaining the viability of PFTs and community pattern under fluctuating environmental conditions. We ask in particular:

i) Are trade-offs necessary for PFT survival in a variable, fire prone environment, if growing in a monoculture?
ii) Do ‘super-types’ necessarily dominate plant communities?
iii) Does the exclusion of ‘super-types’ from the community result in the expected strong increase in PFT richness, diversity, and in changes of community structure?

4.3 METHODS

The aim of this modelling study is to investigate the necessity of trade-offs for the local persistence of Plant Functional Types (PFTs) and for plant community pattern under fluctuating environmental conditions in a highly species rich ecosystem. Simulation experiments are conducted with a spatially-explicit, individual and rule-based model. The biological data and expert knowledge, which has been used to define the model rules and parameterisation, describe woody species of the northern sandplain shrublands near Eneabba, Western Australia, 270 km north of Perth. Non-woody plants make up a separate component of the community and are not modelled here. Detailed descriptions of the vegetation in the field region can be found in Cowling et al. (1987), Enright and Lamont (1989), Lamont et al. (1993, 2007), Enright et al. (1998a, b), Groeneveld et al. (2002) and Perry et al. (2008).

The model area covers a local vegetation patch of 60 m × 60 m, but model analysis is restricted to a core patch of 40 m × 40 m to minimise boundary effects. The model grid is subdivided into 0.5 m × 0.5 m cells, each potentially occupied by a single plant affiliated to one of 288 PFTs. Thus, density for the 40 m × 40 m area has a maximum of 6400 woody plants, matching field density estimates for mapped sites at this scale reported in Chiarucci et al. (2003) and Enright et al. (2007). Each PFT represents a life history strategy based on a set of seven categorical traits (Table 4.1, see section Life history traits). The trait categories define the demographic responses of individuals to ecological processes and environmental factors (Table 4.1; Fig. 4.1; see section Processes). In the following sections we describe the life history traits and processes; a more detailed description of the model can be found in Esther et al. (2008).

4.3.1 Life history traits

Key traits for the demographic behaviour of a species in a fire-prone environment have been derived from data for 156 woody species of the Eneabba sandplain shrublands. These traits are regeneration mode (2 levels), maximum crown diameter (2 levels), seed production (3 levels), seed size (3 levels), drought tolerance (2 levels), dispersal mode (2 levels) and seed bank type (2 levels) (Fig. 4.1; Appendix 4.7.1, for further details see Esther et al. 2008). These trait category combinations lead to 288 theoretically possible PFTs, each exhibiting a potentially different demographic behaviour (Table 4.1). The parameters and equations used in the model are described and listed in the Appendix 4.7.1 ‘Model parameters’, and the Appendix 4.7.2 ‘Equations in model’.

Table 4.1 Traits and their categories defining the plant functional types (PFTs). For each trait the associated attributes are given as well as the model processes in which the attributes are relevant.

Trait	Categories	Associated attributes	Processes
regeneration mode	resprouter non-sprouter	fire survival, longevity, gemination, age to maturity	Fire survival Inter-fire survival Growth
maximum crown diameter	shrub sub-shrub	maximum size, growth rate	Competition Growth Seed production
seed bank type	canopy soil	seed persistence, seed dispersal time, germination rate	Dispersal Germination
seed production	low moderate high	annual maximum seed production	Seed production
seed size	small medium large	seedling survival probability	Establishment
drought tolerance	more less	recruitment probability	Establishment
dispersal mode	short-range long-range	mean dispersal distance	Dispersal

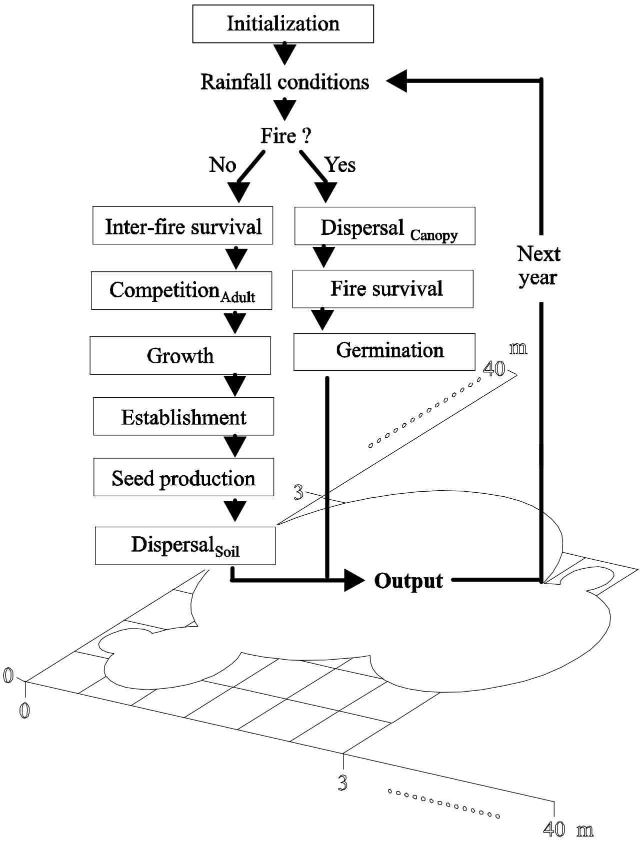

Fig. 4.1 Overview of the model processes (modified after Esther et al. 2008). Individuals are located in the lattice, while the interaction between individuals is modelled using a continuous Zone Of Influence approach.

4.3.2 Processes

After initialization, annual processes are iteratively simulated. Within each time step, all relevant life history processes are simulated for each individual, dependent on stochastic rainfall conditions and fire occurrence. If fire occurs in one time-step, then fire survival, dispersal of canopy-stored seeds, and germination of canopy- and soil-stored seeds are calculated. Otherwise, inter-fire survival, competition between neighbouring plants, growth, establishment, seed production, and dispersal of seeds from species with a soil seed bank, are simulated (see Appendix 4.7.1. for the reference parameter set).

Fire and rainfall conditions. The time between two consecutive fire events (t_f) is randomly determined by a Weibull distribution that was adjusted to produce a minimum interval of six years between fires (*low_cut*) (Esther et al. 2008). The mean inter-fire period (*IFP*) of 13.4 years was matched to field observations for the Eneabba plains (Appendix 4.7.1.; Miller et al. 2007). The annual rainfall condition is randomly assigned as wet (20% of years), average (55%), or dry (25%) based on >100 years of rainfall records from the closest climate station (p_R, Appendix 4.7.1.; Enright et al. 1998a, b; Groeneveld et al. 2002).

Fire-survival. Resprouters, in contrast to non-sprouters, can survive fire, with a probability (p_{f_surv}) which is a function of their age, the time since the last fire (t_f) and rainfall conditions of the current year (Enright et al. 1998b; Groeneveld et al. 2002). The probability p_{f_surv} (a) of an individual reaching age a increases until an age of 9 years, is constant for ages 10 to 40 years, and decreases thereafter at a rate positively correlated to the length of the inter-fire period (Eq. see Appendix 4.7.2; details see Groeneveld et al. 2002). Additionally, the probability of resprouters surviving fire is slightly lower in years classified as ‘dry’ due to drought stress (Appendix 4.7.1).

Dispersal. Seed dispersal depends on seed bank type, dispersal mode and plant crown diameter. Seeds of PFTs with soil seed banks are dispersed each year, while PFTs with canopy seed storage disperse seeds *en masse* after a fire (Enright et al. 2007). The dispersal distance of seeds is drawn from negative exponential functions, with mean dispersal distance (d_m) from the parent (Appendix 4.7.1; Esther et al. 2008). Mean short-range dispersal distance is related to the crown diameter of shrubs and sub-shrubs (greater crown width and plant height of shrubs extending the points of seed release relative to sub-shrubs), while d_m for long distance seed dispersal PFTs is 10-20 times greater than for short-distance dispersal PFTs, facilitating seed dispersal over the entire grid.

Germination – Seeds germinate only in the first year after a fire. While all seeds dispersed from the canopy seed bank germinate, a small fraction of soil-stored seeds remain dormant in the seed bank and so persist until the next fire ($1-f_{g\_soil}$, Appendix 4.7.1).

Inter-fire survival. The survival probability (p_{surv}) of mature plants in years between fire events is dependent on regeneration mode and age. (Appendix 4.7.1).

Competition. Individuals characterised by the same crown diameter type compete because their crowns can overlap. The strength of competition is calculated by the 'zone of influence' (ZOI) approach (Berger and Hildenbrandt 2000; Bauer et al. 2004) for each individual. Under ZOI, the strength of the competitive interaction and the subsequent reduction in growth is relative to the degree of overlap of neighbouring individuals. Growth stops if the strength of competition exceeds a threshold F_{max} (Appendix 4.7.1).

Growth. We differentiate two growth processes: plant regrowth after fire for surviving resprouters, described by the Michaelis-Menten equation (Tietjen and Huth 2006; Esther et al. 2008), and growth from seeds, which is modelled by the logistic equation (Esther et al. 2008). In the case of competition with neighbours, growth is reduced by a relative competition factor. Neighbouring plants can overlap, but the growth of sub-shrubs stops at the centre point of any neighbouring shrub.

Establishment. The establishment probability for a given PFT depends on its drought tolerance, the rainfall conditions and seed size (Appendix 4.7.1). The number of surviving seedlings per cell each year is calculated from a binomial distribution. Years with rainfall above average lead to better recruitment, especially for resprouters (Enright and Lamont 1992). Resprouter seedlings can only recruit under wetter than average conditions in the first year after fire. Seedlings germinating from larger seeds have higher survival rates than seedlings from smaller seeds, especially in dry years. At the same time, their density-dependent intra-specific seedling competition is higher (Lamont et al. 1993; Esther et al. 2008). This density-related competition is described by a power law, with the lowest exponent b for seedlings germinating from large seeds (Appendix 4.7.1, see Esther et al. 2008 for details). In the second year after a fire, one successful recruit from all seedlings within each cell is determined randomly with a probability related to the local PFT seedling abundance (a weighted lottery sensu Chesson and Warner 1981; Lamont and Witkowski 1995). Shrub recruitment is only possible in empty grid cells, i.e. grid cells which are not occupied by a surviving resprouter. Sub-shrubs can establish in cells that are partly covered by a shrub, as long as the centre of the overtopping individual is outside the respective grid cell.

Seed production. Plants start to reproduce at size $m_{s,}$ which is the theoretical size at age to maturity *A1* without competition (Appendix 4.7.1)., Resprouting shrubs and sub-

shrubs resume seed production at earliest two years and one year after fire, respectively, if they have reached the minimum radius m_s required to produce seeds (Appendix 4.7.1).
Annual seed loss from the seed bank is constant (1- v) and is calculated individual-based for canopy storage PFTs, and cell-based for soil seed bank PFTs. We chose parameters so that after 20 years, only 10% of all 20-year-old seeds are still viable.

4.3.3 Simulations

The spatial and temporal dynamics of the 288 virtual PFTs were simulated for a minimum time-span of 1,800 years to allow for convergence to a quasi-stationary state. The output variables, namely the number of individuals per PFT, the number of coexisting PFTs and the Shannon Diversity Index, were recorded five years after the first fire following the minimum time-span to provide a standard reporting time (after transitory seedling dynamics have been resolved).

Initialization. Fire is assumed to have taken place one year before the simulation starts. Thus, the initial age of non-sprouters is one year. The initial age of resprouters is chosen randomly from probability distributions based on empirical size-distributions (crown width) for several common resprouting shrub and sub-shrub species. For individuals characterised by soil seed storage, an initial number of seeds per plant ($Init_{seed}$) were distributed randomly over the lattice (Appendix 4.7.1).

Simulation experiments. We performed two sets of simulation experiments: ‘population level experiments’ and ‘community level experiments’. In the ‘population level experiments’ each PFT was simulated separately to assess its ability to persist under fluctuating rainfall and fire-driven environmental conditions. At the beginning of the simulation all cells in the 60 m × 60 m lattice were occupied, corresponding to a total of 14400 individuals. If a PFT went extinct in all of 20 repetitions (1800 years) then the PFT was deemed non-viable. In the ‘community level experiments’ consecutive simulations were used to identify the influence of ‘super-types’ and trade-offs on community patterns. The first simulation started with all viable PFTs from the ‘population level experiment’. At the end of this simulation the dominant PFT was identified and removed. The model was then again initialized and run without this PFT. This procedure was repeated, removing the dominant PFT each time until only one PFT remained. Each simulation was initialized with 40 individuals per PFT, which were randomly distributed over the whole grid (Appendix 4.7.1; see section Simulations). At the end of each community simulation the relative number of coexisting PFTs was calculated (the number of coexisting PFTs divided by the number of competing PFTs). The relative

Shannon Diversity Index (rSDI) was derived by dividing the SDI divided by the maximum SDI, which corresponds to the situation that all PFTs are present with the same number of individuals. To identify the dominant ‘super-type’ in the community simulation a PFT specific strength *St(x)* was determined by:

$$St(x) = \frac{1}{2}\left(P_x + \frac{\overline{N}_x}{\overline{N}} \right) \tag{4.1}$$

where P_x is the survival probability (percentage of replications where PFT x survived), $\overline{N}_x$ is the mean number of individuals from type x, and $\overline{N}$ is the mean number of all individuals. To calculate the strength *St(x)*, normally ten replications were used, however, to reduce computational time we stopped after four runs if a PFT dominated three of them.

4.4 RESULTS

4.4.1 Population level experiments

Single PFT population dynamics typically showed fluctuations depending on fire frequency and establishment conditions (i.e. rainfall) in the first two years after fire (Fig. 4.2). In spite of these fluctuations the simulated ‘populations’ generally reached a dynamic equilibrium after a few generations. The time span to equilibrium was typically reached sooner for non-sprouters than for resprouters due to their shorter life-spans. Of the 288 theoretically possible PFTs 38 were not viable under the simulated environmental conditions. All non-viable PFTs were non-sprouters with small seed size and low or moderate seed production, or with medium seed size and low seed production (Fig. 4.3a). The remaining 250 viable PFTs were used for the ‘community level experiments’.

4.4.2. Community level experiments

During the standard simulation time of 1800 years the mean number of coexisting PFTs declined strongly (Fig. 4.4). However, a quasi-stationary community dynamic was reached after a period of about 1600 years for the standard parameter set (Appendix 4.7.1; Fig. 4.4).

Of the 250 viable PFTs (including all ‘super-types’) simulated in the first community, 36 PFTs were able to survive at least in one run (4.3b). 23.1 PFTs coexisted on average with a standard deviation (SD) of 2.69 (Fig. 4.5a). The Shannon Diversity Index (SDI) was 2.41 with a SD of 0.11 (Fig. 4.5b). That is a relative number of coexisting PFTs of 9% with a relative SDI of 0.44 (Fig. 4.5c). Most of the coexisting PFTs were present with 100 to 500 individuals (Fig. 4.5a). Two PFTs reached densities of more than 1000 individuals (Fig. 4.5a), including one 'jack-off-all-trades', which had a mean relative abundance of 0.15 (Fig. 4.5a). This 'jack-off-all-trades' type was characterised by the trait expressions *resprouting*, *sub-shrub*, *canopy seed bank*, *high seed production*, *large seeds*, *more drought tolerance* and *long-range dispersal* (Fig. 4.3b). The resulting community contained no PFTs with low seed production or small seeds.

With the consecutive exclusion of 'super-types' in subsequent simulations the community structure remained similar, with a large group of PFTs with individual numbers between 100 and 500 and a few PFTs with more than 1000 individuals (Fig. 4.5a). The maximum mean number of 35.0 ±1.64 of coexisting PFTs (up to 47 PFTs persisted in at least one of 10 runs) was reached after 29 'super-types' were excluded, with an SDI of 2.80 ± 0.13 (Fig. 4.5a). The relative number of coexisting PFTs was 15.6% with a relative SDI of 0.52 (Fig. 4.5c). In this community the strongest PFT showed a relative abundance of 0.098. It was a *non-sprouting*, *shrub*, with *canopy seed bank*, *high seed production*, *large seeds*, *less drought tolerance* and *short-range dispersal* (Fig. 4.3c; Fig. 4.5c). We found resprouters with both typical trade-off characteristics and 'super-types' (Fig. 4.3c). A focus on the trade-off between competition and colonisation shows that the simulation started with 38.1% of resprouters with trait sets that fit into this concept, i.e. large seeds and low seed production, medium seeds and moderate seed production, or small seeds and high seed production. At the end of the simulation this number remained almost unchanged with only 44.7% of the 38 coexisting resprouters fitting into this trade-off concept (Fig. 4.3c). The same applies for seed size vs. seed dispersal. The frequency of resprouters having small seeds and unlimited dispersal or having large seeds with limited dispersal remained nearly constant, beginning with 34.9% and ending with 36.8% (Fig. 4.3c). For the trade–off between resprouting and reseeding, we started with 38% resprouters with low seed production, and ended the simulation with only 7.9% of remaining resprouters characterised by low seed production (Fig. 4.3c). Additionally, two resprouters in this optimised community were 'super-types, characterised by large seeds, high seed production and unlimited seed dispersal. Thus 68.4% of the resprouters fitted into one of these known trade-off concepts.

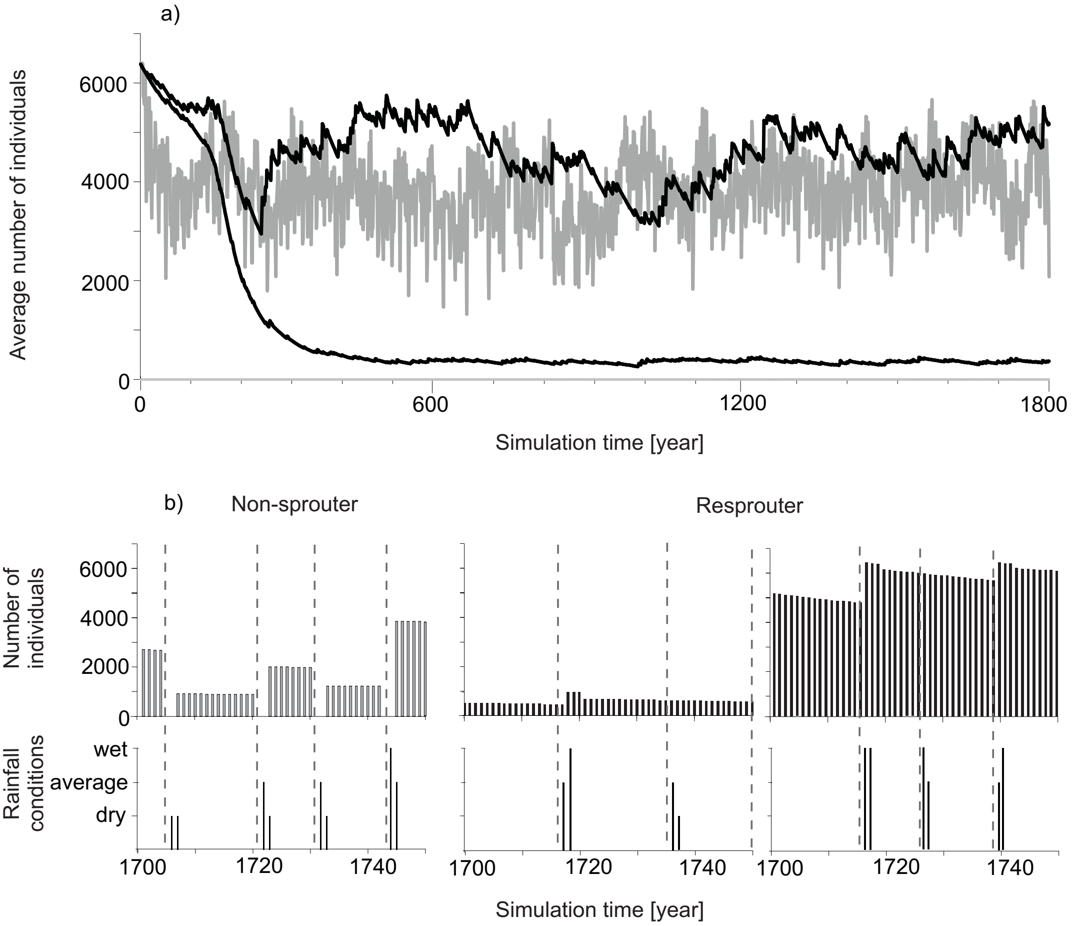

Fig. 4.2 Sample population dynamics for (a) mean of 10 replications of three PFTs simulated separately for a time span of 1800 years (grey line: non-sprouter, black lines: resprouters) and (b) a single run for 50 years, showing also the timing of fire events (dashed grey lines) and rainfall conditions in the first two years after fire. Longer inter-fire periods, average and good rainfall conditions increase recruitment success. Non-sprouters are killed by fire, whereas the number of resprouters is less influenced by fire events.

