



THE UNIVERSITY OF QUEENSLAND
AUSTRALIA

**Pathogen driven change in species-diverse woodlands of the
Southwest Australian Floristic Region: A hybrid ecosystem in a
Global Biodiversity Hotspot**



Carly Lauren Bishop

A thesis submitted for the degree of Doctor of Philosophy at
The University of Queensland in June 2012
School of Agriculture and Food Sciences

Declaration by author

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis. I have clearly stated the contribution of others to my thesis as a whole, including statistical assistance, survey design, data analysis, significant technical procedures, professional editorial advice, and any other original research work used or reported in my thesis. The content of my thesis is the result of work I have carried out since the commencement of my research higher degree candidature and does not include a substantial part of work that has been submitted to qualify for the award of any other degree or diploma in any university or other tertiary institution. I have clearly stated which parts of my thesis, if any, have been submitted to qualify for another award.

I acknowledge that an electronic copy of my thesis must be lodged with the University Library and, subject to the General Award Rules of The University of Queensland, immediately made available for research and study in accordance with the *Copyright Act 1968*.

I acknowledge that copyright of all material contained in my thesis resides with the copyright holder(s) of that material.

Statement of Contributions to Jointly Authored Works Contained in the Thesis

This thesis contains three jointly-authored articles for peer review. These manuscripts have been incorporated into the thesis and form chapters 3, 4 & 7.

Chapter Three

Bishop, C.L., Wardell-Johnson, G.W. & Williams, M.R. 2010. Community-level changes in *Banksia* woodland following plant pathogen invasion in the Southwest Australian Floristic Region. *Journal of Vegetation Science* 21: 888-898.

Carly Bishop was responsible for 70% of conception and design, 80% of analysis and interpretation of data and 80% of drafting and writing; Grant Wardell-Johnson was responsible for 30% of

conception and design, and 10% of drafting and writing; Matthew Williams was responsible for 20% analysis and interpretation of data and 10% of drafting and writing.

Chapter Four

Bishop, C.L., Williams, M.R. & Wardell-Johnson, G.W. 2011. A forest pathogen drives change in plant functional trait composition in the Southwest Australian Floristic Region. *Agriculture, Ecosystems and Environment* 145: 59-66.

Carly Bishop was responsible for 80% of conception and design, 80% of analysis and interpretation of data and 75% of drafting and writing; Matthew Williams was responsible for 20% analysis and interpretation of data and 15% of drafting and writing; Grant Wardell-Johnson was responsible for 20% of conception and design, and 10% of drafting and writing;

Chapter Seven

Bishop, C.L. & Wardell-Johnson, G.W. in prep. Introduced forest pathogen results in hybrid ecosystem in species-diverse woodlands. In preparation for submission to *Ecosystems*

Carly Bishop was responsible for 70% of conception and design, 80% of analysis and interpretation of data and 70% of drafting and writing; Grant Wardell-Johnson was responsible for the remaining percentages of each category. Figure 20 of this chapter will be removed prior to submission for publication and instead referenced to in text. This figure is published by Hobbs *et al.* (2009) and has been included in this thesis for explanation and clarity of existing theory.

Statement of Contributions by Others to the Thesis as a Whole

None

Statement of Parts of the Thesis Submitted to Qualify for the Award of Another Degree

None

Published Works by the Author Incorporated into the Thesis

None

Additional Published Works by the Author Relevant to the Thesis but not Forming Part of it

Bishop, C.L., Wardell-Johnson G.W., Williams, M.R. (2009). How does *Phytophthora cinnamomi* change *Banksia* woodland alpha and beta diversity in the southwest Australian global biodiversity hotspot? (ABSTRACT). In *SERI 2009: World Conference on Ecological Restoration: Making Change in a Changing World: 19th Conference of the Society for Ecological Restoration International, Perth, Western Australia, Australia, Sunday 23 August to Thursday 27 August 2009: Conference Abstracts* Conference Organising Committee, Perth. p. 80

Bishop, C.L., Wardell-Johnson, G.W., Shearer, B.L. (2007). Resilience of *Banksia* woodlands to *Phytophthora cinnamomi* in the Walpole Wilderness Area, SW Western Australia. In *MEDECOS XI: conference proceedings: the International Mediterranean Ecosystems Conference, Perth, Western Australia, Australia, Sunday 2-Wednesday 5 September 2007* (eds D. Rokich, G. Wardell-Johnson, C. Yates *et al.*). Kings Park & Botanic Garden, West Perth. pp. 19–20

Bishop, C.L., Wardell-Johnson, G.W., Shearer, B.L. (2007). Resilience of *Banksia* woodlands to *Phytophthora cinnamomi* in the Walpole Wilderness Area, SW Western Australia (ABSTRACT). In *MEDECOS XI: conference program, information & summary abstracts: the International Mediterranean Ecosystems Conference, Perth, Western Australia, Australia, Sunday 2-Wednesday 5 September 2007* Conference Organising Committee, Perth. pp. 47–48

Acknowledgements

I wish to thank my supervisor Dr Grant Wardell-Johnson for guiding me in the right direction and for accepting, encouraging and assisting development of the central ideas around which this thesis is based. I also wish to thank Grant for inspiring me to think beyond what is currently accepted and to develop and communicate these ideas through my writing.

I also wish to thank Dr Neil Burrows of the Department of Environment and Conservation (Science Division) for his contagious energy and enthusiasm for the project and continued words of encouragement during the trying times of the PhD process.

Dr Matthew Williams also of DEC played a key role in this project though provision of statistical advice. I want to thank Matt for his unwavering patience to my constant questions and periodic

looks of confusion. Thank you also for covering my manuscripts in red pen which has substantially enhanced my writing style leading to publication of thesis chapters.

Thank you to Tub and Jenny Liddelow for providing fantastic hospitality and accommodation during fieldwork. Thank you so much for letting me and my field helpers stay at your Peaceful Bay house which was a home away from home during the long field work stints. Thank you also to my neighbour at Peaceful Bay, Judy, for lending a welcome ear at the end of each day and also for the delicious dinners!

And to Jos Fissioli, who spent weeks traipsing through the wilds of Walpole while we helped each other out with field work. Rain, wind and wild pigs were no deterrent and I still smile at thoughts of driving back to Peaceful Bay tired and hungry but still happy. I especially enjoyed our road trips down south where we dutifully stopped at Bridgetown for cream donuts and a quick look at the op-shop. Your friendship has been invaluable in making the many hours of fieldwork and office work more bearable and memorable.

I also wish to thank my parents for their constant support throughout my studies. I remain ever grateful for their continued love and understanding.

My greatest thanks are to my partner Jeff for his continued support, encouragement and motivation over the past few years. His unwavering understanding and reassurance was crucial to completion of this thesis. Thank you for always showing great interest in my research and for being by my side the whole way through. I dedicate this to you.

Abstract

Human-induced change in natural environments is occurring at unprecedented rates over ecologically brief periods of time. The consequences of such disturbance has been documented in both terrestrial and marine habitats with much focus on disturbance events such as extreme weather events (hurricanes, cyclones etc.), agriculture, altered fire regimes, weeds and climate change. Pathogens are increasingly being recognised as powerful agents of change, though documentation is limited and often restricted to species-level changes. Inextricably linked to the direct changes in species composition are the indirect effects of pathogens on community structure and ecosystem function. Traditional species-based studies looking at pathogen-induced change focus on specific and somewhat one-dimensional shifts in species richness, species cover and un-standardised diversity indices. This project was developed to explore the impact of pathogen disturbance beyond species-level changes using a structured and comprehensive approach that integrates current ecological theories.

This PhD is part of a larger ARC linkage project titled "*Towards a Landscape Conservation Culture – broadening the spatio-temporal scope of ecological studies to anticipate change in Australian forested ecosystems.*" It aims to explore questions regarding biodiversity management using an integrated landscape-level approach to conservation which looks beyond individual species. This is because the performance and persistence of an ecosystem is dependent upon the complexity of relationships between different ecosystem components at a range of spatial scales beyond the species-level.

Through integrating and utilising current ecological theory and frameworks, this thesis links concepts and methods in community ecology to explore disturbance and change. This link is often inadequate in ecological literature and requires bridging through application and testing of theory in field situations or novel research. The practical integration and application of Resilience and Novel Ecosystem theory, forms the basis of the thesis and provides an alternate view of disturbance beyond species-level shifts. Resilience theory suggests that changes in composition and structure lead to an irreversible regime shift. This will be used as a basis to describe pathogen impacts and as criteria for determining if a novel or hybrid ecosystems results. Through this integration I describe changes occurring across spatial scales to provide a comprehensive account

of disturbance in a forest ecosystem. I use the introduction of forest pathogen *Phytophthora cinnamomi* into *Banksia attenuata* woodlands as a case study.

Banksia attenuata woodlands in the high rainfall zone of the Southwest Australian Floristic Region are highly susceptible to *P. cinnamomi* infestation. These woodlands contain a substantial suite of pathogen-susceptible species and are found in low lying areas of the landscape in prime position for pathogen infestation by overland water flow. Due to these factors and obvious disease expression, these *Banksia* woodlands were chosen for investigation.

Using resilience theory as a framework I begin by describing pathogen-induced shifts in species composition and vegetation structure as a basis for further enquiry into shifts in plant functional traits. Using a chronosequence of disease expression replicated across the landscape, I identify changes in species dominance and associated shifts in stand variables (canopy cover, leaf litter and basal area). I also apply uni-variate and multivariate diversity indices that identify change at both the species and community-level. I continue by describing shifts in plant functional trait composition with deduced links to ecosystem function. These shifts in addition to the changes in species dominance and stand variables are then used to determine if a novel or hybrid ecosystem has resulted from pathogen infestation.

This thesis demonstrates that although *Banksia attenuata* woodlands have undergone an irreversible shift in identity (species dominance, beta diversity, stand variables, plant functional trait composition) some original features have been retained including species richness, species diversity and functional diversity. For these reasons, the post-pathogen community identifies as a hybrid ecosystem that is equally speciose despite other substantial pathogen-induced shifts. Following infestation, *Banksia attenuata* woodlands are unlikely to return to their previous state due to changes in site microclimate associated with the substantial shifts in species dominance and related variables.

Keywords

Disturbance; ecosystem function; hybrid ecosystem; novel ecosystem; pathogen; *Phytophthora cinnamomi*; plant functional trait; regime shift; resilience.

Australian and New Zealand Standard Research Classifications (ANZSRC)

060202 Community Ecology (excl. Invasive Species Ecology) 60%, 050102 Ecosystem Function 20%,
050103 Invasive Species Ecology 20%.

TABLE OF CONTENTS

List of figures	xv
List of tables.....	xvi
CHAPTER ONE: INTRODUCTION	1
Background literature.....	1
<i>Concepts of Resilience Theory</i>	<i>1</i>
<i>Criticisms of Resilience Theory</i>	<i>5</i>
<i>Novel, emerging and hybrid ecosystems.....</i>	<i>7</i>
<i>Disturbance</i>	<i>8</i>
<i>Quantifying change and resilience in ecosystems.....</i>	<i>10</i>
<i>Change in vegetation composition and structure</i>	<i>11</i>
<i>Change in ecosystem function, functional diversity and functional redundancy</i>	<i>12</i>
Research justification	15
<i>Pathogen impact at the community-level.....</i>	<i>15</i>
<i>Integration of theoretical frameworks.....</i>	<i>15</i>
Research questions.....	17
Thesis structure.....	18
Study design.....	22
CHAPTER TWO: STUDY AREA	24
The high rainfall zone of the Southwest Australian Floristic Region (SWAFR)	25
Conservation theory.....	27
Geology and soils	28
Climate.....	28
Vegetation	30
Disturbance.....	32
<i>Introduced plant pathogen: Phytophthora cinnamomi</i>	<i>32</i>
<i>Fire.....</i>	<i>34</i>
<i>Interaction between disease and fire.....</i>	<i>36</i>

CHAPTER THREE: COMMUNITY-LEVEL CHANGES IN BANKSIA WOODLAND FOLLOWING PLANT PATHOGEN INVASION	38
Abstract	39
Introduction	40
Methods and materials.....	41
<i>Study area</i>	<i>41</i>
<i>Study design and data collection</i>	<i>42</i>
<i>Data analysis.....</i>	<i>43</i>
Results	45
<i>Community-level changes</i>	<i>45</i>
<i>Change in stand variables – chronosequence data only.....</i>	<i>46</i>
<i>Species-level changes</i>	<i>47</i>
Discussion	49
<i>Community-level changes</i>	<i>49</i>
<i>Species-level changes.....</i>	<i>52</i>
<i>Interacting agents of disturbance</i>	<i>52</i>
Acknowledgements	54
CHAPTER FOUR: A FOREST PATHOGEN DRIVES CHANGE IN PLANT FUNCTIONAL TRAIT COMPOSITION IN THE SOUTHWEST AUSTRALIAN FLORISTIC REGION	56
Abstract	57
Introduction	58
Material and methods	60
<i>Study area</i>	<i>60</i>
<i>Site selection.....</i>	<i>61</i>
<i>Trait measurement.....</i>	<i>62</i>
<i>Pathogen activity</i>	<i>63</i>
<i>Data analysis.....</i>	<i>64</i>
Results	65
<i>Change in community-weighted means (CWM)</i>	<i>65</i>
<i>Change in community-weighted totals (CWT).....</i>	<i>66</i>
<i>Pathogen activity</i>	<i>69</i>
Discussion	69
<i>Community weighted means (CWM) vs. Community-weighted totals (CWT).....</i>	<i>69</i>
<i>Shifts in trait values.....</i>	<i>70</i>
<i>Notes on using community-weighted totals (CWT)</i>	<i>73</i>

Conclusion.....	73
Acknowledgements	73
CHAPTER FIVE: CHANGE IN ABSOLUTE COVER MATTERS!.....	74
Abstract	75
Introduction	75
Derivation of the index.....	76
Testing the index.....	77
Conclusion.....	79
CHAPTER SIX: DOES AN INTRODUCED FOREST PATHOGEN ALTER FUNCTIONAL DIVERSITY?	80
Abstract	81
Introduction	82
Methods	84
<i>Study area</i>	<i>84</i>
<i>Site selection.....</i>	<i>85</i>
<i>Data collection</i>	<i>85</i>
<i>Data analysis.....</i>	<i>86</i>
Results	87
Discussion	89
CHAPTER SEVEN: INTRODUCED FOREST PATHOGEN RESULTS IN HYBRID ECOSYSTEM IN SPECIES-DIVERSE WOODLANDS	92
Abstract	93
Introduction	94
Methods	97
<i>Study area</i>	<i>97</i>
<i>Study design</i>	<i>98</i>
Results	100
<i>Change in species composition and vegetation structure</i>	<i>100</i>
<i>Change in plant functional trait composition</i>	<i>101</i>
Discussion	101
<i>Hybrid or novel ecosystem?</i>	<i>101</i>
<i>Change in vegetation structure and species composition</i>	<i>102</i>
<i>Change in plant functional trait composition</i>	<i>104</i>
<i>An irreversible regime shift</i>	<i>104</i>
<i>Conclusion</i>	<i>106</i>

Acknowledgements	107
CHAPTER EIGHT: CONCLUSION	108
Overview.....	109
Research outcomes	111
Further research.....	115
REFERENCES.....	116