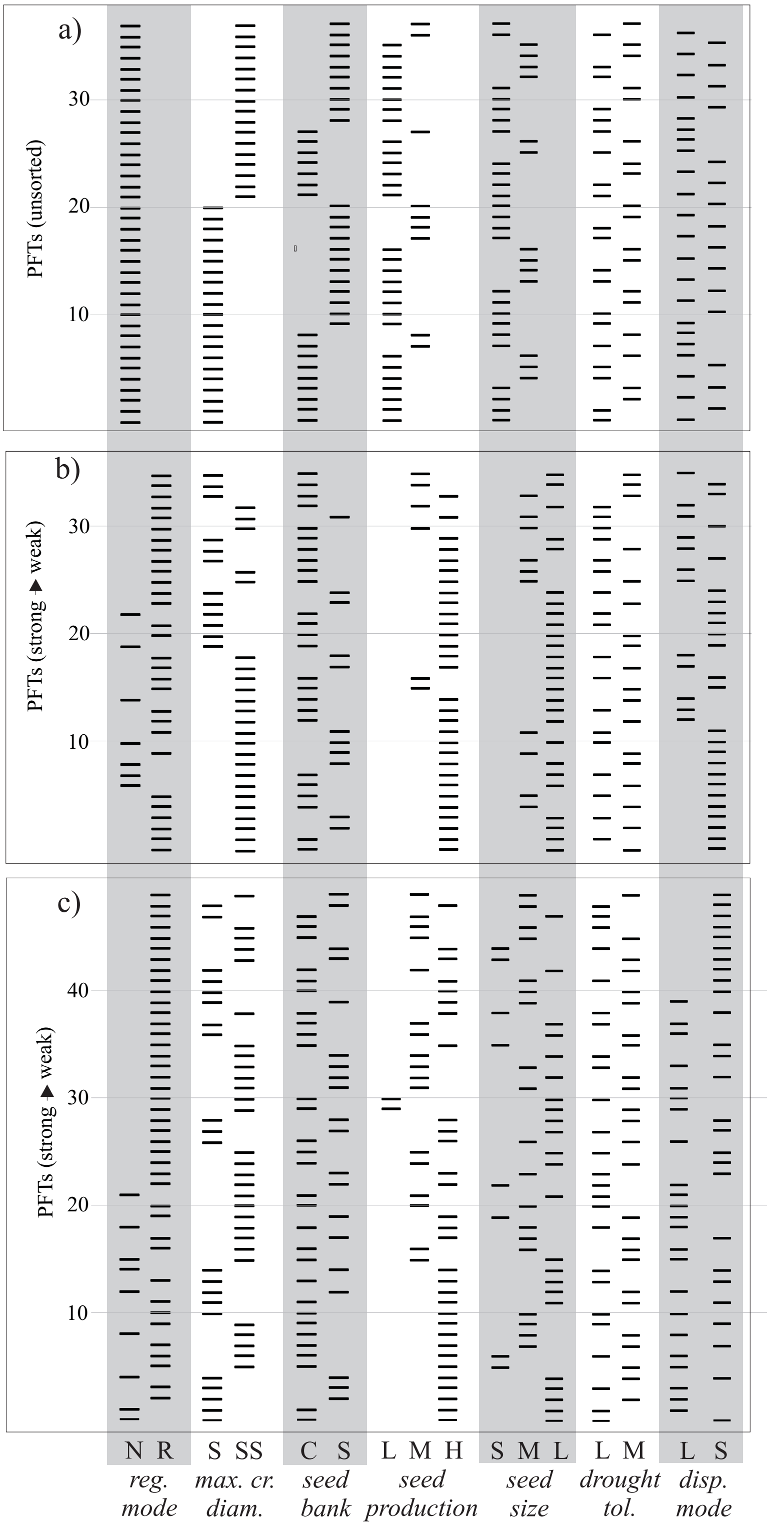

Fig. 4.3 Trait combinations a) of the 38 non-viable PFTs in the 'population experiment', b) of the 36 PFTs, which have persisted in at least one of four runs in the first community initialized with all 250 viable PFTs and c) of the 47 PFTs, which have persisted in at least one of 10 runs, in the communities with the highest mean PFT number (***reg**eneration **mode***: **N** non-sprouter, **R** resprouter**;** **m*ax*i*mum* *crown* *diam*eter**: **S** shrub, **SS** sub-shrub; ***seed bank***: **C** canopy, **S** soil; *maximum **seed production***: **L** low, **M** moderate, **H** high; ***seed size***: **S** small, **M** medium**, L** large; ***drought tol**erance*: **L** less, **M** more; ***disp**ersal **mode***: **S** short-range, **L** long-range).

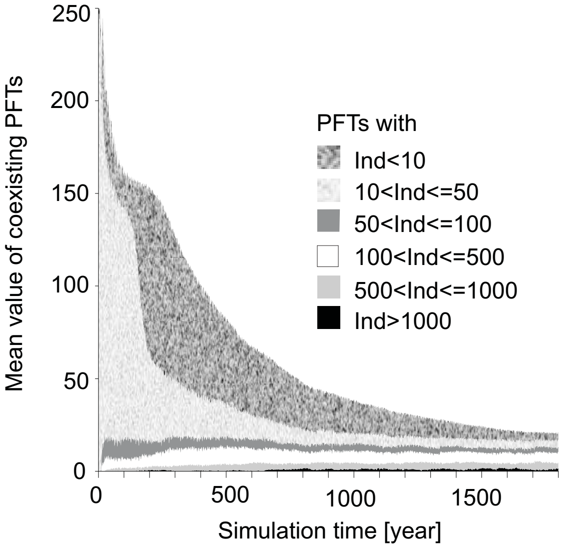

Fig. 4.4 Community dynamics of the 250 viable PFTs simulated together over a run time of 1800 years, averaged for 10 replications using the standard parameter set (Appendix 4.7.1).

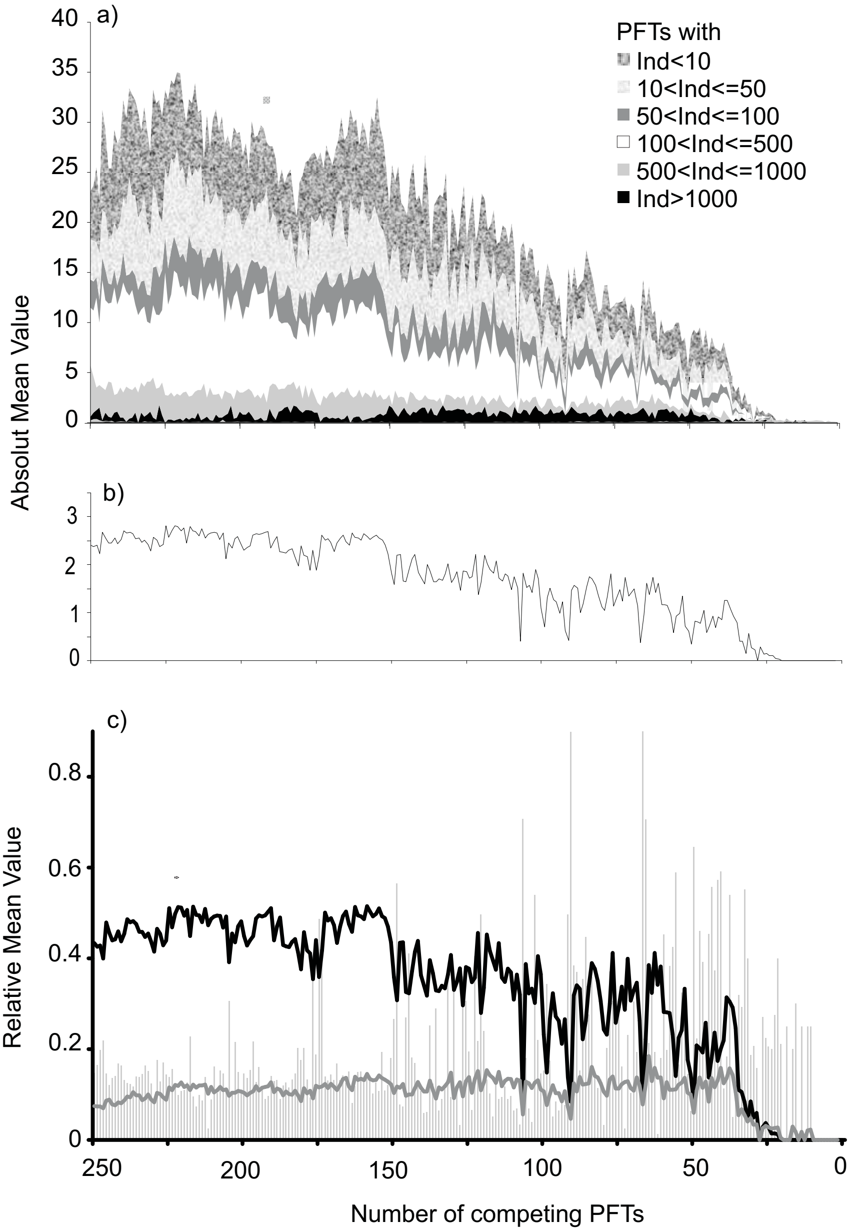

Fig. 4.5 Mean patterns for the 'Community level experiment' resulting from stepwise, successive exclusion of the strongest PFTs: absolute mean values for the number of coexisting PFTs with (a) abundance and (b) the Shannon Diversity Index. And, (c) the relative mean values for the Shannon Diversity Index (black line), the number of coexisting PFTs (grey line) and the relative abundance of the strongest PFT in the community (grey bars).

4.5 DISCUSSION

We investigated the importance of trade-offs and the influence of dominant plant functional types on richness and diversity in species-rich ecosystems using a spatially-explicit, mechanistic model by simulating the life-history processes of individual plants. The virtual community consisted of 288 theoretical plant functional types including trait combinations that consisted of only positive ('super-types') or negative trait expressions ('loser-types'). Our simulations did not support the view that trade-offs are necessary for PFT coexistence. The stepwise exclusion of dominant PFTs led to only a small increase in the diversity and number of coexisting PFTs from initially 23.1 to a maximum of 35.0. In the resulting virtual community only 68.4% of all coexisting resprouters showed at least one of the proposed trade-offs

Furthermore, two PFTs (resprouter, large seed size, high seed production, long-range dispersal mode – but less drought tolerant).of the most diverse community were 'super-types' and did not satisfy any of the proposed trade-off's. These findings are in strong contrast to the assumption that in the absence of trade-offs, communities would be dominated by a single, jack-of all-trades PFT (Rosenzweig 1995; Gordon 2000).

4.5.1. Trade-off mediated species diversity: empirical vs. theoretical studies

Interestingly, the paradigm of trade-off mediated multi-species coexistence, which goes back to early conceptual modelling approaches (Tilman 1994; Clark et al. 2007), has often failed in empirical tests. Though the existence of certain trade-offs has undoubtedly been shown in some ecological systems (e.g. the 'colonisation-competition trade-off: Tilman 1994), other data failed to support clear trade-off patterns at all (Bampfylde et al. 2005; Moles and Westoby 2006; Clark et al. 2007); e.g. Clark et al. (2004) found no empirical support for the competition-colonisation trade-off in forests.

The difficulties in empirically proving the importance of trade-offs to explain multi-species coexistence could indicate either that the importance of trade-offs for multi-species coexistence has been overestimated, or that the empirical evidence is masked by the inherent complexity of these systems and higher-dimensional species differences (i.e. more than three traits are involved) that are even more difficult to detect (Moles and Westoby 2006; Clark et al. 2007). For example, experimental studies on coexistence of plant species are typically based on systematic variations of single plant traits only, while keeping other factors constant (Arii and Parrott 2006; Vandvik and Goldberg 2006). In addition, the short duration of most empirical studies makes it difficult to assess the importance of trade-offs on diversity and species richness – which arise from interactions, potentially across many generations (Bampfylde et al. 2005).

Theoretical and modelling studies also fail to provide a clear picture of the relevance of trade-offs for multi-species coexistence. While several conceptual model studies support the trade-off hypothesis, they mostly demonstrate a putative trade-off mechanism under very restrictive assumptions such as the mean field condition (Tilman 1994; Chesson 2000; Amarasekare and Nisbet 2001; Warren and Topping 2004). Interestingly, single trade-offs seem to become less important as more realistic assumptions are incorporated (Warren and Topping 2004; Bampfylde et al. 2005), e.g. if biotic or abiotic factors create spatial heterogeneity (Jeltsch et al. 1996, 1998; Amarasekare and Nisbet 2001), and if whole life histories are considered (Howard and Goldberg 2001; Moles and Westoby 2006). Bampfylde et al. (2005) present an adaptation of Tilman's theoretical model (Tilman 1994), which more realistically simulates observed processes of gap colonisation in tropical rain forests. They found that a competition–colonisation trade-off is not sufficient to explain species coexistence in tropical rain forests. Likewise, Amarasekare and Nisbet (2001) illustrated that the dispersal-competition trade-off can lose its importance in driving competitive local coexistence if biotic or abiotic factors create spatial heterogeneity.

Our simulated trade-off patterns for a high diversity plant community also showed a lack of evidence for the inevitable need of trade-offs. However, trade-offs are shown to be important for (low competitive) PFTs threatened by environmental stochasticity (in this case, associated with recurrent fire and drought). If trait combinations were too negative, species went extinct even when interspecific competition was excluded. This result indicates that trade-off relations can be important as a basic precondition for (multi-) species coexistence, but may be overestimated as a key mechanism hindering competitive exclusion. This underlines the importance of alternative stabilizing processes such as intra-specific density regulation, which might be a ubiquitous mechanism in plant communities (Chesson 2000).

4.5.2. Dominance and influence of 'super-types'

Our simulation experiments show that 'super-types' are unable to completely dominate the community. This result is particularly interesting in relation to invasive species. There is ongoing debate on the question of what makes an exotic species a successful invader? And, which conditions lead to significant species loss in the native community, as a result of a successful invasive species (e.g. Mihulka et. al. 2006; Sebert-Cuvillier et al. 2007). Although our study was not designed to answer these questions, the results shown here clearly suggest that neither competitive dominance nor an advantageous combination of functional traits automatically leads to community depletion. However, for invasive species, a strong intra-specific density regulation effect may be slowed due to the absence of specific predators and diseases. This agrees with the findings of Arii and Parrott (2006) who examined exotic species of varying competitive abilities. They showed that species required a certain threshold level of competitive ability to establish in a new landscape, but that species with superior competitive ability do not necessarily become dominant in a landscape. In particular, a fluctuating environment may preclude this (Sebert-Cuvillier et. al 2007).

4.6 CONCLUSION

Our results support the view of other recent modelling studies of species interactions indicating the need to move further along the continuum from conceptual and theoretical, to realistic and field-based models in order to better understand the factors determining species coexistence (Gordon 2000; Warren and Toppings 2004; Jeltsch et al. 2008). We could not find strong support that low dimensional trade-offs are necessary to maintain high species richness in a spatially and temporally variable environment. This is in accordance with the neutral model which does not assume any stabilizing mechanisms to maintain species diversity (Hubbell 1997). But, species richness also could be maintained by alternative stabilizing processes, such as regional pool seed immigration (Esther et al. 2008), or local density regulation of seed production or seedling survival (e.g. Chesson and Warner 1981, Higgins et al. 2000). Detecting the mechanisms of coexistence in species-rich communities not only provides the basis for understanding species diversity but is a precondition for successfully addressing key ecological challenges in ecology such as species invasion and climate change impacts.

4.7 APPENDIX

4.7.1 Model parameters

Parameter	Value	Unit	Description of parameter	References
Initialization				
Init_{ind}	14400; 40		number of individuals initialized dependent on scenario (separate simulations; in community simulation)	
Init_{seed}	5; 23; 82		number of seeds in the soil per initialized individual with soil *seed bank* depending on its *maximum seed production* (low; moderate; high) This represents the fraction of seeds (see Table 2).	assumption: 1- f_{g_soil} of the viable seeds produced, accumulated in the soil seed bank over a period of 15 years that did not germinate after fire
Rainfall				
p_R	20; 55; 25	%	probability of good, average and bad rainfall conditions	Enright et al. 1998a, b
Fire				
IFP	13.4	year	mean value of inter-fire periods	Miller et al. 2007
low_cut	6	year	minimum time for fuel load to support a fire	Enright et al. 1998a
Dispersal				
d_d	9.375; 0.53; 1.33	m	mean seed dispersal distance dependent on *dispersal mode* and canopy crown diameter (long-range; short-range sub-shrub; short-range shrub)	Esther et al. 2008
Fire survival				
$p_{f—surv}$	0.997		survival probability for resprouters for age 10 until 40 years if a fire occurs	Groeneveld et al. 2002
$p_{f—addmort}$	0.03		additional mortality probability for resprouters if a fire occurs in a year with bad rainfall condions	Esther et al. 2008
Germination				
f_{g_soil}	0.8		fraction of soil stored seeds germinating after a fire	Esther et al. 2008
Inter-fire survival				
p_{surv}	0.997; 0.979; 0.802		survival probability: for age 3 years until 3/4 of longevity; if older than 3/4 of longevity then dependent on *regeneration mode* (resprouter; non-sprouter)	Enright et al. 1998a, b
L_{resp}; L_{non}	300; 40	year	longevity dependent on *regeneration mode* (resprouter; non-sprouter)	Enright et al. 1998a, b
Competition				
F_{max}	0.5		threshold of neighbourhood strength	Berger and Hildenbrandt 2000
Growth				
R_{max}	2.0; 0.6	m	maximum canopy radius; dependent on *maximum crown diameter* (shrub; subshrub)	Esther et al. 2008
t2	7; 3	year	for re-gowing resprouters; time after fire to reach 98% of the pre-fire size; dependent on *maximum crown diameter* (shrub; sub-shrub)	Enright et al. 1998b; Lamont and van Leeuwen 1988
GR_{max}	0.11; 0.03 0.77; 0.22	m/year	maximum growth rate; dependent on *regeneration mode* (resprouter-shrub, sub-shrub; non-sprouter-shrub, sub-shrub)	Esther et al. 2008
t_H	0.14; 0.06	year	for re-gowing resprouters; time it takes to reach half of the pre-fire size; dependent on *maximum crown diameter* (shrub; subshrub)	Esther et al. 2008
Establishment				
$f_{seedsize}$	0.11; 0.21 0.22; 0.40 0.45; 0.83		fraction of surviving seedlings; dependent on *seed size* (small; medium; large) in the first; second year after germination	Cowling et al. 1987, Enright and Lamont 1989, Lamont et.al 1993
$f_{rainfall}$	1.6; 1.0; 0.4		establishment factor; dependent on rainfall conditions (good; average; bad)	Cowling et al. 1987, Enright and Lamont 1989, Lamont et.al 1993
$f_{tolerance}$	0; -0.05		establishment factor; dependent on d*rought stress tolerance* (more; less)	
b	0.5;0.66;1		power law function exponent describing seedlings intraspecific competition; dependent on *seed size* trait (large; medium; small)	Esther et al. 2008
Seed production				
S_{max}	17; 74; 266		maximum seed production per year; dependent on *maximum seed production* (low; average; high)	Esther et al. 2008
A1	30; 5	year	age at maturity; dependent on *regeneration mode*	Enright et al. 1998a, b; Lamont 1996; Lamont and van Leeuwen 1988
m_s	0.026;0.012 0.066; 0.029	m	plant size necessary to produce seeds; dependent on *regeneration mode* (resprouter-shrub, sub-shrub; non-sprouter-shrub, sub-shrub)	assumption: equals plant size at age A1 if there is no competition
t1	2; 1	year	seed production hiatus after fire (secondary juvenile period); dependent on *maximum crown diameter* (shrub; sub-shrub)	Enright et al. 1998b; Lamont 1988, Lamont et al. 1993
L_{seed}	20	year	seed longevity	Lamont et al. 1991
v	0.89		yearly fraction of stored viable seeds; based on L_{seed}	Esther et al. 2008

4.7.2. Equations in Model

Processes	**Equation**
Fire survival	$p_{f\_surv}(a,t_f) = \begin{cases} \frac{a}{10} & \text{if } a < 10 \textit{ years} \\ 0.997 & \textit{if } 10 <= a < 40 \textit{ years} \\ 0.997 & \textit{if } 40 <= a <= 299 \textit{ years} \\ & \textit{and if } 0 < t_f <= 20 \textit{ years} \\ \frac{300-a}{300-40}\ x\ 0.997 & \textit{if } 40 <= a <= 299 \textit{ years} \\ & \textit{and if } 20 < t_f <= 60 \textit{ years} \\ \frac{100-a}{100-40}\ x\ 0.997 & \textit{if } a <= 100 \textit{ years} \\ & \textit{and if } 60 < t_f <= 299 \textit{ years} \\ 0 & \textit{if } a > 100 \textit{ years} \\ & \textit{and if } 60 < t_f <= 299 \textit{ years} \end{cases}$ $p_{f\_surv}(a,t_f) = p_{f\_surv}(a,t_f) - p_{f\_addition}$ $\textit{if}$ rainfall conditions ='dry' p_{f_surv} fire survival probability, a age, t_f time since last fire, $p_{f\_additon}$ additional mortality because dry rainfall conditions
Competition	$I_k = \frac{1}{A_k}\sum_{i=1}^{n} A_i$ $C = \begin{cases} 1-2I_K & \textit{if } I_k \le F_{\max} \\ 0 & \textit{if } I_k > F_{\max} \end{cases}$ I_k interaction with neighbourhood, A_k is the ZOI of the focal plant k; n number of neighbours, A_i shared area of individual k and I; C relative competition, F_{max} threshold of neighbourhood strength

Growth	$\frac{dR_P}{dt} = \begin{cases} \frac{R_P}{t_H}\cdot\left(\frac{R_P}{R_{pre\_f}}-2\right)+\frac{R_{pre\_f}}{t_H} & if\ \ age > t_f\ \ and\ t_f\ < t2 \\ \frac{GR_{\max}}{R_{\max}}\cdot R_P\left(1-\frac{R_P}{R_{\max}}\right) & else \end{cases}$ $R(t) = C * (Rp(t) - R(t-1)) + R(t-1)\ \ if\ \ R(t-1) < R_{\max}$ *Rp* crown radius, t_H time it takes to reach half of the pre-fire radius R_{pre_f}, GR_{max} maximum growth rate, R_{max} maximum radius, t_f time since fire, *t*2 time needed to reach 98% of the pre-fire crown radius, *R*(*t*) current radius, *C* relative competition, potential crown radius *Rp*
Establishment	$S(t) = S(t-1) * f_{seedsize} * \left(f_{rainfall} + f_{tolerance}\right)\quad if\ \ age < 3$ $N` = N^b$ *S*(*t*)surviving seedlings, *S*(*t*-1) number of seedlings from the previous year, $f_{seedsize}$ seed size factor, $f_{rainfall}$ precipitation conditions factor, $f_{tolerance}$ drought tolerance factor, *N*\` number of seedlings in year 3, *b* seed size specific exponent
Seed production	$N_{ps}(t) = \begin{cases} S_{\max}\times\frac{R(t)}{0.98\,r_{\max}} & \text{if R(t)} < 0.98\,\text{r}_{\max} \\ S_{\max} & else \end{cases}$ $B_i(t) = Seed_{input} + B_i(t-1)\cdot v$ $N_{ps}(t)$ seeds produced per year, S_{max} trait specific maximum seed production per year, *r(t)* current radius, r_{max} trait specific maximum radius, $Seed_{input}$ number of seeds produced in the current year, $B_i(t-1)$ total number of seeds in the seed bank from the previous year, *v* fraction of stored viable seeds, 0.98 threshold because growth following a logistic equation with approximation against r_{max}

4.8 LINK TO THE NEXT CHAPTERS

In this chapter, I investigated the importance of trade-offs to explain coexistence of virtual plant functional types. I showed that low-dimensional trade-offs are not necessary to maintain high species richness in a spatially and temporally variable environment. It can be assumed that there are other stabilizing processes to explain locally high diversity (e.g. density regulation). Therefore I used 288 virtual PFTs created from the traits in field, but not all of them are found in field.