List of figures

Figure 1: The ‘ball in the basin’ conceptual model of regime shifts and thresholds (a) The state of the system is represented by the ball which due to system dynamics is attracted to the pit of the basin. The system can change regimes either by the state changing, or through changes in the shape of the basin (i.e., through changes in processes and system function), as shown in Figure (b) (Resilience Alliance 2005).....	3
Figure 2: The four phases of the Adaptive Cycle (Resilience Alliance 2005).....	4
Figure 3: Conceptual framework of ecosystem properties with structural and functional properties emergent from composition (Lamont 1995, Noss 1990).	10
Figure 4: Increased publication rate of biodiversity & ecosystem function papers (Naeem et al. 2004).	12
Figure 5: Examples of plant traits and associated functions (Lavorel et al. 2007).	14
Figure 6: Resilience theory components (composition, structure & function) used as criteria in <i>Banksia</i> woodland to detect a potential regime shift and determine and describe subsequent novel, hybrid or resilient ecosystem.....	16
Figure 7: Thesis structure and chapter titles. Bracketed numbers refer to research questions addressed in data chapters. * signifies chapter published or in press.	21
Figure 8: Disease chronosequence quadrat placement at each site. This design was replicated 17 times at random sites across the landscape.	22
Figure 9: Location of the Southwest Australian Floristic Region (green line) with average annual rainfall isohyets (from Hopper & Gioia 2004).	25
Figure 10: Rainfall isohyets and associated rainfall zones of the Southwest Australian Floristic Region (Hopper 1979).	26
Figure 11: Temperature and rainfall averages for Walpole (Weatherzone 2011).	29
Figure 12: <i>Banksia attenuata</i> woodland in the high rainfall zone of the Southwest Australian Floristic Region. Key species susceptible to <i>Phytophthora cinnamomi</i> are indicated.....	31
Figure 13: Direct and potential indirect effects of <i>Phytophthora cinnamomi</i> on susceptible plant communities (Shearer & Smith 2000).	34
Figure 14: Constrained ordination of species cover-abundance across disease chronosequence in <i>Banksia</i> woodland of the Southwest Australian Floristic Region ($p=0.001$) with vector overlay of stand variables CC = canopy closure, BA = basal area, LL = leaf litter.	46
Figure 15: Historic (1990 v 2006) dot plot of changes in species cover-abundance following pathogen infestation in <i>Banksia</i> woodland of south-western Australia. Species means are plotted in order of greatest contribution to dissimilarity between healthy and diseased vegetation as derived from the SIMPER routine in PRIMER. Species listed are the top 40% of species contributing to site dissimilarity. Species susceptible to the pathogen are printed in bold. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$	48
Figure 16: Disease chronosequence dot plot of changes in species cover-abundance following pathogen infestation in <i>Banksia</i> woodland of south-western Australia. Species means are plotted in order of greatest contribution to dissimilarity between healthy and diseased vegetation as derived from the SIMPER routine in PRIMER. Species listed are the top 40% of species contributing to site dissimilarity. Species susceptible to the pathogen are printed in bold. ** $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$	49
Figure 17: Change in community-weighted total trait values following disease infestation in <i>Banksia</i> woodland of south-western Australia ($p=0.03$) - Unconstrained ordination: Principal Coordinate Analysis.	66
Figure 18: Change in community-weighted total trait values following disease infestation in <i>Banksia</i> woodland of south-western Australia ($p=0.03$) - Constrained ordination: Canonical Analysis of Principal coordinates.....	67
Figure 19: Relationship between Rao’s index of functional diversity (10 traits) and (a) species richness and (b) Simpson’s diversity index.....	89
Figure 20: Shifts from historical biotic composition and/or abiotic conditions that result in hybrid or novel ecosystems (from Hobbs et al. 2009).....	95

Figure 21: Resilience theory components (composition, structure & function) used as criteria in <i>Banksia</i> woodland to detect potential regime shift and determine and describe subsequent novel, hybrid or resilient ecosystem.....	99
Figure 22: Disease chronosequence with changes listed in white text below corresponding quadrats. Characteristics that were maintained despite disease infestation are listed in black italic text. Chronosequence runs from healthy vegetation through to infested vegetation and was replicated 17 times in spatially separate polygons of <i>Banksia</i> woodland.	102
Figure 23: Thesis structure and chapter titles. Bracketed numbers refer to research questions addressed in data chapters. * signifies chapter published or in press.	110
Figure 24: Resilience theory components (composition, structure & function) used as criteria in <i>Banksia</i> woodland to detect potential regime shift and determine and describe subsequent novel, hybrid or resilient ecosystem.....	111

List of tables

Table 1: Examples of demonstrated regimes shifts resulting in novel/hybrid ecosystems (Resilience Alliance 2004).....	9
Table 2: Diversity and endemism in the Southwest Australian Floristic Region (Bowman 2003).	25
Table 3: Predicted characteristics of Old Climatically Buffered Infertile Landscapes (OCBILs) (Hopper 2009).	28
Table 4: Mean (\pm standard error) cover-abundance of species that changed significantly following infestation for chronosequence and historic data in <i>Banksia</i> woodland of the Southwest Australian Floristic Region. * p <0.05; ** p <0.01; *** p <0.001.	45
Table 5: Vegetation dependant stand variables (mean \pm standard error) in relation to chronosequence disease status in <i>Banksia</i> woodland of the Southwest Australian Floristic Region.	47
Table 6: Plant functional traits measured with deduced links to ecosystem function.	63
Table 7: Change in total species cover across the disease chronosequence by two-way ANOVA with multiple pair-wise comparisons.....	65
Table 8: Pearson's correlations with first & second PCO and CAP axes.....	67
Table 9: Variation in community-weighted means (CWM) and community-weighted totals (CWT) across the disease chronosequence with dominant trait classes printed in bold.....	68
Table 10: Changes in relative (community-weighted means: CWM) and absolute (community-weighted totals: CWT) trait values across the disease chronosequence in species-rich <i>Banksia</i> woodland, southwest Australia. Changes in CWMs and CWTs were measured for six traits at 17 sites, and analysed using analysis of variance; full details of the study are presented elsewhere (Bishop et al. 2011).	78
Table 11: Plant traits used in calculation of Rao's index of functional diversity.	86
Table 12: Results of 2-way ANOVA for species richness and Simpson's diversity index; and PERMANOVA for Rao's index of functional diversity using all traits.	88
Table 13: Change in Rao's index of functional diversity across the disease chronosequence and time since previous fire with p -values.	88
Table 14: Diversity indices and stand variables (mean \pm standard error) in relation to disease status in <i>Banksia</i> woodland of southwest Australia (see Bishop et al. 2010).	100
Table 15: Changes in relative (community-weighted means: CWM) and absolute (community-weighted totals: CWT) trait values across a disease chronosequence in species-rich <i>Banksia</i> woodland, southwest Australia. Changes in CWMs and CWTs were measured for six traits at 17 sites, and analysed using analysis of variance (see Bishop et al. 2011).	101

CHAPTER ONE: INTRODUCTION

Background literature

Concepts of Resilience Theory

Ecosystems are intrinsically resilient to natural disturbances, but through human impact in combination with natural disturbances, substantial and ongoing alteration can result (Vitousek et al. 1997). Ecosystem resilience can be defined as a measure of the capacity of an ecosystem to absorb disturbance without permanently shifting to another regime, i.e. retaining essentially the same basic structure, function, identity and feedbacks (Holling 1973, Walker et al. 2004). This is differentiated from 'engineering resilience' which is the speed at which a system returns to a single steady or cyclic state after disturbance (Holling 1996).

Resilience of an ecosystem may be reduced when external pressures either remove response diversity, remove functional groups of species, remove whole trophic levels; impact on ecosystems via pollution or climate change; or alter disturbance regimes (Folke et al. 2004). The ability of an ecosystem to exhibit resilience to disturbance lies in the functional redundancy of its component plant species (Walker et al. 1999). Functional redundancy is the presence of taxonomically distinct species that exhibit similar ecological functions (Walker 1992, Walker 1995). The presence of functionally redundant species buffers the ecosystem against change by maintaining ecosystem function despite the reduction or removal of species (Walker 1995). As a result of functional redundancy, ecosystems in some cases are able to adapt to a disturbance while retaining basic function and structure

Adaptive cycle: the response of a system that is able to absorb disturbance by going through a series of cyclical changes from destruction through to re-organisation without overall fundamental changes in identity (structure and function) (Holling & Gunderson 2002) cf. regime shift.

Ecosystem resilience: a measure of the capacity of an ecosystem to absorb disturbance without permanently shifting to another regime, i.e. retaining essentially the same basic structure, function, identity and feedbacks (Holling 1973, Walker et al. 2004).

Functional diversity: the extent of functional differences among species in a community (Folke et al. 2004, Petchey & Gaston 2002, Tilman 2001).

Functional group: non phylogenetic, groups of species exhibiting similar functional effects on an ecosystem or having similar responses to disturbance.

Functional redundancy: presence of taxonomically distinct species that exhibit similar ecological functions. Systems with high levels of functional redundancy have increased resilience to disturbance due to the ability to substitute functionally similar species (Walker 1995).

Phase shift: when disturbance initiates shifts between one of four phases of the adaptive cycle: rapid growth, conservation, collapse, and re-organization (Holling & Gunderson 2002).

Regime shift: occurs when a system is unable to absorb a disturbance and results in a fundamental change in the systems identity as characterized by irreversible changes in structure and function and identity (Folke *et al.* 2004; Holling 1973).

Response diversity: the extent of response differences among species in a community to different types of environmental change.

(Levin 1998, Walker & Salt 2006). Once a system can no longer absorb a disturbance, a critical threshold is crossed and the system has experienced a *regime shift* (Folke et al. 2004).

This fundamental ecosystem change is summarised by resilience theory which provides a framework to describe the ability of an ecological system to absorb a disturbance before crossing an irreversible threshold (Folke et al. 2004, Holling 1973, Peterson et al. 1998).

The driving concepts behind resilience theory are:

- Resilience occurs at multiple scales resulting in cross-scale effects known as panarchy;
- Ecosystems exhibit transformability when disturbed and either absorb the disturbance or change basic identity;
- Adaptive cycles describe how ecosystems absorb disturbance and move through different phases to maintain fundamental identity; and
- Regime shifts occur when a system is unable to absorb a disturbance resulting in a fundamental shift in identity.

(Resilience Alliance 2005)

Regime shifts and adaptive cycles are of particular relevance to this project and are discussed further below.

Regime Shifts and Thresholds - Concepts

A regime shift following disturbance (as characterised by a change in ecosystem structure and function) is explained conceptually through the “Ball-in-the-Basin” model (Walker et al. 2004). This model demonstrates the dynamic nature of ecosystems and how they respond to disturbance by either absorbing the impact or shifting to a new regime when the disturbance is too large to accommodate (Figure 1) (Walker et al. 2004). The variables that describe a system are the system’s ‘state’ variables. As a simple example, if a system consists of 3 variables: amounts of grass, shrubs and trees; these variable combine to form the state. The Ball-in-the-Basin model uses the ball to depict the combination of all the variables in a state. The basin is the set of states which have similar structures, functions and feedbacks resulting in the ball moving towards the equilibrium at the bottom of the basin (Walker et al. 2004). The dotted lines represent a *threshold*,

and when a basin is impacted by disturbance, conditions change and structure and function are altered. It is at this point that a regime shift has occurred. The size and depth of a basin is representative of how resilient a system is. Deep, wide basins have higher levels of resilience than shallow, thin basins (Walker & Salt 2006).

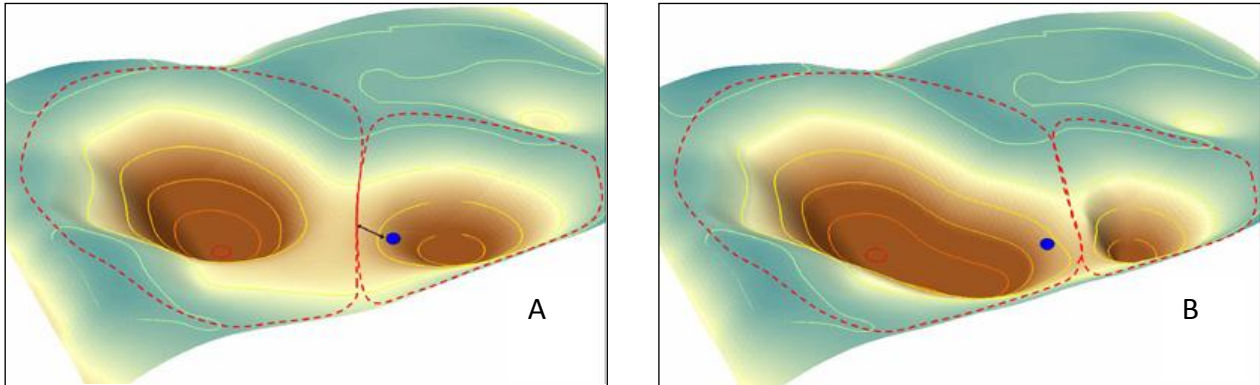


Figure 1: The 'ball in the basin' conceptual model of regime shifts and thresholds (a) The state of the system is represented by the ball which due to system dynamics is attracted to the pit of the basin. The system can change regimes either by the state changing, or through changes in the shape of the basin (i.e., through changes in processes and system function), as shown in Figure (b) (Resilience Alliance 2005).

Adaptive Cycles

The dynamic nature of ecosystems[†] is clearly demonstrated when they experience the different phases of the adaptive cycle. The concept of adaptive cycles was proposed by Holling & Gunderson (2002) and it describes how ecosystems organise themselves in response to external change and pressure.

A system can move through phases in an adaptive cycle which is distinct to a system shifting to a different regime (state). When an ecosystem is able to sufficiently absorb the effects of a disturbance, a threshold is not crossed, but different phases may be observed. A key aspect of the adaptive cycle concept is that when experiencing phase changes a system retains its basic function and structure (Walker & Salt 2006).

The 4 phases of the adaptive cycle are rapid growth, conservation, release and reorganisation (Holling & Gunderson 2002) (Figure 2).

[†] although the term ecosystem is used, the concepts of adaptive cycles apply to all system types from cells through to ecosystems

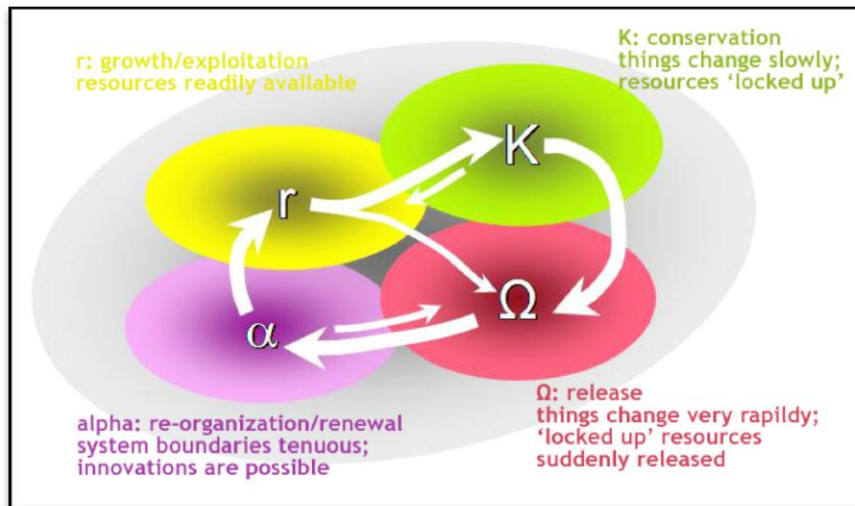


Figure 2: The four phases of the Adaptive Cycle (Resilience Alliance 2005).

The rapid growth phase (*r phase*) is characterised by species that can rapidly colonise an area by exploitation of available resources. These r-strategists (r = instantaneous rate of growth) have the ability to prosper during periods of high environmental variation but operate over relatively short time frames.