In the following chapter I will expand the investigation of processes that maintain local species diversity to the regional spatial scale simulating. In particular I will present how seed immigration does affect species richness and diversity. Therefore the 38 realistic PFTs found at the 40 m by 40 m crest study site at Eneabba (Fig. 3.1) were simulated under different annual immigration rates and the simulation results were systematically compared with the empirical community pattern.

5 ASSESSING THE IMPORTANCE OF SEED IMMIGRATION ON COEXISTENCE OF PLANT FUNCTIONAL TYPES IN A SPECIES-RICH ECOSYSTEM [1]

5.1 ABSTRACT

Modelling and empirical studies have shown that input from the regional seed pool is essential to maintain local species diversity. However, most of these studies have concentrated on simplified, if not neutral, model systems, and focus on a limited subset of species or on aggregated measures of diversity only (e.g., species richness or Shannon diversity). Thus they ignore more complex species interactions and important differences between species. To gain a better understanding of how seed immigration affects community structure at the local scale in real communities we conducted computer simulation experiments based on plant functional types (PFTs) for a species-rich, fire-prone Mediterranean-type shrubland in Western Australia. We developed a spatially-explicit simulation model to explore the community dynamics of 38 PFTs, defined by seven traits – *regeneration mode*, *seed production*, *seed size*, *maximum crown diameter*, *drought tolerance*, *dispersal mode* and *seed bank type* – representing 78 woody species. Model parameterisation is based on published and unpublished data on the population dynamics of shrub species collected over 18 years. Simulation experiments are based on two contrasting seed immigration scenarios: (i) the 'equal seed input number' scenario, where the number of immigrant seeds is the same for all PFTs, and (ii) the 'equal seed input mass' scenario, where the cumulative mass of migrating seeds is the same for all PFTs. Both scenarios were systematically tested and compared for different overall seed input values. Without immigration the local community drifts towards a state with only 13 coexisting PFTs. With increasing immigration rates in terms of overall mass of seeds the simulated number of coexisting PFTs and Shannon diversity quickly approaches values observed in the field. The equal seed mass scenario resulted in a more diverse community than did the seed number scenario. The model successfully approximates the frequency distributions (relative densities) of all individual plant traits except *seed size* for scenarios associated with equal seed input mass and high immigration rate. However, no scenario satisfactorily approximated the frequency distribution for all traits in combination. Our results show that regional seed input can explain the more aggregated measures of local community structure, and some, but not all, aspects of community composition. This points to the possible

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[1] published as Esther A., Groeneveld J., Enright N.J., Miller B.P., Lamont B.B., Perry G.L.W., Schurr F. M., Jeltsch F. 2008. Assessing the importance of seed immigration on coexistence of plant functional types in a species-rich ecosystem. Ecol Model 213: 402-416

importance of other (untested) processes and traits (e.g., dispersal vectors) operating at the local scale. Our modelling framework can readily allow new factors to be systematically investigated, which is a major advantage compared to previous simulation studies, as it allows us to find structurally realistic models, which can address questions pertinent to ecological theory and to conservation management.

5.2 INTRODUCTION

Whether coexistence between plant species is driven by local or regional processes is a fundamental question in community ecology (Tilman and Pacala 1993; Bengtsson et al., 1997; Zobel 1997; Mouquet et al. 2004). The competitive exclusion principle predicts that competition in a homogeneous environment will reduce species diversity (Hardin 1960). However, several stabilising and equalising processes can slow down this reduction, or prevent the decline of diversity. These include both local (Hutchinson 1961; Tilman 1982) and regional processes (Loreau and Mouquet 1999; Leibold et al. 2004; Wildi and Orlóci 2007). From a regional perspective, immigration of individuals can re-establish populations or prevent their local extinction (e.g., Huston and LeAngelis 1994; Hanski 1999). For example, permanent or temporary sink plant populations can be prevented from local extinction by seed input from neighbouring source populations (Pulliam 1988, 2000; Loreau and Mouque 1999; Mouquet and Loreau 2003). These source–sink dynamics (Shmida and Ellner 1984) can be variable in space and time, leading to complex patterns of spatial metacommunities (Leibold et al. 2004; Holyoak et al. 2005; Urban 2006).

These theoretical findings have frequently been observed in plant communities by manipulating immigration processes (Turnbull et al. 1999; Zobel et al. 2000; Foster 2001). Such studies have shown that manipulating immigration rates can drastically alter species composition depending on levels of migration, on seed morphology, on competitive interactions, and on environmental variation (Turnbull et al. 1999; Zobel et al. 2000; Foster 2001; Coomes and Grubb 2003; Kisdi and Geritz 2003; Mouquet et al. 2004; Hiltunen et al. 2006). However, detailed experiments manipulating and analysing seed input in complex, species-rich communities are difficult to conduct. This also complicates the identification of thresholds of necessary seed input for local species survival.

Computer simulation experiments can provide a useful approach where field experiments are precluded due to long timescales and high spatio-temporal and compositional complexity (e.g., Jeltsch et al. 1999; Grimm et al. 2005; Lischke et al. 2007). Although the importance of immigration for local species survival and diversity has been identified in several modelling studies, seed immigration has rarely been the focus of these studies, and most modelling studies integrating regional seed input into community dynamics are either restricted to a limited subset of species of a real community (Wiegand et al. 1995) or focus on more theoretical questions in hypothetical communities (Hubbell 1997; Pachepsky et al. 2001). Currently we are not aware of any modelling study explicitly addressing the role of seed input for community structure in a realistic species-rich, plant community.

In this paper, we apply an individual-based, spatially-explicit and stochastic simulation model to evaluate the effect of different immigration levels on local plant diversity under a temporally varying environment. The model is based on published and unpublished data on the population dynamics of woody species collected in the highly diverse northern sandplain
shrublands, of Western Australia. In the model, species are classified into plant functional types (PFTs) according to selected trait category combinations (Cornelissen et al. 2003). Discrete trait categories define individual responses during the simulation of the important life history processes. We systematically vary the annual total seed mass rates immigrating into the local plant community, distinguishing between two immigration scenarios: (i) the ‘equal seed input number’ scenario, where each of the PFTs from the regional pool contributes the same number of seeds to the overall seed rain (Turnbull et al. 1999; Zeiter et al. 2006), and (ii) the ‘equal seed input mass’ scenario, where the same cumulative seed mass for all PFTs from the regional pool is contained in the seed rain. The latter scenario implies that PFT-specific seed numbers in the seed rain are negatively correlated with seed mass (Mouquet et al. 2004), so that PFTs with larger seeds contribute fewer seeds to the seed rain than do PFTs with smaller seeds (Horn and MacArthur 1972; Hastings 1980; Tilman 1994; Moles and Westoby 2006). This conforms to the competition/colonisation hypothesis (Tilman 1997; Moles and Westoby 2006). To identify the potential role of regional seed input in maintaining local community composition and diversity, we focussed on the following questions:

i) Does seed input from a species-rich regional PFT pool increase local PFT richness and diversity?

ii) If yes, how does this increase depend on the mode (equal seed input numbers vs. equal seed input mass from all PFTs of the regional pool) and the intensity (from low to high) of total mass of seed input?

iii) Can regional seed rain explain the observed complexity of community patterns such as plant trait frequency distributions?

5.3 METHODS

The aim of this modelling study was to investigate the effects of immigration on a species-rich plant community under realistic environmental conditions. Simulation experiments were conducted with a spatially-explicit stochastic individual and rule based model. All biological data used in the model were collected in the northern sandplains of the Mid-West region of Western Australia near the town of Eneabba, 275km north of Perth.

The sandplain is characterised by unconsolidated, acidic and nutrient-poor sands. Maximum temperatures of >40 ◦C are common in the summer months between December and March, and average rainfall is ca. 500mmyear−1, of which 80% falls between May and August (winter), so that summer drought is a major cause of plant mortality, especially for seedlings (Enright and Lamont 1992). The flora is classified as a fire-prone Mediterranean-type sclerophyll shrubland with cover of >70% in mature stands. The plant demographic data used in the model comprise published and unpublished information on the population dynamics of 156 woody species of the sandplain region (Cowling et al. 1987; Enright and Lamont 1989; Lamont et al. 1993; Enright et al. 1998a, b; Groeneveld et al. 2002; Enright and Lamont unpubl. data).

5.3.1 Model description

The model area covers a local vegetation patch of size 60m×60m inclusive of a buffer zone of 10m with results reported for the central 40m×40m area, to minimise boundary effects. The model grid is subdivided into 0.5m×0.5m cells, each potentially occupied by a single plant characterised by its plant functional type (PFT), and so supporting up to a total of 14,400 individuals. The structure of the model with its hierarchical levels is described in the next section. In the model, annual processes are simulated iteratively after initialization and scenario selection (Fig. 5.1; details see section Processes and Simulations). We have incorporated periodic boundary conditions to deal with the spatial scale of seed dispersal, which can extend the size of the buffer zone.

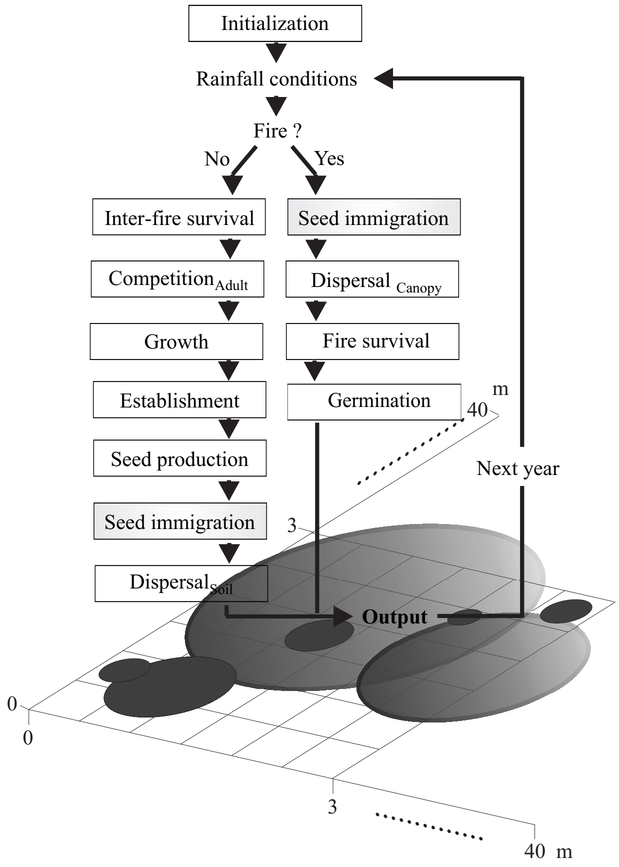

Fig. 5.1 Simplified diagram of the model structure—the lattice with individuals' zone of influence and the flow chart showing iteratively simulated processes, including seed immigration.

5.3.2 Model structure

The model comprises three hierarchical levels: grid (patch), grid cell, individual PFT. The grid consists of grid cells. Environmental processes such as fire and rainfall affect all grid cells in the same way and are therefore state variables of the grid. Grid cells are characterised by their location. Potentially, each cell can be occupied by one adult, which is modelled as an individual, and an unlimited number of seedlings and seeds (in canopy and soil-stored seed banks). Individuals are described by the state variables: PFT, age, current crown radius. Individuals are referred to as seedlings until they are 3 years old, and thereafter they are adults.

Each PFT represents a life history strategy based on a set of seven categorical traits, based on observations for 156 woody species of the Eneabba sandplain shrublands, considered to be most likely to influence the demographic behaviour of species in a fire-prone environment (Table 5.1). The trait categories define the demographic responses of individuals in the simulation which operates iteratively in annual time steps. The traits used are regeneration mode, seed production, seed size, maximum crown diameter, drought tolerance, dispersal mode and seed bank type. We identify 38-plant functional types (from a total of 288 possible PFTs) among the extant woody species, each characterised by a specific trait category combination. The life history trait categories determine an individual's response during the simulation as follows:

Table 5.1 Modelled traits and strategies with examples of woody species

Regeneration mode
Resprouter (*Banksia attenuata, Hakea incrassata*)
Non-sprouter (*Banksia hookeriana, Beaufortia elegans*)

Maximum crown diameter
Shrub (*Banksia hookeriana*, *Banksia menziesii*)
Sub-shrub (*Dryandra carlinoides, Melaleuca scabra*)

Seed bank
Canopy (*Banksia hookeriana, Banksia attenuata*)
Soil (*Jacksonia fasciculata, Leucopogon hispidus*)

Drought tolerance
Less (*Banksia menziesii, Pimelea leucantha*)
More (*Hakea psilorrhyncha, Banksia leptophylla*)

Dispersal distance
Short-range (*Astroloma microdonta, Leucopogon oxycedrus*)
Long-range (*Banksia hookeriana*, *Banksia attenuata*)

Maximum seed production
Low (*Banksia attenuata*, *Banksia menziesii*)
Moderate (*Banksia hookeriana*, *Acacia fagonioides*)
High (*Calothamnus torulosus*, *Melaleuca leuropoma*)

Seed size
Small (*Pityrodia bartlingii, Calytrix superba*)
Medium (*Dryandra tortifolia, Hakea spathulata*)
Large (*Hakea polyanthema*, *Banksia attenuata*)

Regeneration mode describes the response of an individual to fire. While non-sprouters are killed by fire, resprouters survive and re-grow vegetative (Table 5.1). The regeneration mode also influences the longevity, germination, and age at maturity (see processes Fire survival and Inter-fire survival).

Maximum crown diameter distinguishes between two plant categories; shrubs, with a maximum crown diameter of 4.0 m, and sub-shrubs, with a maximum crown diameter of 1.2 m. The maximum size of individuals affects the processes; competition, growth, and seed production. Greater height of shrubs than sub-shrubs is implied, but is not explicitly modelled.

Seed bank type defines whether the seeds of mature plants are stored in a soil or in a canopy (serotinous) seed bank. Seed bank type also influences the time of dispersal and the fraction of germinating seeds (see processes Dispersal and Germination). While soil stored seeds may persist in the soil after parent plants are dead, canopy stored seeds do not persist after parent death.

Seed production describes the maximum number of viable seeds which can be produced per plant per year. We classify three levels: low, medium and high (see process Seed production). Seed production is calculated such that individuals accumulate the estimated mean number of stored seeds as observed in the field 15 years after fire.

Seed size divides plants into three groups characterised by; small seeds (plan area of the largest surface <6.25mm²), medium seeds (6.25–25mm²) and large seeds (>25mm²). Seed size affects the survival probability of seedlings, probability increasing with seed size (see process Establishment).

Drought tolerance determines the recruitment probability in years with low rainfall and is dependent on leaf morphology. Plants with small leaves (<200mm²), needle-leaves or aphylly are characterised by increased tolerance to drought at the seedling stage. In contrast, plants with large leaves (≥200mm²) are characterised by lower drought tolerance (see process Establishment).

Dispersal mode defines whether the mean dispersal distance of seeds is short-range (i.e., local) or long-range (i.e. regional) (see process Dispersal).

5.3.3 Processes

After initialization, annual processes are iteratively simulated. Within each time step, rainfall conditions and fire occurrence are evaluated and the relevant life history processes simulated for each individual. If a fire takes place, fire survival, dispersal of canopy-stored seeds, and germination are calculated. If there is no fire, then inter-fire survival, competition between plants, growth, establishment, seed production, and dispersal of soil-stored seeds are calculated (see Fig. 5.1 and Table 5.2 for the reference parameter set). Seed immigration is simulated in each year, independent of fire occurrence.

Fire and rainfall conditions. The time between two consecutive fire events is a minimum of 6 years (low cut) plus a random time determined by a Weibull distribution (Rinne 1997), with a shape parameter of 2 and a scale parameter of 8.1. The resulting mean inter-fire period (IFP) of 13.4 years conforms to the results of mean fire return interval analysis from satellite image data for the Eneabba sandplains since the 1970s (Table 5.2; Enright et al. 1998a,b; Miller et al. 2007). This lower cut is given by the likely minimum time needed for a sufficient build-up of fuel to carry a fire. The annual rainfall condition (wet, average, dry) is chosen according to a probability distribution generated from rainfall records for 110 years from the closest climate station with long-term rainfall records (Dongara) to the field sites. Years are randomly assigned as wet (20% of years), average

Table 5.2 Model parameters

Parameter	Value	Unit	Description of parameter	References
Initialization				
$Init_{seed}$	5; 23; 82		number of seeds in the soil per initialized individual with soil *seed bank* depending on its *maximum seed production* (low; moderate; high) This represents the fraction of seeds (see Table 2).	assumption: 1- f_{g_soil} of the viable seeds produced, accumulated in the soil seed bank over a period of 15 years that did not germinate after fire
Rainfall				
p_R	20; 55; 25	%	probability of good, average and bad rainfall conditions	Enright et al. (1998a, b)
Fire				
IFP	13.4	year	mean value of inter-fire periods	Miller et al. (2007)
low_cut	6	year	minimum time for fuel load to support a fire	Enright et al. (1998a)
Dispersal				
d_{m_l}	9.375;	m	mean seed dispersal distance if *dispersal mode* is long-range	unpublished
d_{m_s}	0.53; 1.33	m	mean seed dispersal distance if *dispersal mode* is short-range and dependent on canopy crown diameter (sub-shrub; shrub)	unpublished
Fire survival				
p_{f_surv}	0.997		survival probability for resprouters for age 10 until 40 years if a fire occurs	Groeneveld et al. (2002)
$p_{f\_addmort}$	0.03		additional mortality probability for resprouters if a fire occurs in a year with bad rainfall condions	unpublished
Germination				
f_{g_soil}	0.8		fraction of soil stored seeds germinating after a fire	unpublished
Inter-fire survival				
p_{surv}	0.997; 0.979; 0.802		survival probability: for age 3 years until 3/4 of longevity; if older than 3/4 of longevity then dependent on *regeneration mode* (resprouter; non-sprouter)	Enright et al. (1998a, b)
L_{resp}; L_{non}	300; 40	year	longevity dependent on *regeneration mode* (resprouter; non-sprouter)	Enright et al. (1998a, b)
Competition				
F_{max}	0.5		threshold of neighbourhood strength	Berger and Hildenbrandt (2000)
Growth				
R_{max}	2.0; 0.6	m	maximum canopy radius; dependent on *maximum crown diameter* (shrub; subshrub)	unpublished
t2	7; 3	year	for re-gowing resprouters; time after fire to reach 98% of the pre-fire size; dependent on *maximum crown diameter* (shrub; sub-shrub)	Enright et al. (1998b); Lamont and van Leeuwen (1988)
GR_{max}	0.11; 0.03 0.77; 0.22	m/year	maximum growth rate; dependent on *regeneration mode* (resprouter-shrub, sub-shrub; non-sprouter-shrub, sub-shrub)	unpublished
t_H	0.14; 0.06	year	for re-gowing resprouters; time it takes to reach half of the pre-fire size; dependent on *maximum crown diameter* (shrub; subshrub)	unpublished
Establishment				
$f_{seedsize}$	0.11; 0.21 0.22; 0.40 0.45; 0.83		fraction of surviving seedlings; dependent on *seed size* (small; medium; large) in the first; second year after germination	Cowling et al. (1987), Enright and Lamont (1989), Lamont et.al (1993)
$f_{rainfall}$	1.6; 1.0; 0.4		establishment factor; dependent on rainfall conditions (good; average; bad)	Cowling et al. (1987), Enright and Lamont (1989), Lamont et.al
$f_{tolerance}$	0; -0.05		establishment factor; dependent on d*rought stress tolerance* (more; less)	
b	0.5;0.66;1		power law function exponent describing seedlings intraspecific competition; dependent on *seed size* trait (large; medium; small)	unpublished
Seed production				
S_{max}	17; 74; 266		maximum seed production per year; dependent on *maximum seed production* (low; average; high)	unpublished
A1	30; 5	year	age at maturity; dependent on *regeneration mode*	Enright et al. (1998a, b); Lamont (1996); Lamont and van Leeuwen (1988)
m_s	0.026;0.012 0.066; 0.029	m	plant size necessary to produce seeds; dependent on *regeneration mode* (resprouter-shrub, sub-shrub; non-sprouter-shrub, sub-shrub)	assumption: equals plant size at age A1 if there is no competition
t1	2; 1	year	seed production hiatus after fire (secondary juvenile period); dependent on *maximum crown diameter* (shrub; sub-shrub)	Enright et al. (1998b); Lamont (1988), Lamont et al. (1993)
L_{seed}	20	year	seed longevity	Lamont et al. (1991)
v	0.89		yearly fraction of stored viable seeds; based on L_{seed}	

(55%), or dry (25%), without accounting for inter-year correlation (p_R, Table 5.2; Enright et al. 1998a, b; Groeneveld et al. 2002).

Fire-survival. Non-sprouters are killed by fire. Resprouters can survive and re-grow from buried stem tissues after a fire event with a fire survival probability depending on their age, the time since the last fire (t_f) and the rainfall condition of the current year (Enright et al. 1998b; Groeneveld et al. 2002). The fire survival probability ($p_{f\ surv}$) is assumed to increase linearly from 0 to 0.889 until an age of 9 years (details see Groeneveld et al. 2002). For ages 10–40 years the probability is constant, but thereafter slowly decreases (linearly) reflecting a decline in the dormant bank of vegetative buds on the lignotuber at long fire intervals ($p_{f\ surv}$, Table 5.2; Enright et al. 1998b; Groeneveld et al. 2002). Resprouter probability to survive a fire is lower ($p_{f\ surv} - p_{f\ addmort}$) if the rainfall condition is 'dry' in the current year (Table 5.2). Resprouter above-ground biomass is removed by fire and it takes 1 year for mature sub-shrubs and 2 years for mature shrubs to resume seed production (*t1*, Table 5.2; see Seed production).