The conservation phase (*K phase*) is dominated by K-strategists (K = carrying capacity) which are strong competitors with the ability to use resources efficiently, operate across large spatial scales and live for long periods of time. In the late K phase, the system begins to 'lock up' and the longer a conservation phase exists, the smaller the disturbance necessary for transition to the release phase (Holling & Gunderson 2002).

The release phase (*Omega phase*) always follows the conservation phase and transition can be extremely quick. This phase is characterised by the release of accumulated biomass and nutrients, experienced when a disturbance exceeds the systems resilience. Previously tightly bound and stable natural capital is released and available for reorganisation. This is aptly described by Schumpeter's (1950) phrase as "creative destruction".

Following the chaotic release of capital, the ecosystem is highly disorganised and unstable. It is at this point that a system may experience a regime shift (change in structure and function). This reorganisation phase (*Alpha phase*) proceeds to stabilise the ecosystem in preparation for the next rapid growth phase (Holling & Gunderson 2002). A documented example of an adaptive cycle is

seen in North American spruce/fir forests which experience spruce budworm outbreaks (*Choristoneura fumiferana*) (Carpenter et al. 1996, Holling 1978, Ludwig et al. 1997, Walker & Salt 2006). The young forest is characterised by rapid growth through competition and exploitation of resources. Following is the conservation phase (K phase) which exhibits stable and predictable growth for 40 to 120 years. Budworm larvae then peak resulting in substantial defoliation and death of mature trees (release phase). Following release of resources is the reorganisation phase where new opportunities are created through widespread tree death. The forest reorganises itself in preparation for continuation of the cycle through resource exploitation and rapid growth (Walker & Salt 2006).

Adaptive cycles do not always occur in the sequence of phases as described above. It is not possible for a system to go from a release phase back to a conservation phase but all other alternatives can occur (Walker & Salt 2006).

Criticisms of Resilience Theory

A number of criticisms of resilience theory exist including:

- it is theoretical and qualitative with no practical application;
- it is potentially difficult to apply to systems without identifiable alternate states;
- it is reliant on tools from other disciplines to be operational to inform policy;
- is it vague with the term 'resilience' appearing nebulous to policymakers and the general public (Fischer et al. 2009); and
- thresholds can only be identified once they have been crossed.

To address key criticisms, recent resilience literature has emerged which outlines how to conduct a resilience assessment for socio-ecological issues relating to natural resource management. Resilience Workbooks have been released that outline how to apply resilience theory in scientific research (Resilience Workbook for Scientists) and practically through on-ground management (Resilience Workbook for Practitioners) (Resilience Alliance 2007a, Resilience Alliance 2007b). The workbook for practitioners/managers outlines how to conduct a resilience assessment. The results of the assessment can then be used to develop strategies for managing both known and unexpected changes from disturbance.

These workbooks address the main criticism of resilience theory regarding its quantitative application to real world problems and on ground management. The concepts of resilience theory are readily applicable in ecosystems with the key strength being clear problem definition that drives the decision-making process. Resilience researchers have refined theory and developed methods of quantification which have been used to describe and manage ecological issues. A key paper was released by Carpenter *et al.* (2001) which takes resilience theory from metaphor to empirical measurement by using the practical example of lake eutrophication. Additional to this a resilience theory threshold database exists online which has over 100 case studies demonstrating practical application supported by 270 peer-reviewed papers on thresholds and regime shifts (Resilience Alliance 2011).

The resilience framework provides a conceptual background that identifies the key components and boundaries of the system/problem using an interconnected systems based approach (Fischer *et al.* 2009). Using lake eutrophication as an example, a simplified resilience assessment by Carpenter *et al.* (1999) is presented below. The key steps involved are:

- Identify possible regimes: clear water or eutrophic water;
- Identify and measure dependent variables: plant and fish species composition, level of oxygen in water;
- Identify and measure independent variables that control the regime shift: phosphorus in sediments;
- Identify disturbance or threshold trigger: nutrient input from agricultural runoff; and
- Devise management strategies and monitoring programs.

This basic framework can be used to frame ecological problems and quantify the resilience of ecosystems to disturbance.

Resilience theory has also been criticised due to the fact that thresholds are unable to be identified until after they are crossed. Although the exact locations of thresholds are often unknown until after they are crossed, methods to predict thresholds that lead to a regime shifts are being developed (Fischer *et al.* 2009). One method that may inform of potential thresholds is probabilistic analysis. This has been used to estimate phosphorous thresholds that result in lake eutrophication (Carpenter & Lathrop 2008). By estimating probability distributions for thresholds,

Carpenter & Lathrop (2008) were able to inform of potential consequences of differing phosphorus levels and the probability of a regime shift and subsequent eutrophication. Such information can be used to inform of upper and lower thresholds of potential concern which can be built into monitoring and management protocols, and re-assessed as further data is acquired (Carpenter & Lathrop 2008, Fischer et al. 2009).

Novel, emerging and hybrid ecosystems

The resilience threshold of a system can be breached to create an 'emerging' or herein novel ecosystem characterised by new species combinations and altered ecosystem function (Hobbs et al. 2006). Novel ecosystems are created by deliberate or inadvertent human action but although human interference is required for creation of a novel ecosystem, maintenance isn't dependent on it (Hobbs et al. 2006).

Hybrid ecosystem: an ecosystem that retains some pre-disturbance identity (e.g. species diversity) in combination with substantial shifts in function and/or composition (Hobbs et al. 2009)

Novel ecosystem: a disturbance-induced ecosystem that has undergone transformation to result in new species combinations and altered ecosystem function and structure (Hobbs et al. 2006)

In contrast to a novel ecosystem, a system that retains some pre-disturbance characteristics but has undergone substantial shifts in function and/or composition, is described as a hybrid ecosystem (Hobbs et al. 2009). Hybrid ecosystems are thought to be able to return to a pre-disturbance state (Hobbs et al. 2009), though this has yet to be documented. Identifying modified ecosystems as either novel or hybrid is context dependent and may be somewhat arbitrary (Hobbs et al. 2009).

Accepting and managing novel/hybrid ecosystems challenges traditional conservation objectives and initial instincts may deem this pessimistic (Fox 2007, Hobbs et al. 2006). In many circumstances, ecosystem change is irreversible and efforts to conserve or return to a 'natural' state are impossible or require substantial input of scarce resources. When an ecosystems identity is changed beyond recognition, an alternate management approach is required to achieve revised conservation outcomes. Whether or not a novel ecosystem is favourable is an inherently complex decision that will depend on whose perspective is taken (Hobbs et al. 2006).

For this project I use resilience theory as criteria to determine if a novel or hybrid ecosystem results. Allen & Holling (2008) propose that a system that undergoes an irreversible regime shift results in novel combinations of ecosystem elements. This draws a parallel with Hobbs *et al.* (2006) definition of a novel ecosystem.

Disturbance

Numerous regime shifts have been documented in both terrestrial and marine ecosystems from both biotic and abiotic agents of disturbance. Table 1 provides a selection of case studies where regime shifts have been described. These case studies are from a comprehensive database of thresholds examples and references held at <http://www.resalliance.org>.

Although a wide range of vegetation shifts have been described for the obvious agents of change (such as grazing, fire, hurricanes etc.) little attention has been given to the impact of introduced forest pathogens. Although recognised for their potential to cause substantial ecosystem changes, little documentation exists beyond species-level changes, due primarily to lack of information on pre-pathogen forest identity. A prominent Australian forest disease is *Phytophthora cinnamomi* which has particularly impacted the southwestern parts of Western Australia but is also found in Victoria, New South Wales, South Australia, Tasmania and Queensland. Despite recognition in the early twentieth century, documentation of its impacts are limited primarily to species-level changes.

The study area is within the high rainfall zone of the South West Australian Floristic Region (SWAFR) (*sensu* Hopper & Gioia 2004) renowned for its exceptionally high levels of endemism and species diversity. The key agents of disturbance in the SWAFR are fire, *Phytophthora cinnamomi* and climate change and the interactions between these are unknown. However, before such interactions can be explored, ecosystem change from *P. cinnamomi* requires documentation.

Table 1: Examples of demonstrated regimes shifts resulting in novel/hybrid ecosystems (Resilience Alliance 2004).

Change	Location	Original Ecosystem	Novel Ecosystem	How did the change occur?	References
Coral to algae domination	Caribbean Sea, South America	Coral dominated seascape	Brown algae dominated seascape	Herbivorous fish and sea urchins kept brown algae density in check. Fish population significantly reduced by over fishing. Species specific pathogen killed 99% of urchins. Brown algae became abundant and out competed coral growth.	(Hughes 1994, Nystrom et al. 2000)
Vegetation shift – grazing & burning	South-East Asia and Africa	Forest	Grassland	Beyond eight subsistence crops, forest degrades into unproductive grassland. Ungrazed and unburnt grassland will slowly revert to forest providing the seed source is available, but if the grassland has been burned and grazed, then the grassland will effectively be permanent.	(Conway 1997, Trenbath et al. 1989)
Vegetation shift - eutrophication	Florida Everglades, USA	Sawgrass marshes	Cattail, blue-green algae	Soil phosphorus entered marshes from agricultural land. Above 300ppm phosphorus, disturbances such as fire, frost and drought allow cattails and blue-green algae to dominate. In addition, deeper water, as experienced in many channels, favours cattails over sawgrass.	(Gunderson 2001, Newman et al. 1998)
Predator regulation of prey	New South Wales, Australia	High rabbit densities (rabbits escape predator regulation)	Low rabbit densities regulated by predators	High rabbit densities exist with no predator regulation if rabbits experience exceptionally good breeding conditions or if predators are controlled below the predator regulation point. Low rabbit numbers exist with predator regulation if drought or myxomatosis caused rabbit numbers to fall below the predator regulation point. This is reversible with hysteresis.	(Pech et al. 1992)
Rock lobster to whelk domination	West Coast, South Africa	High densities of rock lobsters and seaweeds, but a relative scarcity of other organisms	Rock lobster density low or absent. Community dominated by beds of mussels and large populations of sea cucumbers, sea urchins, and whelks (<i>Burnupena</i> sp.).	Rock lobsters are keystone predators of whelk and mussels, but sharp declines in dissolved oxygen levels combined with over-fishing increases rock lobster mortality. This leads to a substantial increase in the whelk population which when dominant mass-attack rock lobsters. Abundant whelk numbers prevent re-establishment of rock lobster.	(Barkai & McQuaid 1988)
Vegetation shift - hurricane	Nicaragua, Central America	Homogenous species assemblages	Four different species assemblages	Following a hurricane in 1988, there was a 70% mortality rate of forest trees. Post hurricane monitoring revealed four distinct species that diverge over the 12 year study.	(Vandermeer et al. 2004)

Quantifying change and resilience in ecosystems

Biodiversity is defined as “the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems”. This goes beyond taxonomic diversity to include biotic interactions and geography (Naeem et al. 2007). Noss (1990) provides a conceptual framework of ecosystem properties with structural and functional aspects being emergent properties of ecosystem composition (Noss 1990) (Figure 3). These compositional, structural and functional properties are useful indicators for quantifying change. Each component occurs across a range of scales from the cellular up to the landscape level and are integrated to form a complex and non-linear system (Lamont 1995, Noss 1990, Walker & Salt 2006). Whether measurement occurs at the landscape, community, population, species or genetic level; depends upon the nature of the research and the questions being asked (Noss 1990).

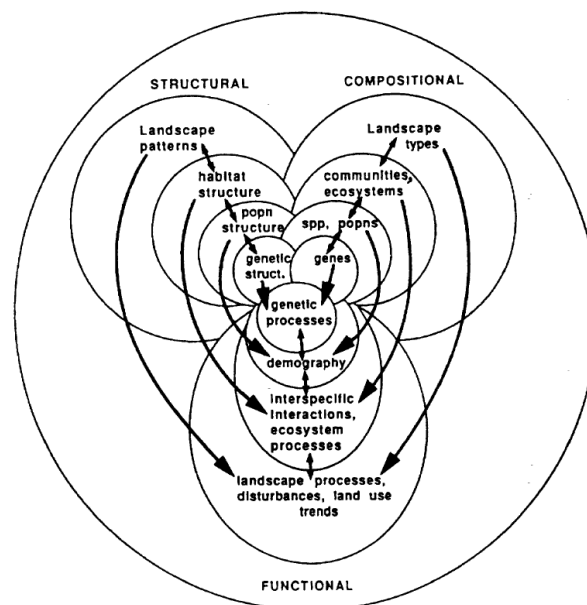


Figure 3: Conceptual framework of ecosystem properties with structural and functional properties emergent from composition (Lamont 1995, Noss 1990).

If one component of an ecosystem is altered by disturbance, questions arise regarding implications for the remaining ecosystem components. Specifically for *P. cinnamomi* this raises questions regarding potential species level loss and the impacts across other ecosystem components (Keighery et al. 1994, Shearer & Dillon 1996a, Shearer & Hill 1989). This study aims to detect and document pathogen-induced changes in plant community composition and structure. It will also determine if change is reflected in plant functional trait composition as a surrogate for shifts in ecosystem function.

Changes in structure, function and composition can be used to quantify resilience and form the basis of resilience theory. A resilient system is able to absorb disturbance without a fundamental change in identity based on ecosystem properties of structure, function or composition (Holling 1973, Walker et al. 2004). As discussed previously, once fundamental changes do occur in response to disturbance, a system can be described as having undergone an irreversible regime shift (Folke et al. 2004, Walker & Salt 2006).

Change in vegetation composition and structure

The visible effects of *P. cinnamomi* have been observed in Western Australia since the 1960's, and existing studies predominantly document compositional and occasionally structural change (e.g. McDougall et al. 2002, Shearer & Dillon 1996a, Shearer & Dillon 1996b, Shearer & Hill 1989). There have been no studies on the functional changes in *Phytophthora* affected ecosystems which in combination with compositional and structural changes can inform on ecosystem resilience and the emergence of novel or hybrid ecosystems. Regions of greatest *P. cinnamomi* impact in Australia are the SWAFR and Victorian forests where long-term studies have documented species changes over the past 30 years (Weste 2003, Weste 1980, Weste 1986, Weste et al. 1999).

Pathogen impact studies in West Australian forests have consistently shown a reduced abundance of susceptible plant species following infestation (McDougall et al. 2002, Podger 1972, Shearer & Dillon 1995, Wills 1992). Decline in susceptible species has a direct impact on vegetation structure leading to simplification and a significant decrease in vegetation density and canopy cover (McDougall et al. 2002, Wills 1992). An indirect effect that has been observed is a change in cover of species not directly susceptible to the pathogen (Davison & Shearer 1989, Havel 1979, McDougall et al. 2002, Shearer & Tippett 1989). For example, McDougall et al. (2005) found an increased abundance of non-susceptible species as the species were able to exploit conditions created by canopy gaps. In contrast, species resistant to *P. cinnamomi* have been found in lower abundances at infested sites. This is also due to indirect effects caused by canopy changes (Shearer et al. 2007). This response was documented for *Lepidosperma angustatum* which is known to be resistant to the pathogen but suffered from increased solar radiation through reductions in canopy cover (Shearer & Dillon 1996b).

A number of studies have documented a decline in species richness at *Phytophthora* affected sites (Keighery et al. 1994, Shearer & Dillon 1996a, Shearer & Hill 1989). However, recent studies in the northern Jarrah forests found that species richness remained constant between infested and uninfested sites and in some cases the presence of the pathogen actually increased species richness (McDougall et al. 2002).