Seed immigration. We randomly distributed an annual total seed input mass of 0.011, 0.11, 1.1 and 11 g/m² over the whole lattice. This total seed input mass is the same for both scenarios, i.e., the distributed seed numbers are either calculated on the basis of (i) equal seed input numbers or (ii) equal seed input mass for all PFTs. The actual seed numbers distributed per PFT thus differ due to the differing specific PFT seed characteristics (for further details see Section 2.2 and Appendix 5.6.1). Seeds are randomly distributed for each PFT.

Dispersal. The time of seed dispersal depends on the seed bank type. Annual seed crops of plants with a soil seed bank are dispersed each year. In contrast, for canopy seed storage PFTs, total accumulated seed stores are dispersed immediately after fire. The distribution of dispersal distances is described by a negative exponential function with an average dispersal distance dm from the parent (Bauer et al. 2002; Groeneveld et al. 2002). We distinguish between short-range ($d_{\mathrm{m\ s}}$) and longer-range ($d_{\mathrm{m\ l}}$) dispersal (Table 5.2). For short-range dispersal this parameter differs depending on the crown diameter trait for shrubs and sub-shrubs (i.e., dispersal distance is greater for shrubs due to the influence of greater crown width and plant height on the points of seed release).

Germination. Germination only occurs after a fire. If a fire occurs, all dispersed canopy seeds germinate (i.e. only estimated numbers of viable seeds are dispersed). For soil-stored seeds, not all seeds germinate, a small fraction of ungerminated seeds remaining dormant in the seed bank ($1-f_{\mathrm{g\ soil}}$, Table 5.2).

Inter-fire survival. Mature plants survive each year in the absence of fire with a probability (p_{surv}) which depends on the age of the plant (Table 5.2). Overall survival declines such that by the time the assumed maximum longevity has been reached, at least 99% of all plants have died (L_{resp}, L_{non}, Table 5.2).

Competition. Competition can occur between individuals of the same crown diameter type. To calculate competition, the "zone of influence" (ZOI) approach is used. Here, the influence of competition on a plant depends on the distance from, and the size of, its neighbours (Berger and Hildenbrandt 2000; Weiner et al. 2001; Aiko 2004; Bauer et al. 2004). The plant is characterised by its stem position and a circular zone of influence around this position (Berger and Hildenbrandt 2000; Weiner et al. 2001; Bauer et al. 2004). We assume the ZOI to be equal to the canopy area. To quantify the *n* neighbours influence on an individual *k*, the interaction with neighbourhood I_k is calculated as:

$$I_k = \frac{1}{A_k} \sum_{i=1}^{n} A_i \qquad (5.1)$$

where *Ai* denotes the area which is shared by ZOI's of individual *k* and *I*, and *Ak* is the ZOI of the focal plant *k*.

The interaction with neighbourhood determines the relative competition, *C*:

$$C = \begin{cases} 1 - 2I_K & if\ \ I_k \leq 0.5 \\ 0 & if\ \ I_k > 0.5 \end{cases} \qquad (5.2)$$

where $F_{\max}$ is the threshold of neighbourhood strength (details see Berger and Hildenbrandt 2000; Bauer et al. 2002).

Growth. Neighbouring plants are allowed to overlap. But the growth of sub-shrubs stops at the centre point of any neighbouring sub-shrub. We differentiate two growth processes: plant regrowth after fire for surviving resprouters, described by the Michaelis-Menten equation (5.3a) (Tietjen and Huth 2006), and growth from seeds, which is described by logistic equation (5.3b) (Bauer et al. 2002). Regrowth after fire is described by equation 5.3a until the plant has reached 98% of its pre fire diameter, which is at age t_2. After that, growth of resprouters is also described by logistic Eq. (5.3b):

$$\frac{dRp}{dt}=\begin{cases}\frac{Rp}{GR_{\max}}*\left(\frac{Rp}{R_{pre\_f}}-2\right)+\frac{R_{pre\_f}}{GR_{\max}} & if\ \ age>t_f\ \ or\ t_f<t2 \qquad (5,3a)\\ GR_{\max}*\frac{Rp}{R_{\max}}\left(1-\frac{Rp}{R_{\max}}\right) & else\end{cases}$$

(5.3b)

where; GR_{max} is the maximum growth rate, Rp is crown radius, $R_{pre\_f,}$ is pre-fire radius, R_{max} is maximum radius, t_f is time since fire, and t_2 is the time needed to reach 98% of the pre-fire crown radius. Maximum growth rate is calculated using the assumption that individuals reach 98% of their maximum crown radius at an age of 60% of longevity when growing without competition. The actual radius R(t) depends on the relative competition C (Eq. 5.2) and potential crown radius Rp (Eq. 5.4).

$$R(t)=C*(Rp(t)-R(t-1))+R(t-1) \qquad if\ \ R(t-1)<R_{\max} \tag{5.4}$$

Establishment. The establishment phase incorporates survival and recruitment of seedlings up to three years. In the first two years after germination the number of surviving seedlings in each cell and for each PFT, $S\ (t)_,$ is calculated as,

$$S(t)=S(t-1)*f_{seedsize}*\left(f_{rainfall}+f_{tolerance}\right) \qquad if\ \ age<3 \tag{5.5}$$

Where $S(t\text{-}1)$ is the number of seedlings from the previous year, $f_{seedsize}$ is the survivorship factor associated with seed size, $f_{rainfall}$ represents the effect of precipitation conditions, and $f_{tolerance}$ the factor for drought tolerance (Table 5.2). The highest number of survivors is obtained for seedlings growing from large seeds with higher drought tolerance in wet years. First year seedlings of resprouters only survive in wet years. We also consider a density-depend intra-specific seedling competition, reflecting lower seedling survival in monospecific stands compared to mixed stands found in seedling experiments (Lamont et al. 1993; B. Lamont unpublished data). We use the power law:

$$N^{'}=N^{b} \tag{5.6}$$

where N is the number of seedlings of a particular PFT and b is an exponent ranging from 0 (only one seedling can survive) to 1 (no intra-specific competition) considering the different seed sizes (b; Table 5.2). After 2 years, one seedling is chosen within each cell as the successful recruit, and thereafter occupies it alone. The identity of the successful recruit is determined randomly, weighted by local PFT seedling abundance (lottery competition sensu Chesson and Warner 1981; Lamont and Witkowski 1995; Groeneveld et al. 2002).

Recruitment is impossible in cells already occupied by a mature individual, and density in some cells may have declined to 0 in any case (especially under drought conditions). Establishment of shrubs is inhibited in cells covered by neighbouring shrubs or sub-shrubs, and sub-shrubs cannot establish in cells where the cell centre is covered by the canopy of a neighbouring sub-shrub.

Seed production. Individuals start to reproduce after reaching a particular fraction of their maximum potential size, depending on regeneration mode and crown diameter (*m*s, Table 5.2). Without competition this size is reached at the age of maturity, *A*1. Seed production of mature resprouting shrubs recommences 2 years after fire for shrubs and 1 year after fire for sub-shrubs (*t*1, Table 5.2). For reproducing individuals seed production increases linearly (Bauer et al. 2002). The number of seeds $Bi(t)$ in the seed bank of a cell i is calculated by:

$$B_i(t) = Seed_{input} + B_i(t-1) * v \tag{5.7}$$

where $Seed_{input}$ is the number of seeds produced in the current year, $B_i(t-1)$ is the total number of seeds in the seed bank from the previous year, and v is the fraction of stored viable seeds after losses to spontaneous germination, decay and granivory. The yearly loss of stored seeds is defined such that after 20 years 90% of all 20-year-old seeds in the seed bank have died.

5.3.4 Simulations

The spatial and temporal dynamics of the community consisting of 38 PFTs commences with the initialization and runs for a minimum of 1800 years, a time-span within which the community appears to reach a quasistationary state (Table 5.3).

Initialization. One hundred individuals per PFT are randomly distributed over the whole lattice, so that 3800 of 14,400 cells are occupied at the start of the simulation. We also tested an initial distribution of individual numbers based on field abundance for each PFT but this did not significantly alter the results and so is not presented here. The last fire is assumed to have taken place 1 year before the simulation starts. Thus, the initial age of non-sprouters is 1 year. The age of resprouters is chosen at random from probability distributions based on field size-distribution data for the most frequent resprouter sub-shrub, *Hibbertia hypericoides*, and shrub, *Banksia attenuata*. For individuals characterised by soil seed storage, 15, 23 or 82 seeds per plant, depending on their maximum seed production, were distributed randomly over the lattice ($Init_{seed}$, Table 5.2). This represents the fraction of seeds accumulated in the soil seed bank (over a period of 15 years) that did not germinate after fire (see Table 5.2).

Table 5.3 Trait characteristics of the 38 simulated plant functional types, shaded lines show coexisting PFTs if there is no regional seed input.

	regeneration mode		*max. crown diameter*		*seed bank type*		*max. seed production*			*seed size*			*drought tolerance*		*dispersal mode*	
PFT	nonsprouter	respouter	shrub	subshrub	canopy	soil	low	moderate	high	small	medium	large	less	more	limited	unlimited
1	x		x		x		x					x		x		x
2	x		x		x			x				x	x			x
3	x		x			x			x	x				x		x
4	x		x			x			x		x			x	x	
5	x			x	x		x				x			x		x
6	x			x	x		x					x		x		x
7	x			x	x			x		x				x		x
8	x			x		x		x			x			x	x	
9	x			x		x		x				x		x	x	
10	x			x		x			x	x				x		x
11	x			x		x			x		x			x		x
12		x	x		x		x			x				x		x
13		x	x		x		x					x	x			x
14		x	x		x		x					x		x	x	
15		x	x		x			x		x				x		x
16		x	x		x			x				x	x			x
17		x	x			x	x			x				x		x
18		x	x			x		x				x	x			x
19		x		x	x		x			x				x		x
20		x		x	x		x				x		x		x	
21		x		x	x		x				x		x			x
22		x		x	x		x				x			x	x	
23		x		x	x		x				x			x		x
24		x		x	x		x					x	x		x	
25		x		x	x		x					x	x			x
26		x		x	x			x		x			x			x
27		x		x	x			x		x				x		x
28		x		x	x			x				x		x		x
29		x		x	x				x	x				x		x
30		x		x		x	x			x			x			x
31		x		x		x	x			x				x		x
32		x		x		x	x				x		x		x	
33		x		x		x	x				x			x	x	
34		x		x		x		x		x				x		x
35		x		x		x		x			x		x			x
36		x		x		x			x	x			x			x
37		x		x		x			x	x				x		x
38		x		x		x			x		x			x	x	

Scenarios. For the seed immigration experiments we randomly distributed an annual total seed input mass of 0.011, 0.11, 1.1 or 11 g/m² over the whole lattice. This covers a wide range of possible seed immigration rates and encompasses empirical data estimates for seed banks in our study area (0.73 g/m² to 5 g/m² seeds accumulated by a stand age of 15 years; Enright et al. 2007 and Enright unpublished data), as well as the highest value for seed immigration reported in a field study (10 g/m²; Mouquet et al., 2004). We used two seed input scenarios leading to the same overall seed input mass: (i) equal seed number per PFT (0.0161, 0.161, 1.61, or 16.1 seeds/m², respectively), and (ii) equal seed mass per PFT. In the latter case, seed input mass was divided between all PFTs based on 11 PFTs with large seeds (50.00 mg/seed), 14 PFTs with medium seeds (8.58 mg), and 13 PFTs with small seeds (0.77 mg), resulting in lower seed immigration numbers for large seeds (0.0634, 0.634, 6.34, 63.4

seeds/m²) and higher numbers for moderate (0.4707, 4.707, 47.07, or 470.7 seeds/m²) and small seeded PFTs (4.8648, 48.648, 486.48, or 4864.8 seeds/m²), respectively representing an external seed rain of 1.2% large seeds, 8.8% medium and 90.0% small, see Appendix 5.6.1).

Output. After 1800 years we continue to simulate until an inter-fire period of at least 15 years appears. Fifteen years after the last fire the number of coexisting PFTs, including the number of individuals in each PFT, the Shannon diversity index, and the distribution of traits among all coexisting individuals (i.e., the relative densities of traits) were recorded as model output. The mean values of output data over 20 iterations are used to analyse the system with regard to the initial questions.

Analyses. To analyse the effects of immigration on Shannon diversity and number of coexisting PFTs, we fitted a generalized linear model (GLM; with quasi-binomial error), and a linear model (LM), in R [version 2.3.1] (R Development Core Team 2006). Both started with a maximal model that contained both immigration intensity and seed input scenario effects, and their interaction. We then performed backward stepwise model simplification (Crawley 2002), retaining model terms significant at $p < 0.05$. In a second set of analyses, we compared the fit of model predictions to field data on trait frequencies for different scenarios and immigration levels. Model fit was quantified as the log-likelihood of obtaining the data given the model prediction (Hilborn and Mangel 1997). The best fitting scenario-immigration level combination thus has the highest log-likelihood (note that log-likelihood values are always negative). In the calculation of log-likelihoods, we assumed binomial errors for binary traits and multinomial errors for traits with more than two states. As an indicator of the overall fit of a scenario-immigration level to all trait distributions, we also calculated the sum of the log-likelihoods for all individual traits.

5.4 RESULTS

5.4.1 Effects of seed immigration on number of coexisting PFTs

Without seed immigration only 13 (median) of the 38 PFTs are able to coexist at the end of the simulations (Fig. 5.2). The number of coexisting PFTs increases if seed immigration is included. At low to moderate levels of seed immigration, e.g., 0.11 g/m², 34 PFTs coexist (median, equal seed number scenario) after 1800 simulated time steps (Fig. 5.2), increasing to the observed field number of 38 PFTs for high levels of seed immigration (Fig. 5.3a). The number of coexisting PFTs is associated with a significant interaction between immigration intensity and seed input scenario (GLM, $F(1,156) = 4.5$, $P < 0.05$). The number of coexisting PFTs differs significantly for low and moderate seed immigration levels, but not for the two highest immigration levels (i.e., 1.1 and 11 g/m², Fig. 5.3a). The equal seed mass scenario produces higher PFT richness at low seed immigration levels than does the equal seed number scenario: for the equal seed input mass scenario the median is 32 persisting PFTs for the lowest seed immigration level 0.011 g/m², while at all higher seed immigration levels all 38 PFTs coexist, apart from a few rare outlier simulations (Fig. 5.3).

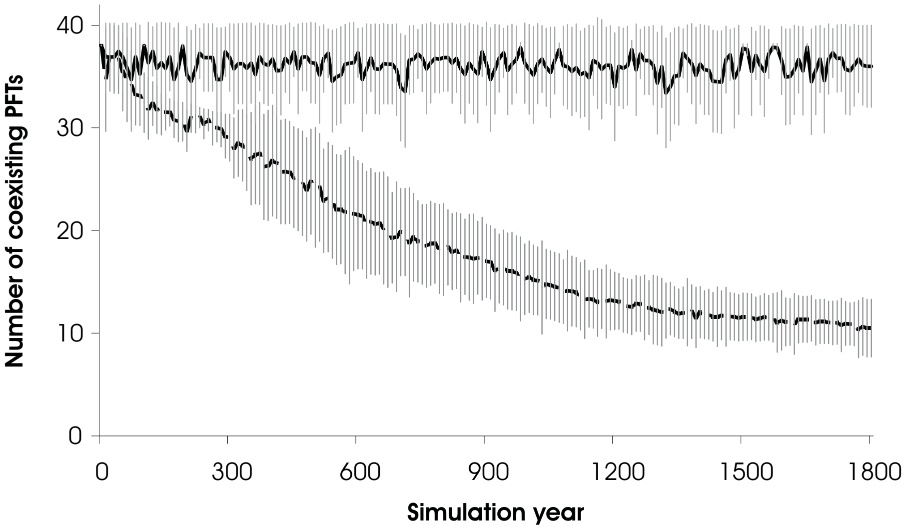

Fig. 5.2 Number of coexisting PFTs without seed immigration (mean—dashed black line, error bars present standard deviation) and with a moderate seed immigration rate of 0.11 g/m2 based on the equal seed input mass scenario (black line).

5.4.2 Effects of seed immigration on diversity

Without seed immigration, the median Shannon diversity index (SDI) is 1.67 after 1800 simulated years (Fig. 5.3b) compared to a SDI of 2.88 calculated from the field data. The SDI increases to more realistic values with increasing immigration rates (Fig. 5.3b). The level of diversity is associated with a significant interaction between immigration intensity and seed input scenarios (LM, $F(1,156) = 13.6$, $P < 0.05$). The SDI increases significantly with increasing immigration intensity, with significant differences also between the equal seed input number and equal seed input mass scenarios. For the same immigration level, the SDI is always higher for the equal seed input mass per PFT scenario, excepting for the highest seed immigration level (11 g/m²) where this ordering is reversed (Fig. 5.3b). For an immigration intensity of 0.011 g/m² a median SDI of 1.9 is obtained (Fig. 5.3b), while for an immigration level of 0.11 g/m² median SDI is 2.74. The highest value, 3.36, is reached at 1.1 g/m², but falls slightly at 11 g/m² to 3.09.

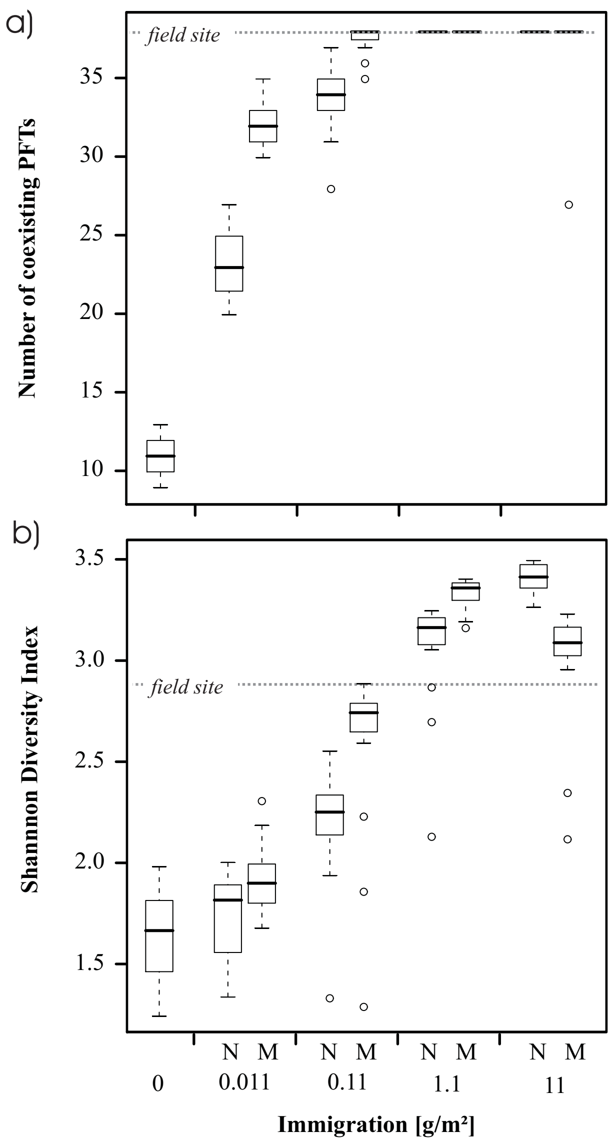

Fig. 5.3 Box and whisker plots of (a) number of coexisting PFTs and (b) Shannon diversity index, in relation to immigration intensity levels and seed input scenarios: equal seed input numbers (*N*) and equal seed input masses (*M*) for all PFTs. Centre, bottom and top lines of the box plots are the median, 25th and 75th percentiles, respectively. Whiskers are 1.5 times the interquartile range;
outliers are data points which lie beyond the extremes of he whiskers.

5.4.3 Effects of seed immigration on trait distribution

Without seed immigration we can reproduce two of the empirical trait frequencies, maximum crown diameter and drought tolerance with log-likelihood values of 57.97 and 21.86, respectively (Fig. 5.4; Table 5.4). However, the other trait distribution patterns differ more widely from the field observed patterns. Seed immigration markedly improves the fit of most, but not all, traits in relation to the levels observed in the field data.

Regeneration mode. The fraction of non-sprouting individuals observed in the field is 0.4. Simulations without seed immigration gave a non-sprouter fraction of 0.22

(loglikelihood =−573.21). There is no clear trend between the fraction of non-sprouting individuals and the level of seed immigration. The highest fraction of non-sprouters, 0.357, and the highest log-likelihood (−33.25) is reached for the 1.1 g/m² level of seed immigration (equal seed number scenario, Table 5.4).

Maximum crown diameter. Seventeen percent of individuals in the field are shrubs, the rest (83%) are sub-shrubs (Fig. 5.4). Without seed immigration the fraction of shrubs is 0.13 with a log-likelihood of −57.97 (Table 5.4). This fraction increases to 0.178 at a seed immigration intensity of 0.011 g/m² and shows the highest fit to field data (log-likelihood =−4.65).

Seed bank type. Forty-two percent of individuals in the field had a canopy seed bank while the remaining 58% were soil stored (Fig. 5.4). Without seed immigration, individuals with canopy seed bank dominated the community (log-likelihood =−1071.69, Table 5.4). However, the fraction of individuals with canopy seed storage decreases with increasing immigration intensity down to a minimum of 0.46 in the equal seed input mass scenario with 11 g/m² seed immigration (log-likelihood =−27.96).

Maximum seed production. Thirty-eight percent of individuals in the field are characterised by low and high seed production (respectively), and 24% by moderate seed production (Fig. 5.4). Without seed immigration PFTs with low seed production go extinct, and the fraction of individuals with high seed production is >0.43. With increasing immigration intensity the fraction of individuals with low seed production increases. The match between empirical and simulated distributions of trait characteristics was best for the highest level of seed immigration in the equal seed input mass scenario with fractions for low, moderate, and high seed production of 0.38, 0.27, and 0.35 (log-likelihood =−29.75).

Seed size. Forty-five percent of field individuals are characterised by small seeds, 43% by medium seeds and 12% by large seeds (Fig. 5.4). In simulations without seed immigration, individuals with large seeds dominate with a fraction of 0.5. The fractions of individuals with small and medium seeds are 0.24 and 0.26. The equal seed input mass scenario has a stronger positive effect on the fraction of small seeds than the equal seed input number scenario. The best match – 0.43, 0.28, 0.29 for the fractions of individuals with small, medium and large seed – results from a seed immigration level of 0.11 g/m² in the seed mass input scenario, but remains a poor fit overall (loglikelihood =−576.89).

Drought tolerance. Twenty-one percent of field individuals are less drought tolerant (Fig. 5.4). Simulations without seed immigration result in a community similar to the observed field community with a fraction of less drought tolerant individuals of 0.18 (log-likelihood =−21.86, Table 5.4). This fraction decreases with immigration intensity in the equal seed input number scenario with negative impact on similarity. In the equal seed input mass scenario the fraction of less drought tolerant individuals does not change much at all. Best performance is achieved for seed immigration intensity 0.11 gm^{-2} in the equal seed input mass scenario with a fraction of less drought tolerant individuals of 0.19 (log-likelihood = −8.21).

Dispersal mode. Thirty-one percent of field individuals have short-range seed dispersal (Fig. 5.4). PFTs with short-range dispersal are suppressed in the community if there is no seed immigration. This fraction increases only if we assume equal seed input number and high immigration intensity, with a maximum simulated value of 0.3 (log-likelihood of −5.45, Table 5.4). None of the models (five levels of seed immigration for each of the two scenarios) could reproduce the observed field frequency distributions for all seven traits. Measuring the overall fit using the sum of the log-likelihoods, the equal seed input mass shows a better result than the equal seed input number scenario at each of the immigration levels. The best sum of log-likelihood values (−1879.42) is obtained assuming immigration by equal seed input mass per PFT at a level of 1.1 g/m^2 (Table 5.4).

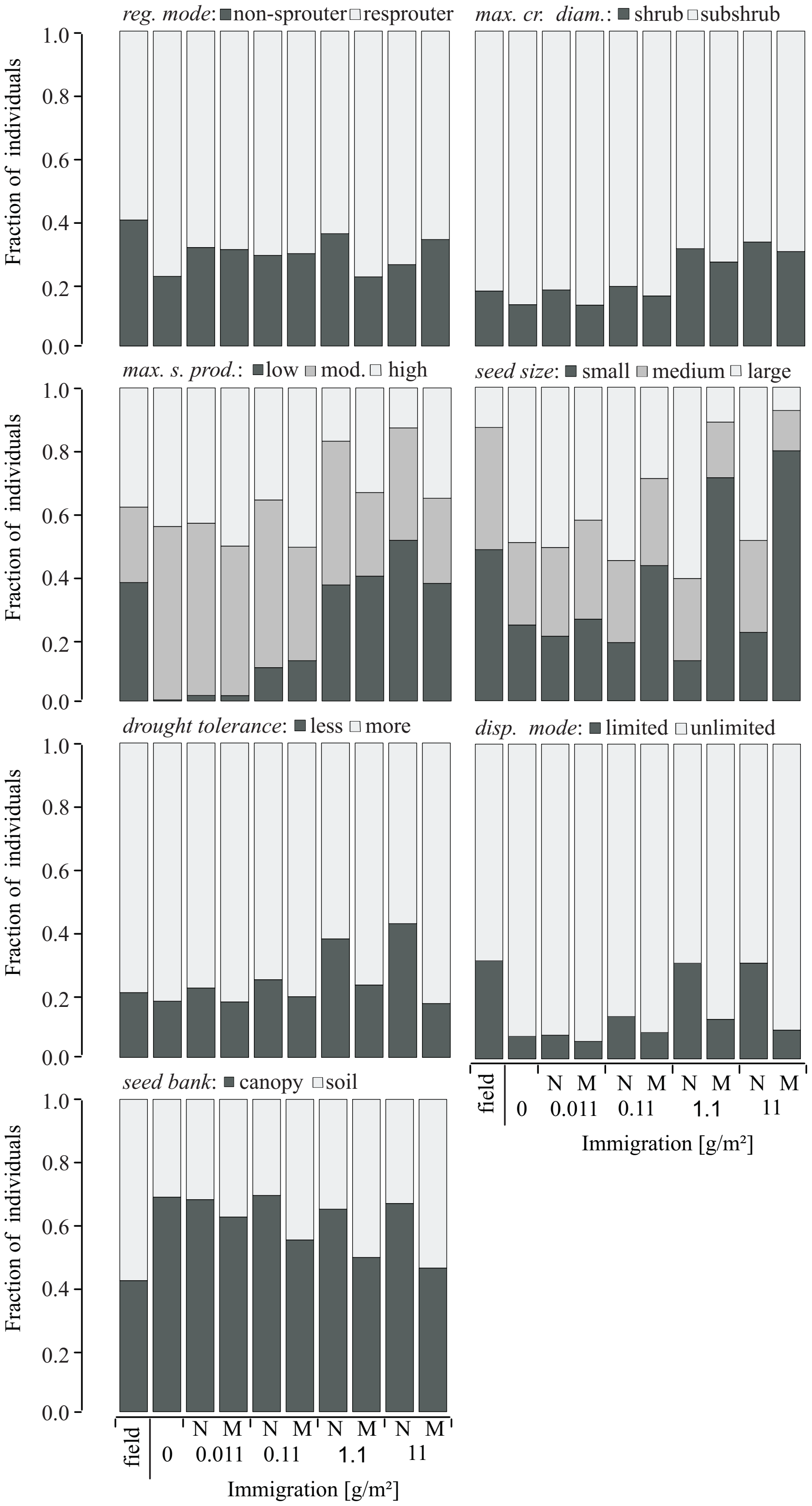

Fig. 5.4 Fraction of individuals per plant trait in the field data and the mean value from simulations by immigration intensity level and mode of seed input; equal seed input number (*N*) and equal seed input mass (*M*) for all PFTs combined (abbreviations: **reg**eneration mode, **max**imum **cr**own **diam**eter, **max**imum **s**eed **prod**uction, **disp**ersal mode).

Table 5.4 Log-likelihood model fits for the simulated *versus* observed trait frequency distributions for individuals across all PFTs. The best model fit for each trait (and for all traits summed) is indicated in bold type.

SI level	Scenario	reg. mode	crown diam.	seed bank	seed prod.	seed size	stress tol.	disp. mode	sum
0		-573.25	-57.97	-1071.69	-10568.82	-2211.99	-21.86	-1789.31	-16294.90
0.011	N	-124.44	**-4.65**	-1004.91	-6437.69	-2528.31	-8.89	-1690.62	-11799.50
	M	-143.69	-61.55	-602.64	-6316.41	-1598.65	-24.61	-2259.65	-11007.20
0.11	N	-209.16	-9.36	-1119.58	-2192.92	-3023.22	-37.78	-739.41	-7331.44
	M	-187.34	-10.65	-244.52	-1410.40	**-576.89**	**-8.21**	-1508.61	-3946.62
1.1	N	**-33.25**	-335.19	-768.18	-1130.09	-4195.31	-483.64	-5.60	-6951.26
	M	-585.09	-171.68	-82.36	-43.94	-980.00	-16.36	-837.12	**-2716.54**
11	N	-341.33	-434.80	-904.34	-1447.35	-2275.80	-760.33	**-5.45**	-6169.40
	M	-63.92	-295.86	**-27.69**	**-29.75**	-1841.04	-33.10	-1351.63	-3642.99

5.5 DISCUSSION

We investigated the impact of seed immigration intensity on plant functional type (PFT) richness, diversity and trait frequency distribution (relative abundance) in a simulated species-rich plant community based on field data for a Mediterranean-type, fire-prone shrubland in Western Australia. We developed a mechanistic, generic simulation model based on the life-history attributes of individuals for 38 different PFTs derived from long-term field data. This spatially-explicit and trait-based model allowed us to systematically test whether seed immigration is able to reproduce three layers of plant community structure in a highly diverse ecosystem: PFT richness, PFT diversity, and relative trait distribution.

Our simulation results show that moderate to high levels of seed input can explain the first two components of community structure (i.e., species richness and diversity), while only some aspects of trait distribution were satisfactorily reproduced. For PFT richness and Shannon Diversity Index, the results show that immigration of seeds is a potential explanation for coexistence and diversity patterns. Without seed immigration the simulated community represents an isolated vegetation patch. Under these conditions the model predicts that the initially species-rich community would decline towards a community which is dominated by only a few PFTs. These findings are consistent with findings of the neutral theory, even though it differs substantially from our modelling approach. In the neutral theory isolated local communities comprised of functionally identical species (as opposed to our functionally differentiated PFTs) drift towards the mono-dominant state in the absence of immigration (Hubbell 1997). Seed rain from the so-called metacommunity avoids species loss and results in the observed empirical pattern of community structure (Hubbell 1997). However, the timescales of species extinction differ considerably between our study (millennia—see Fig. 5.2) and the evolutionary time-scales required in neutral theory. This discrepancy was also found in previous simulation studies that have tested the basic assumptions of neutral theory (Zhang and Lin 1997). The important role of dispersal between patches, and the general patterns of local population extinction and recolonisation are widely discussed and analysed in the context of metapopulations (Shmida and Ellner 1984; Holt 1993; Hanski 1999; Pulliam 2000; Mouquet and Loreau 2002). However, the system investigated here is more like a community containing a set of sink populations than a community of metapopulations. Immigrant seed rain enables more plant functional types to persist in small numbers rather than to re-establish vital local populations that themselves provide large seed outputs which might re-colonise other extinct patches (Hanski 1999). The key to coexistence in this framework is spatial variance in fitness (Amarasekare and Nisbet 2001), which is mainly caused by spatial heterogeneity in the fire regime (Groeneveld et al. 2002). Plant functional types that are inferior within the investigated local patch coexist because they continuously immigrate from other patches, where they are more abundant due to different local fire history, more suitable local edaphic conditions, or chance effects (Brown and Kodric-Brown 1977; Pulliam 1988; Loreau and Mouquet 1999; Mouquet and Loreau 2003). Another precondition for source–sink dynamics is long-range dispersal of propagules to maintain the seed rain. There is recent empirical evidence that long distance dispersal in plants is much more frequent than has been assumed in the past. For example, genetic analyses for the fire-killed shrub, *Banksia hookeriana*, show that long distance dispersal (up to 2.5 km) may be quite frequent after fire, facilitating recolonisation of temporarily lost habitat (He et al. 2004).

Our model suggests that diversity is a function of both seed immigration as a regional process, and local competitive processes associated with differences in demographic parameters and responses to fire. These differences alone are not sufficient to maintain diversity in the sense of limiting similarity. On the contrary, the differences in ecological traits are limiting. To compensate different competitive abilities, local processes (such as intra-specific competition) and regional processes are of major importance. However, in our case not all community patterns, especially plant functional trait distributions can be fully explained by immigration alone (e.g., seed bank type). Additional local processes and plant traits causing feedbacks between density and demographic processes, which were not necessary to explain species richness, could improve the model performance substantially. Further research is needed in order to assess additional processes or traits. One possible trait could be *dispersal vector*, differing between wind and various forms of animal-dispersed seeds (e.g., animal dispersal leading to a more clumped distribution of seeds than in dispersal by wind). In respect to these findings, those of certain sowing experiments are of particular interest, where it has been shown that external seed input does increase species richness and plant cover in some natural communities (Tilman 1997). The composition of seed rain is most often dominated by small seeded species (Moles and Westoby 2006), and since seed mass is generally considered to correlate with competitive ability, the dominance of small seeds in seed rain supports the colonization–competition trade off (Turnbull et al. 1999; Mouquet et al. 2006). Turnbull et al. (1999) and Richards and Lamont (1996) showed empirical evidence for recruitment limitation by strongly competitive, large seeds and therefore for this trade-off. Our simulation results are in accordance with these findings. The equal seed input scenario, which considers a size-biased seed rain composition, produced much better results than the equal seed input number scenario.

However, it is difficult to determine empirically the amount of immigrant seed needed to maintain the current species diversity and community structure of a given ecosystem. Models allow the quantification of parameters that are difficult to measure in the field (Turnbull et al. 2000; Mouquet and Loreau 2003). The seed rain varies enormously between different communities (Loreau and Mouquet 1999; Turnbull et al. 1999; Eskelinen and Virtanen 2005; Hiltunen et al. 2006). Mouquet et al. (2004) used 4 g/m² as low and 10 g/m² as high (more than 17,000 seeds/m² depending on tested scenarios) immigration intensity to show the supporting effect of immigration on local diversity. Zeiter et al. (2006) in a seed addition experiment in grassland in Switzerland assumed a density of 4444 seeds/m² (grass and forbs), similar to high event seed rains in semi-natural meadows. These values seem too high for the shrublands examined here, considering the large number of PFTs (and individuals) with low seed production and resulting low accumulation of seeds in the seed banks (Enright et al. 2007). We estimate that about 0.11–1.1 g/m² is realistic. This means in the case of the equal seed input number scenario an overall immigration of around 6–60 seeds/m². In contrast, in the equal seed mass scenario 54–540 (mostly light) seeds/m² were distributed per year.

Our approach allows us to investigate not only patterns of species richness and species diversity, but also patterns of the frequency distribution of plant functional type traits, such as regeneration mode and seed size, among individuals in a community. Most empirical and previous modelling studies focus on species-poor (sub-)systems or hypothetical systems that only allow consideration of aggregated measures of diversity (Loreau and Mouquet 1999; Hiltunen et al. 2006; Zeiter et al. 2006). We are able to attribute the importance of relevant factors by a combination of empirical and modelling work, where the long-term empirical knowledge can further be extrapolated in space and time, as it is needed, to achieve sufficient answers (Kareiva and Andersen 1988). Seed immigration has been shown, as in our study, to positively contribute to species coexistence and diversity. However, consideration of detailed trait abundance patterns shows that seed immigration is not yet able to describe all important community-level parameters. So, the most important lesson to learn from this is that most coexistence and diversity studies dealing only with species richness and diversity would never be capable of detecting such fundamental patterns.

5.6 APPENDIX

5.6.1 Seed immigration (SI) rates depending on scenario and level

			PFTs with seed size			
SI scenario		SI level	large	medium	small	sum
equal seed input number	seeds g/m²	0.011	0.0089	0.0019	0.0002	0.011
		0.11	0.0886	0.0193	0.0016	0.110
		1.1	0.8861	0.1935	0.0161	1.096
		11	8.8613	1.9346	0.1614	10.957
	seed No./m²	0.011	0.1772	0.2256	0.2093	0.612
		0.11	1.7722	2.2556	2.0932	6.121
		1.1	17.7222	22.5557	20.9318	61.210
		11	177.2218	225.5565	209.3176	612.096
equal seed input mass	seeds g/m²	0.011	0.0032	0.0040	0.0037	0.011
		0.11	0.0317	0.0404	0.0375	0.110
		1.1	0.3172	0.4037	0.3749	1.096
		11	3.1718	4.0369	3.7485	10.957
	seed No./m²	0.011	0.0634	0.4707	4.8649	5.399
		0.11	0.6344	4.7066	48.6486	53.990
		1.1	6.3435	47.0662	486.4857	539.895
		11	63.4354	470.6616	4864.8568	5398.954
		g/seed	0.0500	0.0086	0.0008	0.059
		No. of PFTs	11	14	13	38

5.7 LINK TO THE NEXT CHAPTER

In the previous two chapters 4 and 5, I investigated the importance of local processes (low dimensional trade-offs) and regional processes (seed immigration) for the maintainance of local species diversity. In contrast to the low dimensional trade-offs which are not necessary to explain PFT richness seed rain composition has a strong influence on local community pattern. With increasing immigration rates the simulated number of coexisting PFTs and Shannon diversity quickly approaches values observed in the field. The assumption of equal seed mass for each PFT in seed rain resulted in a more diverse community than did the assumption of equal seed number per PFT in seed rain.

Climate change will change the seed rain composition. Most studies ignore this effect, when investigating impact of climate change in local communities. Thus I show in the next chapter the sensitivity of plant functional types and the related plant community to climate change under consideration of changes in local and regional processes. For the sensitivity analysis I used classification trees.

6 SENSITIVITY OF PLANT FUNCTIONAL TYPES TO CLIMATE CHANGE: CLASSIFICATION TREE ANALYSIS OF A SIMULATION MODEL[1]

6.1 ABSTRACT

Question: The majority of studies investigating the impact of climate change on local plant communities ignores changes in regional processes, such as immigration from the regional seed pool. Here we explore: (i) the potential impact of climate change on composition of the regional seed pool, (ii) the influence of changes in climate and in the regional seed pool on local community structure, and (iii) the combinations of life history traits, i.e. plant functional types (PFTs), that are most affected by environmental changes.

Location: Fire-prone Mediterranean-type shrublands in south-western Australia.

Methods: Spatially-explicit simulation experiments were conducted at the population level under different rainfall and fire regime scenarios to determine the effect of environmental change on the regional seed pool for 38 PFTs. The effects of environmental and seed immigration changes on local community dynamics were then derived from community-level experiments. Classification tree analyses were used to investigate PFT-specific vulnerabilities to climate change.

Results: The classification tree analyses revealed that the responses of PFTs to climate change are determined by specific trait characteristics. PFT-specific seed production and community patterns responded in a complex manner to climate change. For example, an increase in annual rainfall caused an increase in numbers of dispersed seeds for some PFTs, but decreased PFT-diversity in the community. Conversely, a simulated decrease in rainfall reduced the number of dispersed seeds and diversity of PFTs.

Conclusions: PFT interactions and regional processes must be considered when assessing, how local community structure will be affected by environmental change.

6.2 INTRODUCTION

Climate change is receiving widespread scientific attention as a major threat to biodiversity, potentially causing species range shifts and losses, population declines and species extinctions (Thomas et al. 2004; De Boeck et al. 2007). While there is clear evidence that climate change has significant ecosystem-level impacts (e.g., Hughes 2003), the direction and magnitude of effects on communities is less certain (Chesson 2000; Brooker et

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[1] online available at Journal of Vegetation Science as Esther A., Groeneveld J., Enright N.J., Miller B.P., Lamont B.B., Perry G.L.W., Blank F.B., Jeltsch F. Sensitivity of plant functional types to climate change: classification tree analysis of a simulation model.

al. 2007; Barnard and Thuiller 2008). Long-term monitoring along natural climate gradients and climate manipulation experiments provide some indications as to the responses of species, communities and ecosystems to climate change (Dunne et al. 2004; Nippert et al. 2006), but are expensive, time-consuming, and have limitations in controlling factors and replication (Dunne et al. 2004). In particular, spatio-temporal environmental variability is often disregarded in such empirical studies for the sake of feasibility (Dunne et al. 2004; De Boeck et al. 2007). To overcome these limitations, modelling has become an important additional approach (Guisan and Zimmermann 2000).

There are many theoretical approaches available for examining the potential effects of climate change on plant species and communities (Botkin et al. 2007; Jeltsch et al. 2008). Bioclimatic envelope models (e.g., Huntley et al. 2004; Thuiller et al. 2005) and spatially-explicit mechanistic models (e.g., Tews et al. 2006; Brooker et al. 2007) have been utilized widely to develop response scenarios for one or a few species. Climate envelope models use the current correlation of species distributions and climatic variables to predict future changes in species occurrences by considering climate change scenarios on a macroecological scale (Bakkenes et al. 2002; Huntley et al. 2004; Thuiller et al. 2005). However, the predictive power of such model-based approaches is limited because they often ignore key ecological processes such as dispersal or demography (Thomas et al. 2004; Brooker et al. 2007; Morin and Lechowicz 2008).

The need to incorporate key ecological processes into models has been demonstrated by several simulation studies for theoretical communities, or communities consisting of a small number of species (Pausas 2003; Brooker et al. 2007). Also, the possible trait-related response of species to climate change has been illustrated using spatially-explicit mechanistic models (Mouillot et al. 2002; Pausas and Bradstock 2007; Keith et al. 2007; Jeltsch et al. 2008). However, most modelling studies thus far have neglected potentially important regional processes such as seed immigration. Recent theoretical efforts to characterize community assembly processes have emphasized the importance of interactions between local and regional processes (Levine and Murrell 2003). Whether or not a species is a long-term resident in the local community depends to some extent on its presence in the regional species pool (Chesson 2000; Esther et al. 2008), and this pool may change over ecological time, especially as environmental conditions change (Levine and Murrell 2003; Davis 2005). Furthermore, local communities and the regional seed pool are interdependent due to a positive abundance–range size relationship (Schurr et al. 2007). Thus, to understand local community dynamics in the light of global change, it is essential to understand the interdependence between local dynamics and the regional seed pool. In this study we assess the influence of predicted climate changes on plant functional type diversity of the species rich Mediterranean-type shrublands of south-western Australia (SWA), simulating local community dynamics under possible changes in regional seed immigration. We are unaware of any previous modelling study that seeks to address the effects of climate change on the structure of a species-rich, local plant community considering the impacts of both local and regional processes.

Recent climate change scenarios for SWA predict changes in annual average rainfall between -20% and +5% by 2030 (CSIRO 2001, 2007; Williams et al. 2001). Due to global warming and increased atmospheric CO_2, higher biomass production and higher rainfall variability are also expected (IPCC 2007), possibly resulting in more frequent fires (Williams et al. 2001; Pausas and Bradstock 2007). Reflecting the uncertainty in climate predictions we test change scenarios with different rainfall and fire regimes and compare results with a base-line (no change) scenario representing present conditions. We use a spatially-explicit, rule-based and individual-based model developed from field data for the biodiverse Mediterranean-type fire-prone shrublands in SWA to address the following questions:

i) What is the potential impact of climate change on the regional seed pool?

ii) What community structure will emerge under changes in climate and the regional seed pool?

iii) Which particular combinations of life history traits, i.e. plant functional types, are most affected by climate change?