The role of *P. cinnamomi* in vegetation change has generally focussed on species-level change (e.g. Shearer et al. 2004a, Shearer & Dillon 1996b, Shearer & Dillon 1995). Although many susceptible species are structurally dominant, (Shearer et al. 2007, Shearer & Dillon 1996b, Shearer & Dillon 1995) there is little quantification on how the pathogen changes vegetation structure or function (Shearer & Dillon 1996a). An exception is Wills (1992) who observed that in the Stirling Ranges, different growth forms had differing susceptibility levels. It was found that close to 50% of woody perennials surveyed were susceptible to the pathogen with herbaceous perennials, annuals and geophytes apparently unaffected (Wills 1992). McDougall (2002) also identified structural change but in the northern Jarrah Forests near Perth (400 km from the study area).

Change in ecosystem function, functional diversity and functional redundancy

Concern over the loss of biodiversity relates directly to its functional significance and provision of essential ecosystem services (Walker & Langridge 2002). Despite the inherent interconnectedness of biodiversity and ecosystem function, investigating these relationships is relatively recent in ecological research (Folke et al. 2004, Naeem et al. 2007). This is demonstrated by the growth in publication of papers integrating biodiversity and ecosystem concepts (Figure 4) (Naeem et al. 2004).

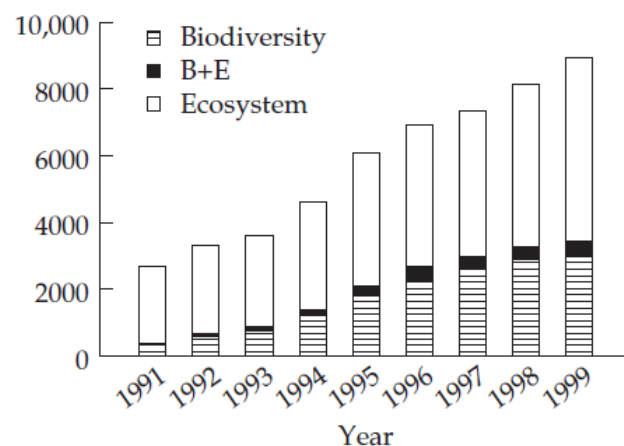


Figure 4: Increased publication rate of biodiversity & ecosystem function papers (Naeem et al. 2004).

Measuring functional trait composition, functional diversity and functional redundancy is a comprehensive approach to explore ecosystem change and resilience. This is because the functional traits of individual species (namely the dominants) determine the effect on ecosystem function and not species taxonomic identity (Allen et al. 2005, Grime 1998, Hooper et al. 2004, Naeem & Li 1997).

Ecosystem function – functional trait composition

The importance of species biomass to ecosystem function is described by Grime's (1998) Mass Ratio Hypothesis. Grime (1998) suggests that those species with the greatest biomass have the greatest contribution to ecosystem function while relatively insensitive to the species richness of subordinate and transient species (Aarssen 1997, Huston 1997). Some studies have suggested a correlation between species richness and ecosystem function suggesting that species-rich communities are more resilient to disturbance (e.g. Kareiva 1996, Kareiva 1994, Naeem et al. 1994, Naeem et al. 1995, Tilman 1996). As summarised by Huston (1997), these studies failed to recognise the importance of species abundance which was not incorporated into data analyses.

Measuring changes in plant effect trait composition weighted by species abundance can be used to generate hypothesis about the impact of disturbance on ecosystem function. Such effect traits have been identified for plant species with deduced links to ecosystem function. Using shifts in aggregated plant traits provides a method that is suitable for investigations into ecosystem function change (Cornelissen et al. 2003).

Plant functional trait (effect trait): measurable characteristics of plant species that link to ecosystem functions. Dominant traits have the greatest influence on ecosystem function.

Plant trait analysis is a parsimonious method requiring substantially less financial and time expenditure than traditional quantitative laboratory techniques that rely on vegetation destruction. For example, conventional measurement of specific annual net primary productivity (SANPP) involves harvesting, sorting, drying and weighing standing biomass at replicated sites. Garnier *et al.* (2004) have demonstrated a relationship between traditionally collected SANPP values and the relatively easily collected leaf trait values for specific leaf area, dry matter content and nitrogen concentration. Strong correlations were revealed between SANPP and these leaf traits which demonstrates the ability to use plant traits as surrogates to identify change in

productivity (Lavorel et al. 2007). Figure 5 shows additional links between functions and measurable plant traits.

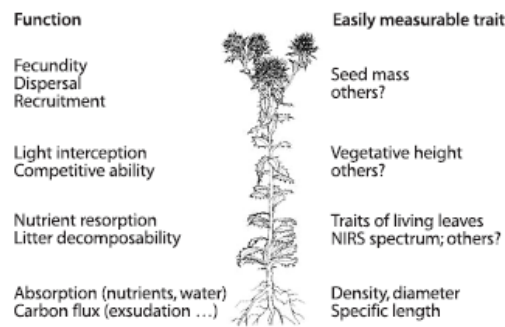


Figure 5: Examples of plant traits and associated functions (Lavorel et al. 2007).

Hypotheses generated through the use of plant traits and their deduced links with ecosystem function will require quantification and clarification using traditional techniques. However, this is beyond the scope of the project both financially and temporally, but most importantly robust justification would be required for further study using the traditional destructive techniques as the study sites are located within an ecologically sensitive reserve recognised for its significant conservation value.

Functional diversity and redundancy

Functional diversity and functional redundancy analysis provide further depth when exploring ecosystem resilience. Functional diversity is the extent of functional differences among species in a community and incorporates functional traits of individual species (Petchey & Gaston 2002, Tilman 2001). Changes in functional diversity can be used to determine trait changes in response to disturbance or environmental

Functional diversity: the extent of functional differences among species in a community (Folke et al. 2004, Petchey & Gaston 2002, Tilman 2001).

Functional redundancy: the presence of taxonomically distinct species that exhibit similar ecological functions. Systems with high levels of functional redundancy have increased resilience to disturbance due to the ability to substitute functionally similar species (Walker 1995).

gradients. Where functional diversity quantifies how different individual species are functionally, functional redundancy is the presence of species that exhibit similar ecological functions (Walker 1995). Ecosystems with high levels of functional redundancy exhibit multiple species that contribute to the same ecosystem function and hence intrinsically have a higher level of resilience than an assemblage with low functional redundancy (Walker 1995).

Research justification

Pathogen impact at the community-level

Plant pathogens have a major impact on forested ecosystems by shaping plant community dynamics & diversity; and by altering community structure and composition (Burdon et al. 2006, Castello et al. 1995, Gilbert 2002, Holdenrieder et al. 2004, Shearer & Smith 2000). Understanding the roles of pathogens (and roles at different scales) in producing landscape pattern is an important challenge in landscape ecology (Turner 2005).

Although plant pathogens have received recognition as agents of ecological change, there has been relatively little focus on their effects at the community/landscape scale compared to other forms of disturbance such as logging, fire or cyclones (Burdon et al. 2006, Castello et al. 1995).

Selected examples exist in the northern hemisphere including:

- Chestnut Blight (*Cryphonectria parasitica*) in North America and Europe;
- Dutch Elm Disease (*Ophiostoma novo-ulmi*) in North America and Europe;
- Sudden Oak Death (*Phytophthora ramorum*) in California; and
- *Fusarium* dieback of *Acacia koa* in Hawaii (Burdon et al. 2006).

These examples embrace an emerging field of research that is successfully combining plant pathology and landscape ecology to address pathogen invasions beyond the species-level. Landscape pathology has developed due to the recognition that pathogens exert impacts at a range of spatial scales (Burdon et al. 2006, Holdenrieder et al. 2004, Kitron 1998, Turner 2005).

Although the examples above have recognised rudimentary changes at a landscape scale, quantification of changes in species composition, plant community structure and function has yet to be documented for a plant pathogen. This study aims to explore compositional and structural changes as well as potential changes in ecosystem function through shifts in plant trait composition.

Integration of theoretical frameworks

This project uses the novel integration and application of theoretical frameworks to provide a comprehensive and quantitative documentation of change in a plant community.