6.3 METHODS

6.3.1 Plant Functional Type model

The simulation model is based on 38 plant functional types (PFTs) derived from empirical data for 156 plant species occurring on the Eneabba Sandplains (see species list in Appendix 6.6.1), Western Australia using the following seven plant traits; regeneration mode, seed production, seed size, maximum crown diameter, drought tolerance, dispersal mode and seed bank type (Enright et al. 1998a, b; Groeneveld et al. 2002; Lamont et al. 2007; Esther et al. 2008). Each plant trait can take one of two or three values (Table 6.1; for details see Esther et al. 2008). In the model the local dynamics of the 38 PFTs are simulated in annual time steps on a 60 m by 60 m grid, with analyses restricted to a core area of 40 m by 40 m to minimize boundary effects. The grid is divided into 0.5 m by 0.5 m cells, each potentially occupied by a single plant from one of the 38 plant functional types (PFT).

Table 6.1 Trait characteristics of 38 simulated Plant Functional Types (PFT) and their responses to environmental change compared to the 'no change' scenario. PFT responses are presented as the average number of dispersed seeds per year for the 'Population level experiment' (white - increased, grey - unaffected, black - decreased) and as the difference in survival probability between the environmental change scenarios and the 'no change' scenario for the 'Community level' experiment.

Trait PFT	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
reg. mode																																						
nonsprouter	×	×	×	×	×	×	×	×	×	×	×																											
respouter												×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
max. cr. diam.																																						
shrub	×	×	×	×								×	×	×	×	×	×	×																				
subshrub					×	×	×	×	×	×	×								×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
seed bank type																																						
canopy	×	×			×	×	×					×	×	×	×	×			×	×	×	×	×	×	×	×	×	×	×									
soil			×	×				×	×	×	×						×	×												×	×	×	×	×	×	×	×	×
max. seed prod.																																						
low	×				×	×						×	×	×			×		×	×	×	×	×	×	×					×	×	×	×					
moderate		×					×	×	×						×	×		×								×	×	×						×	×			
high			×	×						×	×																		×							×	×	×
seed size																																						
small			×				×			×		×			×		×		×							×	×		×	×	×			×		×	×	
medium				×	×			×			×									×	×	×	×									×	×		×			×
large	×	×				×			×				×	×		×		×						×	×			×										
drought tol.																																						
less		×											×			×		×		×	×			×	×	×				×		×			×	×		
more	×		×	×	×	×	×	×	×	×	×	×		×	×		×		×			×	×				×	×	×		×		×	×			×	×
dispersal mode																																						
limited				×				×	×					×						×		×		×								×	×					×
unlimited	×	×	×		×	×	×			×	×	×	×		×	×	×	×	×		×		×		×	×	×	×	×	×	×			×	×	×	×	
Population level experiment																																						
5%	▒	▒	▒	▒	□	▒	□	▒	▒	▒	▒	□	▒	□	▒	▒	▒	▒	□	▒	▒	□	▒	□	□	▒	▒	▒	▒	▒	▒	▒	□	▒	▒	▒	▒	□
-10%	■	▒	■	▒	■	■	■	■	▒	■	▒	■	■	■	■	▒	▒	■	■	■	■	■	■	■	▒	■	▒	▒	▒	■	■	■	■	■	▒	▒	▒	▒
-20%	■	▒	■	▒	■	■	■	■	▒	■	▒	■	■	■	■	■	▒	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
-10% -2	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Community level experiment																																						
5%	▒	▒	▒	▒	■	▒	▒	▒	■	▒	▒	▒	▒	■	▒	▒	▒	□	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	■	▒	▒	▒	▒	▒	▒
-10%	▒	▒	▒	▒	■	▒	■	□	■	▒	▒	▒	▒	▒	▒	▒	▒	□	▒	▒	▒	■	■	■	▒	▒	▒	▒	▒	■	▒	■	■	▒	▒	▒	▒	▒
-20%	▒	▒	▒	▒	■	▒	▒	▒	■	▒	▒	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
-10% -2	■	■	■	■	■	■	■	■	■	■	■	■	■	■	▒	■	■	■	■	■	■	■	■	■	■	■	■	▒	▒	■	■	■	■	■	■	▒	■	▒

A detailed description of the PFT model is presented in Esther et al. (2008). However, in order to facilitate understanding we briefly describe the structure and logic of the model here (Fig. 6.1). The local plant community pattern, such as the number and abundance of PFTs, depends on local processes and on seed immigration from the regional seed pool (Fig. 6.1). Local processes are computed for each individual, taking into account interactions among environmental factors, plant functional traits and spatial position (Fig. 6.1; Table 6.1). If a fire occurs, then survival (of resprouting PFTs), dispersal of seeds (of canopy seed bank PFTs), and germination of seeds (all PFTs) are simulated. Inter-fire survival, competition between plants, growth, establishment, seed production and dispersal (of soil seed bank PFTs) are considered annually during inter-fire periods. Table 2 contains a detailed description of all model parameters.

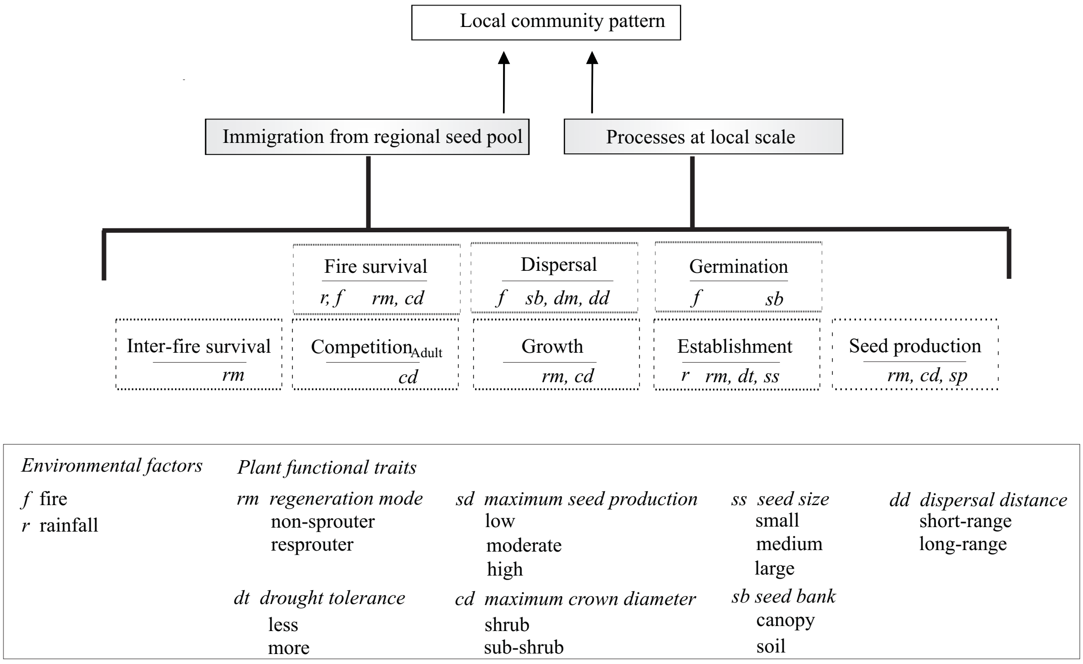

Fig. 6.1 Causal chart showing how the local community pattern depends on processes and plant functional traits in the model.

6.3.2 Processes

Dispersal of seeds depends on the following traits: seed bank type, dispersal distance and maximum crown diameter. Thus, annually produced seeds of those PFTs with soil seed banks are dispersed each year, while seeds accumulated in canopy seed banks are dispersed immediately after fire. The average dispersal distance is described by a negative exponential function. The average dispersal distance (d_d) differs for shrubs and sub-shrubs and also depends on the dispersal mode of the PFT (short-range vs. long-range, Table 6.2).

Fire-survival of resprouters is calculated for years in which fires occur, with the probability of fire survival (p_{f_surv}) increasing linearly to an age 9 years, being constant between 10 and 40 years, and decreasing linearly thereafter. Fire survival probability is reduced if the rainfall condition is 'dry' in the current year ($p_{f\_surv} - p_{f\_addmort}$). Resprouter above-ground biomass is removed by fire and it takes 1 year for mature resprouter sub-shrubs and 2 years for mature resprouter shrubs to resume seed production (*t1*, Table 6.2, and see Seed production). Non-sprouters do not survive fires.

Germination occurs only after fire, at which time all canopy stored seeds and a fraction of soil-stored seeds (f_{g_soil}) germinate (Table 6.2).

Inter-fire survival is calculated for each year during inter-fire periods. Mature plants survive with a probability (p_{surv}) that depends on their age (Table 6.2). The probability of an individual reaching the assumed maximum longevity (L_{resp}, L_{non}) is 0.01 (Table 6.2).

Competition can occur between individuals of the same crown diameter type (i.e. within, but not between, sub-shrubs and shrubs). We used the 'zone of influence' (ZOI) approach to calculate for each plant the influence of its neighbours (Berger and Hildenbrandt 2000; Bauer et al. 2004). The more the crown is overlapped by neighbouring crowns the more the growth of the plant is reduced (Esther et al. 2008).

Growth, in the absence of competition, comprises two processes: plant regrowth after fire for surviving resprouters, described by the Michaelis-Menten equation (Tietjen and Huth 2006; Esther et al. 2008), and growth from seeds that is modelled by the logistic equation (Esther et al. 2008). In the case of competition with neighbours, growth is reduced by a relative competition factor, as described above. Neighbouring plants can overlap, but the growth of sub-shrubs stops at the centre point of any neighbouring shrub, whereas shrubs can overtop sub-shrubs.

Establishment is described by the post-fire recruitment and survival of seedlings. Plant establishment is only possible in empty cells, i.e. no stem of an adult plant is located in this grid cell. Number of surviving seedlings of each PFT in each grid cell depends on seedling *drought tolerance*, *seed size* and rainfall conditions (Table. 6.2). The number of surviving seedlings per cell per year is calculated from a binomial distribution. Resprouter seedlings only survive under wet conditions during the first year (Enright and Lamont 1992). Seedlings germinating from large seeds have higher survival rates than seedlings from small

Table 6.2 Parameter set used in the model.

Parameter	Value	Unit	Description of parameter	References
Initialization				
$Init_{ind}$	14400; 40		number of individuals initialized dependent on scenario (separate simulations; in community simulation)	
$Init_{seed}$	5; 23; 82		number of seeds in the soil per initialized individual with soil *seed bank* depending on its *maximum seed production* (low; moderate; high) This represents the fraction of seeds (see Table 2).	assumption: 1- f_{g_soil} of the viable seeds produced, accumulated in the soil seed bank over a period of 15 years that did not germinate after fire
Rainfall				
p_R	20; 55; 25	%	probability of good, average and bad rainfall conditions	Enright et al. 1998a, b
Fire				
IFP	13.4	year	mean value of inter-fire periods	Miller et al. 2007
low_cut	6	year	minimum time for fuel load to support a fire	Enright et al. 1998a
Dispersal				
d_d	9.375; 0.53; 1.33	m	mean seed dispersal distance dependent on *dispersal mode* and canopy crown diameter (long-range; short-range sub-shrub; short-range shrub)	Esther et al. 2008
Fire survival				
p_{f_surv}	0.997		survival probability for resprouters for age 10 until 40 years if a fire occurs	Groeneveld et al. 2002
$p_{f\_addmort}$	0.03		additional mortality probability for resprouters if a fire occurs in a year with bad rainfall condions	
Germination				
f_{g_soil}	0.8		fraction of soil stored seeds germinating after a fire	Esther et al. 2008
Inter-fire survival				
p_{surv}	0.997; 0.979; 0.802		survival probability: for age 3 years until 3/4 of longevity; if older than 3/4 of longevity then dependent on *regeneration mode* (resprouter; non-sprouter)	Enright et al. 1998a, b
L_{resp}; L_{non}	300; 40	year	longevity dependent on *regeneration mode* (resprouter; non-sprouter)	Enright et al. 1998a, b
Competition				
F_{max}	0.5		threshold of neighbourhood strength	Berger and Hildenbrandt 2000
Growth				
R_{max}	2.0; 0.6	m	maximum canopy radius; dependent on *maximum crown diameter* (shrub; subshrub)	Esther et al. 2008
t2	7; 3	year	for re-gowing resprouters; time after fire to reach 98% of the pre-fire size; dependent on *maximum crown diameter* (shrub; sub-shrub)	Enright et al. 1998b; Lamont and van Leeuwen 1988
GR_{max}	0.11; 0.03 0.77; 0.22	m/year	maximum growth rate; dependent on *regeneration mode* (resprouter-shrub, sub-shrub; non-sprouter-shrub, sub-shrub)	
t_H	0.14; 0.06	year	for re-gowing resprouters; time it takes to reach half of the pre-fire size; dependent on *maximum crown diameter* (shrub; subshrub)	
Establishment				
$f_{seedsize}$	0.11; 0.21 0.22; 0.40 0.45; 0.83		fraction of surviving seedlings; dependent on *seed size* (small; medium; large) in the first; second year after germination	Cowling et al. 1987, Enright and Lamont 1989, Lamont et.al 1993
$f_{rainfall}$	1.6; 1.0; 0.4		establishment factor; dependent on rainfall conditions (good; average; bad)	Cowling et al. 1987, Enright and Lamont 1989, Lamont et.al 1993
$f_{tolerance}$	0; -0.05		establishment factor; dependent on d*rought stress tolerance* (more; less)	
b	0.5;0.66;1		power law function exponent describing seedlings intraspecific competition; dependent on *seed size* trait (large; medium; small)	Esther et al. 2008
Seed production				
S_{max}	17; 74; 266		maximum seed production per year; dependent on *maximum seed production* (low; average; high)	
A1	30; 5	year	age at maturity; dependent on *regeneration mode*	Enright et al. 1998a, b; Lamont 1996; Lamont and van Leeuwen 1988
m_s	0.026;0.012 0.066; 0.029	m	plant size necessary to produce seeds; dependent on *regeneration mode* (resprouter-shrub, sub-shrub; non-sprouter-shrub, sub-shrub)	assumption: equals plant size at age A1 if there is no competition
t1	2; 1	year	seed production hiatus after fire (secondary juvenile period); dependent on *maximum crown diameter* (shrub; sub-shrub)	Enright et al. 1998b; Lamont 1988, Lamont et al. 1993
L_{seed}	20	year	seed longevity	Lamont et al. 1991
v	0.89		yearly fraction of stored viable seeds; based on L_{seed}	
Seed immigration				
S_{input}	48.65; 4.71; 0.63	No/ m²	yearly seed immigration from region in standard scenario on level of 0.11 g/m² dependent on seed size (small, medium, large)	Esther et al. 2008

seeds (B. Lamont unpublished data), especially in dry years. At the same time, density-dependent intra-specific seedling competition is more intense for large seeded PFTs than for medium and small seeded PFTs (Lamont et al. 1993; B. Lamont unpublished data; Esther et al. 2008), with the strength of density regulation related to seed size by a power law (*b*; Table 6.2). The sole successful post-fire recruit is determined for each cell (not already occupied by a resprouter) at two years after fire, at random, but with a probability proportional to the PFT seedling abundance in the cell (*sensu* Chesson and Warner 1981; Lamont and Witkowski 1995).

Seed production incorporates annual seed production, and loss of seeds from seed banks. Plants start to produce seeds at diameter size $m_{s,}$ which is their theoretical size at maturity, age *A1*, without competition (Table 6.2). Annual seed production increases with crown radius. Mature regrowing resprouter shrubs and sub-shrubs may re-commence seed production 2 years and 1 year, respectively, after fire (*t1*, Table 6.2). Seed loss from seed banks is constant (1- *v*) and calculated per individual for canopy seed banks, and for each PFT within each cell in the case of soil seed banks, so that after 20 years 10% of all 20-year-old seeds are still viable (Table 6.2).

6.3.3 Simulation experiments

We considered one base-line and four environmental change scenarios: three with modified rainfall conditions (5% increase, 10% decrease and 20% decrease respectively, covering the range of predicted rainfall changes (CSIRO 2001, 2007) and one with a moderate rainfall reduction (-10%) in combination with a reduced mean fire return interval (by 2 years from 13.4 years). We test these scenarios in ‘population level experiments’ and ‘community level experiments’ to assess the sensitivity of each of the 38 PFTs to environmental change. We infer from the population experiments the composition of the seed rain and the regional seed pool, respectively. In the following we describe the environmental change scenarios and the experiments in detail.

Change in the amount of rainfall is modelled as changes in the probability distribution for wet, average, and dry years. We used rainfall records for 118 years at Dongara, the closest climate station with a long term record to the Eneabba field sites (Fig. 6.2; Enright et al. 1998a) to calculate probability distributions. If the annual rainfall exceeded 555 mm, years were classified as ‘wet’, while annual rainfalls of less than 376 mm were classified as ‘dry’. A rainfall amount between these thresholds represented average rainfall conditions. Considering these thresholds the classification of Dongara annual rainfall records led to a distribution of 20% for 'wet', 55% for 'average' and 25% for 'dry' years. We used this probability distribution in the base-line scenario (Enright et al. 1998a; Fig. 6.2).

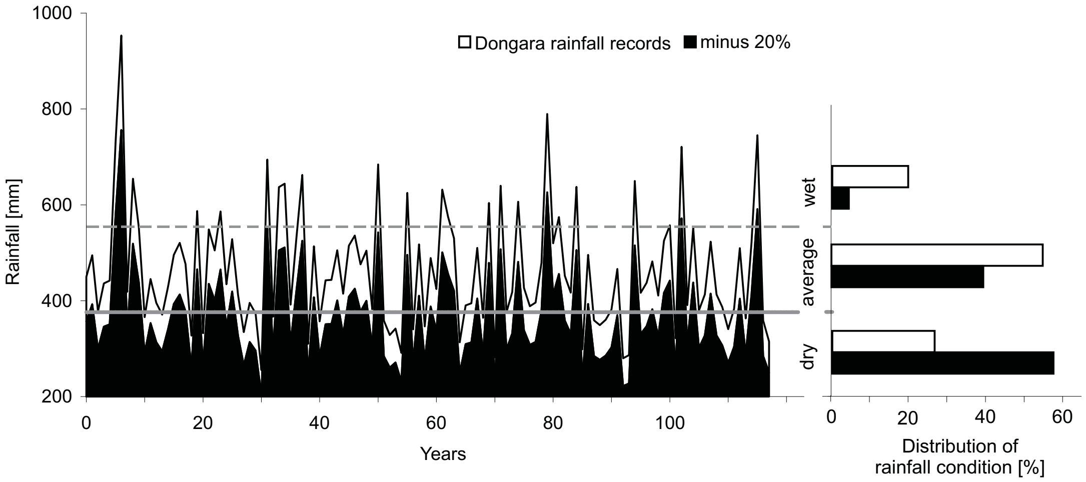

Fig. 6.2 Left: Dongara annual rainfall records for 118 years (1884 – 2001) with levels for differentiation of dry, average and wet years indicated by solid and broken lines. Right: White bars show the % distribution of rainfall years (dry, average and wet years) over the period of records, while black bars show the distribution for the change scenario '-20% rainfall' after 30 years of climate change.

To consider projected change in rainfall conditions for the scenarios we used the annual Dongara rainfall amounts and calculated a linear change in annual rainfall over the first 30 simulation years until the annual rainfall had increased by 5%, or decreased by 10% or 20%. Using these thresholds we recalculated the probabilities for good, average and bad years for the new rainfall scenarios (Fig. 6.2; as an example, for -20% rainfall: 4.2% wet years, 39% average years, and 56.8% dry years). After the 30 year transition period the rainfall condition distributions used in the simulation remained constant.

For the *inter-fire intervals*, the time between two consecutive fire events is determined randomly from a two-parameter Weibull distribution shifted by six years, with a resulting mean inter-fire period of 13.4 years. This is in agreement with the results of fire return interval analysis from satellite image data for the Eneabba Sandplain since the 1970's (Miller et al. 2007). We chose a shape parameter of 2 and a scale parameter of 8.1 and added six years to every chosen fire interval, so that no fire intervals < 6 years were possible. This lower cut is given by the minimum time needed for a sufficient build-up of fuel to carry a fire. We used this in the base-line and the rainfall scenarios. To test the effect of a combination of reduction in mean fire return interval and rainfall changes we combined a reasonable decrease in the mean inter-fire interval of 2 years with a moderate rainfall scenario that assumes a rainfall change of -10%. Thus, the scale parameter of the Weibull distribution changed linearly over 30 years; from 8.1 to 6.07. After 30 years the parameters of the Weibull distributions remained constant at the new level.

Experiments at the population level assess the sensitivity of PFTs to environmental changes and changes in seed production that are subsequently considered as changes in seed immigration in the 'local community level experiments'. The assessment of PFT response to environmental change is analysed in three steps; each PFT was simulated separately under a particular environmental change scenario, the change in number of dispersed seeds was calculated, and the response of each PFT to each scenario was classified.

First, we simulated the spatial and temporal dynamics of each of the 38 PFTs for the five scenarios separately without seed immigration. The simulations started with 144 000 individuals, so that each cell was occupied by one individual, and progressed under base-line conditions for a pre-run time of 500 years to reach a quasi-stationary state. This quasi-stationary state was then used as the starting point for each scenario (base-line, +5%, -10%, -20%, -10%-2), with each scenario simulating 2500 years. To assess the sensitivity of PFTs of a species-rich community to possible environmental changes at the population and community level we compared the results of the base-line scenario (Esther et al. 2008) with four environmental change scenarios.

We repeated each of the five scenarios six times. For each simulated year the mean number of released seeds was calculated as the moving average of the previous 500 years to reduce stochastic fluctuations and derive general trends in seed dispersal. Next, the ratio of the number of seeds released in each of the change scenarios relative to the base-line scenario was determined. And finally, classification of the PFTs' response to the scenario was assessed using the last 1000 years of these ratio series. A PFT was classified as having a positive response if this ratio exceeded 1.05 in more than 950 time steps of the last 1000 years. When the ratio was lower than 0.95 for more than 950 time steps the response was classified as negative. In all other cases the reaction was classified as unresponsive. A positive or a negative reaction led to a changed number of immigrating seeds in the 'community level experiments' (Table 6.2).

Experiments at the community level assess the sensitivity of the PFT community to changes in seed immigration under environmental changes. The community initially consists of 38 PFTs. Each simulation starts with a pre-run of 1,800 years to allow for a quasi-stationary state of the community to arise, during which time the parameterisation of the base line scenario is used. After this pre-run we simulate a minimum simulation time of 1,800 years. In the environmental change scenarios, rainfall and inter-fire intervals change linearly from the parameterization of the base-line scenario to the parameterization of the environmental change scenario over 30 years. The total annual seed immigration in the base-line scenario is 0.11 g/ m², divided equally by mass among PFTs. Thus, more small seeds than large seeds are in the seed rain, with rates depending on seed size (S_{input}, Table 6.2; Esther et al. 2008). The seed rain from the regional seed pool into the local community is randomly distributed for each PFT over the whole grid in the simulation experiments. In the 'local community experiments' we altered the number of immigrating seeds for those PFTs that showed a significant (positive or negative) response in the preceding population level experiments by multiplying, annually, the number of immigrating seeds from the base-line scenario by the ratio of seeds dispersed in the environmental change scenarios *versus* base-line scenario. Five years after the first fire following the minimum simulation time of 1,800 years, the number of coexisting PFTs, and the distribution of traits among all coexisting individuals (i.e. the relative densities of traits) were recorded, with results presented as the average over 20 runs. Additionally, the Shannon diversity index (SDI) was calculated using the abundance of PFTs (Begon et al. 1996). Differences in model outputs (number of coexisting PFTs and SDI) between the base-line scenario and each environmental change scenario were tested using Wilcoxon signed-rank tests for two groups. The statistical tests were carried out using 'R' (version 2.6.0; R Development Core Team 2007).

Sensitivity of PFTs' to environmental change was analysed by the 'classification and regression trees' method (CART) using the RPART library (Therneau and Atkinson 1997) in 'R' (version 2.6.0; R Development Core Team 2007). CART aims to explain the behaviour of a categorical variable (classification trees) or a continuous variable (regression trees) from a suite of predictor variables using binary recursive partitioning rules that are based on thresholds in categorical or continuous predictor variables (Breiman et al. 1984; De'ath and Fabricius 2000). CART works by searching through a set of predictor variables to find the ones that reveal significant patterns and relationships between predictors and targets. CART creates decision trees that are separated into two nodes at each split making this method robust and comprehensible. At each split a predictor is chosen that looks for the largest class in the database and strives to isolate it from all other classes. This procedure is repeated as long as further segmentation is required. CART repeats the search process recursively for each derived node, thereby creating a tree structure (De'ath and Fabricius 2000). Cross-validation is used to express the explanatory power of the tree using sub-sets of the whole data-set as training data. Accuracy of cross-validation is expressed by the cross-validation error (xe). The absolute error (ae) shows how many cases cannot be classified by the generated tree. In our case the CART analyses were performed using the trait category combinations as explanatory variables. The dependent variable was the behaviour of the PFTs (positive, negative, unresponsive) as affected by climate change, assessed in terms of the number of dispersed seeds in the population experiment and by the survival probability in the community experiments. The outcomes of the CART analysis indicate the probability of PFTs with distinct trait characters reacting positively, negatively or not at all to environmental change.

6.4 RESULTS

6.4.1 Consequences of climate change on seed dispersal

All 38 PFTs were simulated individually without seed input from the regional pool to assess the local effects of environmental change on the rate of long distance dispersal. The response is described by the proportion of seeds produced in the environmental change scenarios and in the base-line scenario, considering year 1000 to year 2000 of the total of 2500 simulated years.

Scenario ‘+5%’ was the only scenario where any PFTs had an increase in seed production (positive reaction) compared with the base-line scenario: 10 PFTs showed an increase (Table 6.1; Fig. 6.3a). The number of PFTs with no change in number of dispersed seeds decreased in order ‘+5%’ (with 28), ‘-10%’ (14), ‘-20%’ (5), and ‘-10%-2’ (0) and there were commensurate increases in the number of PFTs with a negative response (Fig. 6.3a).

The *CART analysis* showed that all trait characteristics were represented within the sensitive PFTs (Table 6.1; Fig. 6.4). In the ‘+5%’, maximum seed production was the first split in the tree. For PFTs with high and moderate seed production the probability of increasing seed production seeds is only 0.1, while for PFTs with low seed production and limited dispersal the probability is 0.67 (Table 6.1; Fig. 6.4). PFTs with low seed production, unlimited dispersal and a soil seed bank show no clear response to a 5% increase in rainfall. PFTs with canopy seed banks in combination with large and medium seed size show a positive reaction with a probability of 0.28. In combination with small seeds, all PFTs react

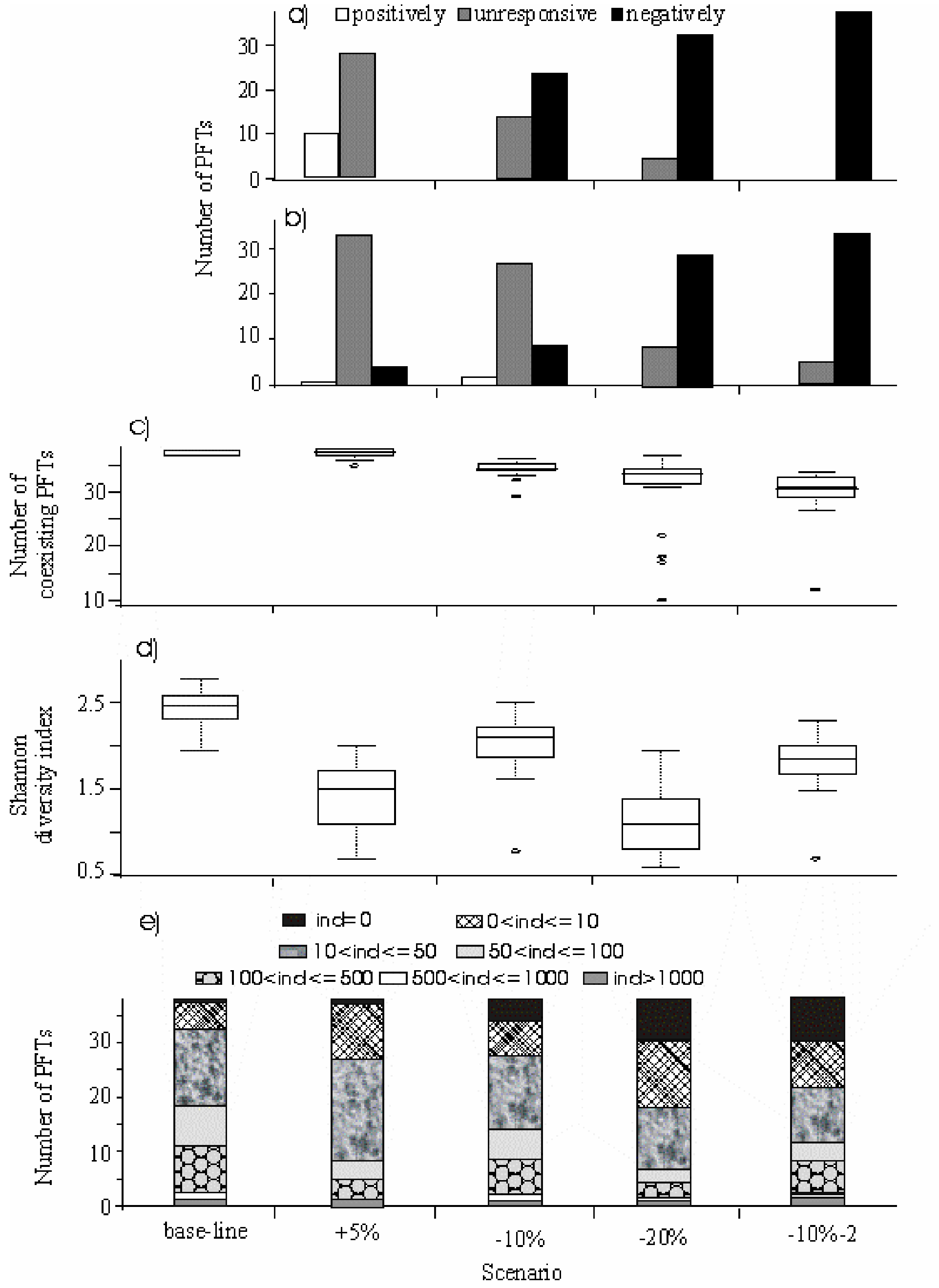

Fig. 6.3 Numbers of PFTs reacting positively, negatively or unresponsive (i.e. no significant change) for the five change scenarios. (a) 'Population level experiment' showing changes in seed production within the last 1000 simulated years. 'Community level experiment' showing (b) changes in survival probability, (c) number of coexisting PFTs, (d) PFT- Shannon diversity index and (e) abundance (number of **ind**ividuals) distribution of PFTs. Centre, bottom and top lines of the box plots are the median, 25th and 75th percentiles, respectively. Whiskers are 1.5 times the inter-quartile range; outliers are data points that lie beyond the extremes of the whiskers.

positively. In scenario ‘-10%’ there are differences between PFTs with low seed production that react negatively to a decrease in rainfall with a probability rate of 0.89, while those with high and moderate seed production among large and medium seed size react negatively with a probability of 0.25 (Table 6.1; Fig. 6.4). Small-seeded resprouters react negatively with a probability of 0.4 and all of the non-sprouters react negatively. In scenario ‘-20%’ regeneration mode was the first split. Resprouters react negatively with a probability of 0.96. The same rate applies for non-sprouters with high seed production (Table 6.1; Fig. 6.4). Non-sprouters with low and moderate seed production in combination with large and medium seed size react negatively with a probability of 0.2. In combination with small seeds, all non-sprouters react negatively (Table 6.1; Fig. 6.4). Changes in the fire regime (‘-10%-2’) reduced seed production in all PFTs, except for one non-sprouter (Table 6.1; Fig. 6.4).

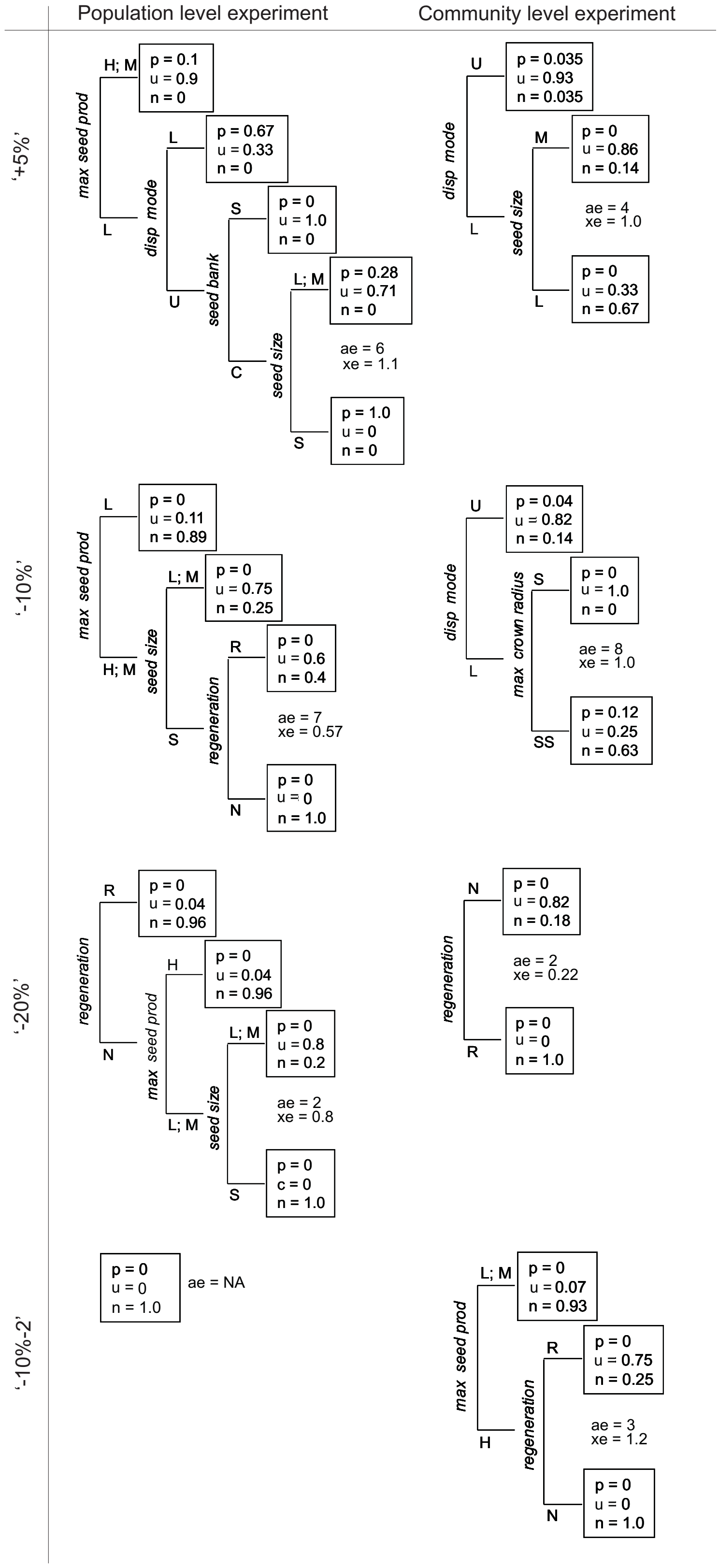

Fig. 6.4 Classification and regression tree model describing the variance in the reaction of PFTs to climate change. Traits functioned as splitting nodes (SN). White boxes are the terminal nodes (TN). Each SN was split into two 'daughter' nodes (e.g. in scenario '+5%' population level experiment: the primary SN is maximum seed production with split to high and moderate on one side and low on the other side). Each TN shows the probability of the PFTs for a positive (**p**) negative (**n**) or unresponsive (**u**) reaction expressed by number of dispersed seeds in the population level experiments and by survival probability in the community level experiments. (**ae** absolute error, **xe** cross-validation error, ***regeneration** mode*: **R**esprouter, **N**on-sprouter, ***max**imum **seed prod**uction*: **H**igh, **M**oderate, **L**ow; ***seed size***: **S**mall, **M**edium, **L**arge; ***seed bank***: **S**oil, **C**anopy; ***disp**ersal **mode***: **L**imited, **U**nlimited; ***max**imum **crown diameter***: Shrub, Sub-Shrub)

6.4.2 Consequences of climate change on community pattern

The assessment of PFT sensitivity to rainfall and inter-fire interval changes is based on the comparison between the survival probability of the PFTs in the environmental change scenarios and the base-line scenario averaged over 20 runs. The median number of coexisting PFTs was 38 in both the ‘base-line’ scenario and ‘+5%’ scenario, (Fig. 6.3c). In the other environmental change scenarios the number of coexisting PFTs was lower (p<0.001). The worst case was scenario ‘-20%’ with a median number of 31 coexisting PFTs.

The Shannon diversity index (SDI) for all environmental change scenarios was significantly lower (p<0.001) than in the ‘base-line’ scenario (SDI = 2.44, Fig. 6.3d). The value decreased in the order ‘base line’, ‘-10%’, ‘-10%-2’ ‘+5%’ ‘-20%’, with the -;20%’ scenario having the lowest SDI (1.08). The abundances of individual PFTs also changed compared with the ‘base-line scenario’ (Fig. 6.3e), with more rare PFTs (<100 individuals) in the environmental change scenarios than in the ‘base-line’ scenario (Fig. 6.3e).

In ‘+5%’ and ‘-10%’ we found one and two PFTs respectively with a low increase in survival probability compared with the base-line scenario (Table 6.1; Fig. 6.3b). Furthermore, 4 of the 38 PFTs at‘+5%’ showed a decreased survival probability trend and 33 PFTs showed no trend. The number of PFTs with unchanged survival probability decreased in the order 5%’ (33 PFTs), ‘-10%’, ‘-20%’, ‘-10%-2’ (5 PFTs), while the number of PFTs with a negative trend in survival increased (Fig. 6.3b).

The *CART analysis* showed that PFTs with all trait combinations were affected by climate, while there were also differences between traits (Table 6.1; Fig. 6.4). In ‘+5%’, dispersal mode was the first split. The probability of PFTs with unlimited seed dispersal reacting positively and also negatively is 0.035. PFTs with limited dispersal and medium seed size react negatively with a probability of 0.14. In scenario ‘-10%’, PFTs with unlimited dispersal mode react negatively with a probability of 0.14 and positively with a probability of 0.04. The survival probability of shrubs with limited dispersal mode was unchanged, and sub-shrubs with limited dispersal mode showed a negative reaction with a probability of 0.63: their probability of a positive reaction was 0.12 (Table 6.1; Fig. 6.4). In scenario ‘-20%’ non-sprouters react negatively with a probability of 0.18. Resprouters consistently showed a negative reaction in survival probability. In scenario ‘-10%-2’, PFTs with a low or moderate seed production reacted negatively at a rate of 0.93 (Table 6.1; Fig. 6.4). Resprouters with high seed production showed a negative response in this scenario with a probability of 0.25. The survival rate decreased for non-sprouters with high seed production (Table 6.1; Fig. 6.4).

6.5 DISCUSSION

6.5.1 Consequences of climate change on populations

We found that changes in rainfall and fire regime affect the number of dispersed seeds among 38 PFT-defined populations. While, these changes can arise at the individual level, as observed in field studies along rainfall gradients (Hovenden et al. 2007; Lamont et al. 2007), they may also be an effect of landscape-level processes where regional species abundances are affected (Brooker et al. 2007; Schurr et al. 2007). The potential for environmental factors to influence an individual's seed production has been demonstrated in empirical and modelling studies of temperate grassland species (Hovenden et al. 2007), woody plants of Mediterranean-type vegetation (Groeneveld et al. 2002) and semi-arid shrublands (White et al. 2008). Hovenden et al. (2007) showed that flowering and seed-production among perennial woody dicots responded strongly to free air CO_2-enrichment and 2° C warming. Based on field experiments and modelling studies, Brooker et al. (2007) found that reductions in establishment success resulted in a reduction of numbers of adults and subsequently to a decrease in seed availability. However, there were differences in magnitude and direction of the effect depending on the species and environmental factors (Levine and Murrell 2003; Brooker et al. 2007).

Life history traits determine a plant's reaction to changed environmental conditions (Pausas 2003; Brooker et al. 2007; Levine and Murrell 2003), so that not all species respond in the same way to such changes. For example, Hovenden et al. (2007) found that warming increased the fraction of the population that flowered in perennial grasses but not in other growth forms. In our model, the trait characters that describe *maximum seed production*, *regeneration mode* and *seed size* drove the sensitivity of PFTs to rainfall change. Low seed production caused sensitivity to changes in rainfall, with the number of dispersed seeds positively correlated to changes in the rainfall. Small-seeded PFTs were more sensitive to rainfall decrease than medium and large seeded PFTs. Resprouter PFTs were also more sensitive to changes in rainfall than non-sprouter PFTs, since the establishment of their seedlings depends on good rainfall conditions after fire (Enright et al. 1998b). Groeneveld et al. (2002) argued that regeneration mode (non-sprouter vs. resprouter) largely determines the response of PFTs to fire regime change. Here we found negative impacts on the number of dispersed seeds for both non-sprouters and resprouters if fire frequency was increased in conjunction with decreasing rainfall (-10%).

Since seed immigration is an important process maintaining local species diversity, the assessment of changes in seed rain composition is necessary for the prediction of species responses to climate change (Chesson 2000; Duguy and Vallejo 2008; Esther et al. 2008; Fitzpatrick et al. 2008; Thuiller et al. 2008). Even minor changes in seed availability can have substantial implications for community composition and structure (Levine and Murrell 2003; Hovenden et al. 2007). We discuss below the effects of climate change on local communities by explicitly considering the changes in regional seed rain based on the results of the population experiments. Although we did not include interactions between PFTs and spatial heterogeneity when calculating the seed rain change (Holderegger et al. 2007; Suter et al. 2007; Perry et al. 2008), the population-level approach allowed us to test, for the first time, the main community-level effects of changes in seed numbers under scenarios of environmental change.

6.5.2 Consequences of climate change on community patterns

Many empirical and modelling studies show that climate change can have a negative impact on biodiversity and the potential to alter communities (Thomas et al. 2004; Klanderud 2008; Heller and Zavaleta 2009). Using climate envelopes, Bakkenes et al. (2002) predicted major changes in biodiversity in Europe by 2050. On average, 32% of the European plant species present in 1990 would disappear locally by 2050. Walker et al. (2006) used a meta-analysis of plant community measurements from standardized warming experiments at 11 locations across the tundra biome to predict that warming will cause a decline in biodiversity across a wide variety of tundra habitats, with a shift from herbaceous to woody communities. Thomas et al. (2004) predicted declining numbers of species globally, with rates depending on the magnitude of climate change. A decline in species diversity with changing climatic conditions also occurs in our simulation experiments, which are based on a mechanistic approach. The same applies to PFT richness in all of our declining rainfall scenarios, but not in the increased rainfall scenario.

While the aggregated descriptors of community structure, such as number of coexisting PFTs and the Shannon diversity index, are negatively correlated with environmental change, we found that individual PFTs respond differentially to change. The number of PFTs with many individuals decreased in favour of PFTs with fewer individuals, i.e. most ‘PFTs’ became less abundant while a few PFTs increased in abundance. We showed that differences in the magnitude of effects depended on the PFT trait characteristics, interactions between PFTs and direction of climate change. Our finding are similar to that of Mouillot et al. (2002), who combined a climate change model with a multispecies functional model and showed that changes in the survival probabilities of the PFTs depended on specific plant traits and the direction and magnitude of environmental changes. An increase in fire frequency led to a shift from Mediterranean-type, maquis woodland to shrub-dominated landscapes (Mouillot et al. 2002). In our study, *regeneration mode*, *seed dispersal*, *seed size* and *maximum crown diameter* best explained sensitivity to changing rainfall, whereas *drought tolerance*, *seed bank type* and *seed production* level were less important. Resprouter survival probability was more strongly negatively affected by a reduction in rainfall than was that of non-sprouters, while non-sprouters were more sensitive to shorter inter-fire intervals, as previous studies have suggested (Groeneveld et al. 2002). Investigating two non-sprouter and one resprouter species in fire-prone shrublands, Groeneveld et al. (2002) showed that increases in the length of the inter-fire period greatly advantaged non-sprouters and disadvantaged resprouters. However, we found that shorter fire intervals combined with lower rainfall negatively affected both non-sprouters and resprouters. We identified that the separate components of change affect each PFT differently: shorter fire intervals impact more on non-sprouters, and lower rainfall more on resprouters. This illustrates the complexity of predicting plant population responses to global environmental change (Walker et al. 2006).

Different plant species face different risks due to climate change, because their responses to climate vary (Klanderud 2008; Morin and Lechowicz 2008). Thus, ignoring differences in life history traits may result in erroneous predictions of species’ responses (Mouillot et al. 2002; Brooker et al. 2007; Morin and Lechowicz 2008; Reyes and Casal 2008). Keith et al. (2007) compared long-term observations with model results for PFTs in fire-prone, species-rich, edaphically variable heathland in south-eastern Australia and found strong agreement in abundance changes for field and model predictions when life history traits and fire frequency changes were considered.

Most studies investigating the impacts of climate change on species assume that regional processes, such as seed immigration rates, are constant in time (Chesson 2000) even though there are indications that: (i) seed immigration is affected by climate change (Chesson 2000; Levine and Murrell 2003; Brooker et al. 2007) and (ii) these effects are central to community composition and structure (Hovenden et al. 2007; Duguy and Vallejo

2008; Esther et al. 2008). Our results show that small changes in regional seed rain may have significant effects on community diversity, the number of coexisting PFTs and the survival of PFTs, depending on their traits. However, our model also shows that change in survival probabilities cannot be explained by changes in the composition of the seed rain alone. Rather, interactions between PFTs blur the impact of changes in the seed rain on community structure. Using a simple process-based model, Brooker et al. (2007) found that changes in biotic processes at both the local and regional scales may determine whether species will persist, or whether there is a catastrophic collapse of populations. It is also important to recognise that PFT-specific responses to climate change are not necessarily additive, due to the complex nature of interactions between them. Thus, quantitative assessments of how climate change will alter community structure and species ranges must deal with interdependent ecological processes at the local and the regional scales (Brooker et al. 2007; Levine and Murrell 2003; Keith et al. 2007; Duguy and Vallejo 2008).

6.6 APPENDIX

6.6.1 Species list with nomenclature following Paczkowska and Chapman (2000)

Acacia barbinervis subsp. *borealis*
Acacia fagonioides
Acacia spathulifolia
Actinostrobus acuminatus
Adenanthos cygnorum subsp. *cygnorum*
Allocasuarina humilis
Allocasuarina microstachya
Andersonia heterophylla
Astroloma microdonta
Astroloma pallidum
Astroloma sp. Red
Astroloma xerophyllum
Baeckea camphorosmae
Banksia attenuata
Banksia candolleana
Banksia hookeriana
Banksia lanata
Banksia leptophylla var. *melletica*
Banksia menziesii
Beaufortia elegans
Boronia cymosa
Boronia ramosa
Bossiaea eriocarpa
Calectasia narragara
Calothamnus hirsutus
Calothamnus longissimus
Calothamnus quadrifidus
Calothamnus sanguineus
Calothamnus torulosus
Calytrix depressa
Calytrix flavescens
Calytrix fraseri
Calytrix sapphirina
Calytrix sp.
Calytrix superba
Comesperma confertum
Comesperma sp. (blue)
Commersonia pulchella
Conospermum incurvum
Conospermum stoechedis
Conospermum wycherlyi
Conothamnus trinervis
Cristonia biloba
Cryptandra myriantha
Cryptandra pungens
Darwinia neildiana
Darwinia speciosa
Daviesia decurrens
Daviesia divaricata
Daviesia nudiflora
Daviesia pedunculata
Daviesia quadrilatera
Daviesia triflora
Diplopeltis huegelii subsp. *subintegra*
Dryandra bipinnatifida subsp. *multifida*
Dryandra carlinoides
Dryandra fraseri
Dryandra lindleyana subsp. *media*
Dryandra nobilis
Dryandra sessilis var. *cygnorum*
Dryandra shuttleworthiana
Dryandra stenoprion
Dryandra tortifolia
Dryandra tridentata
Eremaea beaufortioides
Eremaea ebracteata var. *ebracteata*
Eremaea violacea ssp. *violacea*
Gastrolobium acutum
Gastrolobium capitatum
Gompholobium shuttleworthii
Gompholobium tomentosum
Grevillea eriostachya
Grevillea preissii subsp *glabrilimba*
Grevillea vestita ssp. *isopogoides*
Hakea candolleana
Hakea costata
Hakea eneabba
Hakea incrassata
Hakea lissocarpha
Hakea polyanthema
Hakea prostrata
Hakea psilorrhyncha
Hakea spathulata
Hakea stenocarpa
Hakea trifurcata
Hemiandra sp.
Hibbertia crassifolia
Hibbertia hypericoides
Hibbertia sp. aff. *hypericoides*
Hibbertia sp.3
Hibbertia spicata ssp. *spicata*
Hovea pungens
Hypocalymma xanthopetalum
Isopogon divergens
Isopogon tridens
Isotropis cuneifolia ssp. *cuneifolia*
Jacksonia fasciculata
Jacksonia floribunda
Jacksonia restioides
Labichea cassioides
Lambertia multiflora
Lasiopetalum drummondii
Leptospermum oligandrum
Leptospermum spinescens
Leucopogon sp. aff. *tenuis*
Leucopogon conostephioides
Leucopogon sp.
Leucopogon hispidus
Leucopogon oxycedrus
Leucopogon sp.3
Leucopogon sp.5
Lysinema ciliatum
Melaleuca leuropoma
Melaleuca scabra
Melaleuca trichophylla
Mirbelia spinescens
Petrophile brevifolia
Petrophile drummondii
Petrophile linearis
Petrophile macrostachya
Petrophile rigida
Petrophile scabriuscula
Petrophile serruriae
Phyllanthus calycinus
Phymatocarpus porphyrocephalus
Pileanthus filifolius
Pimelea leucantha
Pimelea sulphurea
Pityrodia bartlingii
Ptilotus stirlingii subsp stirlingii
Scaevola eneabba
Scholtzia involucrata
Scholtzia umbellifera
Stachystemon axillaris
Stenanthemum notiale ssp. *chamelum*
Stenanthemum pomaderroides
Sterculiaceae sp.1
Stirlingia latifolia
Synaphea spinulosa
Thryptomene sp.
Thysanotus fastigiatus
Thysanotus sparteus
Thysanotus triandrus
Unident ericoid leaf
Verticordia sp. *7*
Verticordia argentea
Verticordia chrysanthella
Verticordia densiflora ssp. *caespitosa*
Verticordia grandis
Verticordia monodelpha
Verticordia nobilis
Verticordia ovalifolia
Verticordia pennigera
Xanthorrhoea acanthostachya
Xylomelum angustifolium

7 GENERAL DISCUSSION

The main objective of this thesis was to understand processes promoting local multi-species coexistence in fire-prone, Mediterranean-climate regions. For this purpose I developed a spatially-explicit, individual-based model, based on expert knowledge and data from the Eneabba field sites of Western Australia. The model simulates the life-history of individual plants. The individuals are grouped in plant functional types (PFTs), which are characterised by important demographic traits and responses to environmental conditions such as precipitation and fire. Potential coexistence mechanisms, seed immigration and trade-offs are explored systematically with the simulation model. In addition, the impact of seed immigration on community under simulating the impact of climate change was analysed thoroughly. In the following sections, I will discuss content-related issues and the limits of the model.

7.1 Potential coexistence mechanisms: low-dimensional trade-offs and seed immigration

In Chapter 4 and Chapter 5 I assessed the effects of low-dimensional trade-offs and seed immigration, respectively, to investigate their importance on the maintenance of species diversity in real multi-species communities. Trade-offs are based on the assumption that energy and resources are limited for plants. Due to the costs involved in development and maintenance of life history traits, the competitiveness of plants is constrained by certain inevitable trade-offs (e.g. Crawley 1997). To date, it is largely low-dimensional (i.e. between only two traits) trade-offs that have been considered, although with different results in term of explaination for species coexistence (Lamont and Groom 1998; Tilman 1994; Cornelissen et al. 2003; Moles and Westoby 2006). One main result in Chapter 4 was that low-dimensional trade-offs cannot fully explain multi-species communities. Although PFTs with trait combinations in conflict with the simple trade-off concepts (such as high seed production and resprouting) were involved in community simulations, the Shannon diversity index (SDI) and number of coexisting PFTs was high in my model study. Additionally, the SDI did not increase explicitly, if strong PFTs were excluded from the community simulations. The results are in contrast to the general assumption that 'jack-of-all-trade' or super-species combining all advantageous life history attributes would dominate communities (Rosenzweig 1995; Gordon 2000). The results are in accordance with empirical work of multi-species communities (Clark et al. 2004; Chave 2004) and simulation studies (Jeltsch et al. 1996, 1998; Amarasekare and Nisbet 2001; Warren and Topping 2004; Clark et al. 2007) incorporating more realistic processes and whole life histories. Thus, other mechanisms such as seedling competition or high-dimensional differences in life history could be more important for stabilizing local multi-species communities.

High dimensional differences in life history were not considered as coexistence mechanisms in the results described here. This theory is based on the huge number of trait differences among species, which lead to advantages and disadvantages in space and time (Clark et al. 2007). Thus, it can be that simple trade-offs evolve as part of a wide spectrum of life history traits (Clark et al. 2004; Moles and Westoby 2006; Clark et al. 2007). Using a theoretical mathematical approach Moles and Westoby (2006) showed by that besides seed size and seed number, longevity, maturity age and plant growth could be involved in facilitating coexistence by leading to equivalent fitness. The investigation of such high dimensional differences in life history for fire-prone Mediterranean-climate communities under realistic environmental conditions could be a promising way to improve our understanding (see future research).

A further stabilizing coexistence mechanism explaining high numbers of PFTs could be density-dependent, intra-specific seedling competition. This effect has not been discussed in this thesis. However, it was implemented as a model rule, based on observations by Lamont et al. (1993), who found lower seedling survival in monospecific stands compared to mixed stands. Seedling survival rates increase with seed size, especially in dry years, such that seed size variation underlies variation in density-dependent intra-specific seedling competition (Lamont unpubl.; Shilo-Volin et al. 2005; Moles and Westoby 2006; Tormo et al. 2008). Coexistence seems to be possible as long as intraspecific competition is stronger than interspecific interactions, a hypothesis that arose also from classical Lotka-Volterra models (ordinary differential equation models, ODE) (e.g. Hardin 1960; Hutchinson 1961; May 1973). Classical ODE models neglect other processes, such as spatial interactions, sources of environmental and demographic stochasticity, which are important to explain multi-species coexistence (Jeltsch et al. 1996, 1998; Howard and Goldberg 2001; Moles and Westoby 2006). Thus, the uncertainty in terms of density-dependent, intra-specific seedling competition clearly poses the need to systematically explore its effect on local multi-species communities under realistic environmental conditions (Shilo-Volin et al. 2005; Tormo et al. 2008).

Seed immigration, was not considered in the investigation of trade-offs in Chapter 4. It is, however, in contrast to low dimensional trade-offs, an important stabilizing mechanism for local coexistence (see Chapter 5). In Chapter 5 it is shown that seed rain consisting of equal seed mass per PFT leads to a more realistic pattern of the Shannon diversity index and number of coexisting PFTs than did seed rain consisting of equal seed numbers per PFT. This is agreement with the competition/colonisation hypothesis (Tilman 1997; Moles and Westoby 2006), because seed numbers in the seed rain are negatively correlated with seed mass (Mouquet et al. 2004). However, this trade-off does not seem to explain multi-species coexistence, as both the equal seed mass per PFT and the equal seed number per PFT seed rain concepts lead to high Shannon diversity indices (Chapter 5). In case of seed immigration it would be interesting to detect realistic seed densities: their rates vary strongly between communities and between experiments in previous studies (Loreau and Mouquet 1999; Turnbull et al. 1999; Mouquet et al. 2004; Eskelinen and Virtanen 2005; Hiltunen et al. 2006; Zeiter et al. 2006). We estimated the seed rain to be 540 seeds per m² and year in maximum at the Eneabba shrublands (see Chapter 5). Due to the sensitivity of the community to seed rain composition, further detailed empirical and modelling investigations would be useful (see future research).

7.2 Impact of climate change on plant functional types and community structure

It is hypothesized that seed immigration will be altered by climate change (Levine and Murrell 2003; Davis 2005; Nathan et al. 2008; Kuparinen et al. 2009). This could drastically affect species diversity because seed immigration is important for plant coexistence at the local scale (Turnbull et al. 1999; Zobel et al. 2000; Foster 2001; Coomes and Grubb 2003; Kisdi and Geritz 2003; Mouquet et al. 2004; Hiltunen et al. 2006). Chapter 6 shows the potential response of the vegetation at the Eneabba field sites to climate change, with a focus on altered seed rain composition. In accordance with other studies, the response of PFTs depends on plant traits and the direction and magnitude of climate change (Mouillot et al. 2002; Levine and Murrell 2003; Brooker et al. 2007; Fitzpatrick et al. 2008). In this study a change in the seed rain composition always reduced the Shannon diversity index at the community level. The same applies for the number of coexisting PFTs, except when the seed rain increases. However, the changes in survival probabilities can not be solely explained by changes in the composition of the seed rain. Interactions between PFTs, such as seedling competition, blur the impact of changes in the seed rain on community structure.

Investigations on the effects of climate change on dispersal and spread of plants are rare (Nathan et al. 2008; Kuparinen et al. 2009). In a recent study on seed dispersal by wind Kuparinen et al. (2009) show that an increase in temperature may promote plant movement in boreal forests. One important factor for plant movement by long-distance dispersal is seed availability (Groeneveld et al. 2008; Kuparinen et al. 2009). Although in my study the calculations of seed rain change are based on simulations of single PFTs interactions among PFTs and spatial heterogeneity are neglected , For the first time this approach allows to test the potential community effects of changes in seed numbers under environmental change. The consequences of climate change will be changes in reproductive rates leading to altered seed immigration rates and changes in coexistence patterns in these local multi-species communities. Therefore, studies evaluating the effects of climate change on future plant distributions fail if they ignore changes in seed immigration (see also Chesson 2000; Kuparinen et al. 2009). Altered seed immigration at the local scale also affects processes at larger scales (Thomas et al. 2004; Brooker et al. 2007; Morin and Lechowicz 2008) and should be considered in models evaluating plant distribution at large scales. For example the predictive power of climate envelope models seems to be limited due to the fact that predictions of future species occurrences are only based on current correlation of species distributions and climatic variables (Bakkenes et al. 2002; Huntley et al. 2004; Gusian and Thuiller 2005; Heikkinen et al. 2006). One reason for this might be their spatial scale. Due to the complexity of local processes influencing dispersal, it might be difficult to make predictions at the global scale. However, Guisan and Thuiller (2005) discuss a general hierarchical modelling framework for integration of disturbance, dispersal and population dynamics within species distribution models to overcome this problem. To obtain more realistic predictions of species distribution, the model basis could include general rules of biotic interactions, dispersal behaviour and population dynamics (Guisan and Thuiller 2005). BIOMOD developed by Thuiller et al. (2009) demonstrates another approach, the ensemble forecasting of species distributions. This tool considers a wide range of techniques, including the envelope model approach and different dispersal assumptions. It shows the prediction range and allows consideration of the uncertainties of different approaches.

7.3 Model limitations

To improve ecological understanding as a basis for conservation measures, a number of traits relevant to species coexistence have been investigated in the fire-prone shrublands of southwest Australia, including: differences between regeneration traits (Enright et al. 1998a, b), seed bank dynamics (Lamont et al. 1991), seed production and seedling survival (Cowling et al. 1987; Enright and Lamont 1989; Lamont et al. 1993), and coexistence mechanisms of selected species (e.g., Enright et al. 1998a, b; Lamont et al. 2007). In this thesis much of this knowledge was used to develop a complex simulation model to investigate potentially important mechanisms for multi-species coexistence. The individual-based, spatially-explicit modelling approach allowed integration of much of the information of these former studies. Therewith the study goes further than it would have been possible with field investigations, theoretical models or models of only a few species. And, the model results show that by using structurally realistic assumptions the importance of low-dimensional trade-offs is diminished and the role of seed immigration is emphasised.

The complex model helped to point out key processes unconsidered so far in realistic multi-species communities. For example although regional seed input could explain more aggregated measures of local community structure, more detailed aspects of community composition in terms of relative abundances of plant traits could not be explained. This revealed that further research needs to be done to find the missing traits and processes. One interesting aspect would be the trait dispersal vector, distinguishing between wind and various forms of animal-dispersed seeds (Calviño-Cancela et al. 2006, 2008; DeFalco et al. 2009). Animal dispersal, by emus or ants, led to clumped distribution of selected seeds, and could explain the community compositions (see future research).

Uncertainties in model processes such as density regulation (Chapter 4) and values such as seed immigration rates (Chapter 6) should be minimized by further studies. My climate change study only gives an impression of the effects of altered seed immigration. Spatial heterogeneity of vegetation by patchiness of fire-events or landscape formations remains unconsidered (Groeneveld et al. 2002, 2008). However, it certainly influences the composition of seed rain and the seed input on local communities (Rees et al. 2000; Zavaleta et al. 2007; Gómez-Aparicio 2008; Groeneveld et al. 2008). My studies highlight the importance of seed immigration as a key process for biodiversity maintenance, which should be in the focus of further investigations (see future research).

8 FUTURE RESEARCH

The complex modelling work of my study on the basis of a unique empirical data set has invoked new questions and revealed further needs for research. For example, since low-dimensional trade-offs failed to explain high diversity (Chapter 4) an interesting topic for future research would be the analysis of other stabilizing mechanisms. In Chapter 4 I focused on trade-offs between two plant traits (e.g. colonisation vs. competition), but neglected trade-offs involving more than two plant traits. However, it is possible, that there are complex trade-offs between the evolved Eneabba plant traits such as seed production, maturity age, life span, and regeneration, creating competition compensation (Howard and Goldberg 2001; Moles and Westoby 2006). Investigations of this aspect could possibly give new information, why so many species can coexist.

Furthermore, the process of density regulation as a potential mechanism explaining high biodiversity pattern on local scale is worth systematic exploration (e.g. Chesson and Warner 1981; Higgins et al. 2000). In the model density regulation is described by a power law function, with a seed size specific exponent (see 4.7.2). However, this functional relationship between seed size and the strength of density regulation needs further empirical and modelling investigations to ensure the accuracy of the translation of this process into models.

Results from chapter 5 showed that the distribution in terms of seed dispersal could not be explained. One explanation for this shortcoming could be that the differences among dispersal vectors were neglected and should be included in future studies. For the Eneabba region Calviño-Cancela et al. (2006) classified several dispersal vectors, such as anemochory (wind), myrmecochory (ants) and vertebrate endozoochory (inside vertebrate animals). In contrast to the anemochory that leads to single seed distributions, vertebrate endochory by Emus leads to clumped seed distributions on a long-range scale with a maximum of 600 km. Myrmechory leads to short-range clumped seeds distribution in distances of usually <2m (Calviño-Cancela et al. 2006, 2008; De Falco et al. 2009). The differences in dispersal vectors could lead to variances in seed densities with follows for establishment rates of seedlings and coexistence pattern.

My model investigation highlights that there is a deficiency of empirical data on the amount and composition of the seed rain and its variability (Chapter 5 and Chapter 6). It would be possible to detect the number and mass of seeds with seed traps (see for example Gómez-Aparicio 2009) at the four study sites of Eneabba. The resulting data could be directly used in my modelling framework. This is a major advantage of this model compared to more conceptional models, as it allows improving iteratively the model by including more realistic processes and hence, to address questions on ecological theory, conservation management and the implications of climate change.

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10 DANKSAGUNG

Ich möchte mich bei allen herzlich bedanken, die mich während meiner Doktorarbeit ausdauernd und konstruktiv unterstützt haben! Erwähnen möchte ich:

Meine Betreuer Prof. Dr. Florian Jeltsch und Dr. Jürgen Groeneveld, vor allem wegen ihrer intensiven fachlichen Unterstützung.

Die australischen und neuseeländischen Kooperationspartner: Prof. Neal J. Enright, Ben P. Miller, PhD, Prof. Byron B. Lamont, George L.W. Perry, PhD die viel Zeit aufwendeten und ihr Expertenwissen und ihre Daten für das Modell zur Verfügung stellten. Thanks guys!

Die Koautoren - Dr. Frank M. Schurr, Dr. Britta Tietjen, Dr. Benjamin Blank - wegen ihrer kompetenten Unterstützung.

Die Gutachter meiner Arbeit: Prof. Dr. Florian Jeltsch, Prof. Neal.J. Enright, Prof. Dr. Uta Berger und Prof. Dr. Christine Rademacher.

Dr. habil. Volker Grimm, der mich an das wissenschaftliche Schreiben herangeführt hat.

Die ehemaligen Studien- und Arbeitskollegen der Universität Potsdam, für ihre Unterstützung und das gute Arbeitsklima.

Die Arbeitsgruppe „Wirbeltierforschung“ des Julius Kühn-Instituts, die mich in Ihrer Runde aufgenommen und mir tolle beruflichen Perspektiven eröffnet hat.

Meine Eltern, Geschwister und ihre Familien, die allesamt viel Verständnis zeigten, wenn mal wieder keine Zeit war.

Die Familie Blank, im Besonderen aber *Benjamin*, der mich langjährig intensiv unterstützt hat.

Meine Arbeit wurde finanziert durch die Deutsche Forschungsgemeinschaft (DFG Projekt102JE 207/2) und zusätzlich unterstützt durch das Australian Research Council (DP0343511).