Resilience theory provides the framework for the project and guided development of the key research questions that explore compositional, structural and functional change (Figure 6). These components which underpin resilience theory were used as criteria to determine the identity of the post-pathogen ecosystem as either novel, hybrid or resilient. Change in species composition and structure was identified using traditional methods and data from botanical surveys. Using plant functional traits to explore functional change in plant communities is a novel approach that can be used in lieu of traditional time intensive and expensive methods. The plant functional trait approach can generate hypotheses regarding pathogen-induced functional change to guide future ecosystem-function related research pertaining to *P. cinnamomi*.

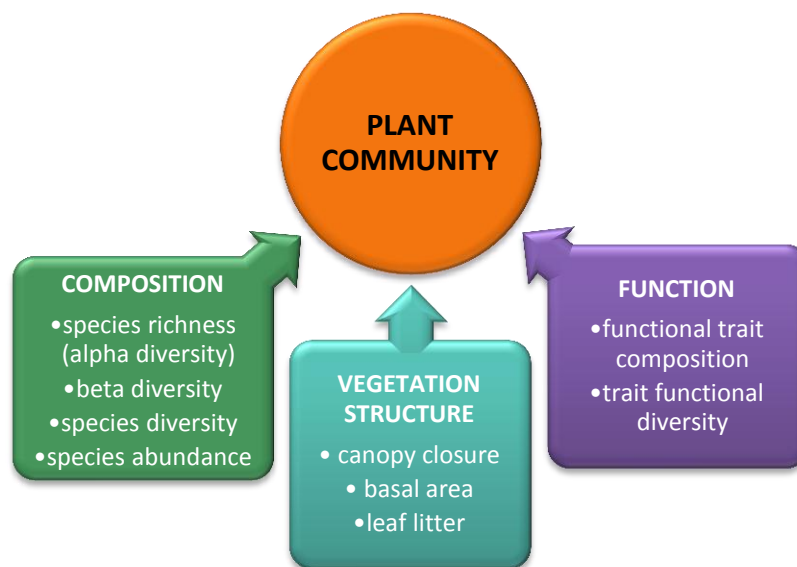


Figure 6: Resilience theory components (composition, structure & function) used as criteria in *Banksia* woodland to detect a potential regime shift and determine and describe subsequent novel, hybrid or resilient ecosystem.

This study will determine if the ecosystem has absorbed the pathogenic disturbance or collapsed and changed its basic function and structure. If basic ecosystem identity has changed, a novel or hybrid ecosystem will result dependent on the extent of change.

Research questions

The key research question this study explores is:

Does *Phytophthora cinnamomi* infestation result in a novel or hybrid ecosystem characterised by a change in *Banksia* woodland composition, structure and/or function?

The research question reflects the resilience theory framework to describe pathogen-induced change in species composition, structure and function. Such changes, known as a *regime shift*, describe a system that has undergone a fundamental change in structure and function. Shifts in floristic composition are also explored which is inherently linked to both vegetation structural and functional change. A series of specific sub-questions relating to floristic composition, vegetation structure and functional trait shifts have been developed to systematically explore the central research question. These sub-questions are listed below.

CHANGE IN FLORISTIC COMPOSITION

- 1) How do species abundances change along a disease chronosequence and over time?
- 2) Does alpha or beta species diversity change along a disease chronosequence and over time?

CHANGE IN VEGETATION STRUCTURE

- 3) How does plant community structure change?
- 4) How does the pathogen impact the stand variables; basal area, leaf litter, canopy closure and bare ground?

CHANGE IN PLANT FUNCTIONAL TRAIT DIVERSITY AND COMPOSITION

- 5) Are there changes in the site productivity traits specific leaf area (SLA) and leaf dry matter content (LDMC)?
- 6) Does the pathogen alter nutrient cycling rates?
- 7) Does pathogen introduction alter *Banksia* woodlands capacity for carbon immobilisation?

- 8) A: Does the dominance of particular root patterns change following disease infestation?
- B: What are the potential implications regarding hydraulic lift and site water balance?
- 9) Does *Phytophthora cinnamomi* alter the functional diversity of species-diverse *Banksia* woodlands?
- 10) Do *Banksia attenuata* woodlands exhibit functional redundancy as characterised by the presence of functionally similar species?

Thesis structure

Following this introductory chapter, **Chapter Two** will describe the biophysical aspects of the study area and provide a background to the key disturbance types of the region. Chapters Three to Seven are data chapters that combine newly obtained data with existing empirical data in the case of chapter 3. This is followed by conclusions in Chapter 8. Figure 7 outlines the thesis structure and indicates where in the thesis each research questions will be investigated.

Chapter Three explores community-level changes in *Banksia* woodland following plant pathogen invasion both along the disease chronosequence and by re-sampling of historic quadrats. Data are used comparatively to test for validity of the newly established space-for-time transects. Floristic cover and a series of site specific stand variables (leaf litter, basal area, canopy closure & bare ground) are recorded for each site to assess pathogen induced change in vegetation structure. Changes in both alpha and beta species diversity are assessed in conjunction with cover changes for individual species. These data provide a community-level perspective of change from *P. cinnamomi* which is poorly documented in the literature. This chapter addresses research questions 1 to 4 and has been published in the Journal of Vegetation Science (Bishop et al. 2010).

Chapter Four explores change in functional trait composition following pathogen invasion. Shifts in plant functional trait abundances are measured across the disease chronosequence to provide an indication of change in ecosystem function. The chapter is centred on Grime's (1998) Mass Ratio hypothesis which suggests that ecosystem function is dominated by those species with greatest biomass and comparatively insensitive to subordinate species. Based on deduced links with ecosystem functions, changes in trait abundances can provide an indication of pathogen induced

change in ecosystem function. The results generate a series of hypothesis regarding functional change requiring future verification and clarification using traditional quantitative techniques. This chapter explores research questions 5 to 8 and has been published in a functional trait special issue in the journal *Agriculture, Ecosystems and Environment* (Bishop et al. 2011).

Chapter Five evolved from the previous functional trait chapter and applies a modified diversity index. The traditional community-weighted mean index (CWM) provides insight into functional change through trait analysis (Garnier et al. 2004). Community-weighted means incorporate change in *relative* species cover and I apply a modified community-weighted total (CWT) index which uses *absolute* species cover. The chapter further explains the importance of including *absolute* cover change when inferring functional change from trait shifts. The use of absolute cover is in line with the Mass Ratio hypothesis (Grime 1998) as the CWT index incorporates change in total cover which is not incorporated in the traditional CWM index. Both indices should be applied comparatively.

Chapter Six explores shifts in Rao's index of functional diversity (RIFD) which identifies changes in trait variance. The chapter explores research questions 9 and 10 to complement chapter 4 which identified shifts in trait composition through abundance. Rao's index of functional diversity identifies shifts in trait variance to ascertain if the forest pathogen is generating functional convergence (homogenisation) or divergence (Lepš et al. 2006, Rao 1982). The chapter also examines the extent of functional redundancy in *Banksia* woodlands by determining the presence of functional similar species. This has implications for resilience to disturbance as systems that have high levels of functional redundancy (i.e. many functionally similar species) may be able to maintain ecosystem function when disturbed.

Chapter Seven provides a synthesis of key findings from the previous data chapters and places the results in a theoretical framework based on resilience theory (Folke et al. 2004, Holling 1973, Peterson et al. 1998) and novel ecosystems (Hobbs et al. 2006, Hobbs et al. 2009). Resilience theory is used as criteria to determine and describe the extent of disturbance impact. The chapter explores the key research question regarding formation of a novel or hybrid ecosystem through pathogen infestation. Through synthesis of results from past chapters into the resilience theory framework, a pathogen-induced regime shift is documented with substantial changes in species

abundance, community structure and functional trait composition. Although *Phytophthora cinnamomi* infested *Banksia* woodlands have undergone substantial change and subsequent regime shift, some pre-disturbance characteristics have been retained. These include species diversity and functional diversity which result in the post-pathogen ecosystem identifying as hybrid and not novel.

Chapter Eight outlines the main conclusions of the study and directions for future research. The chapter also indicates how the research questions have been addressed.

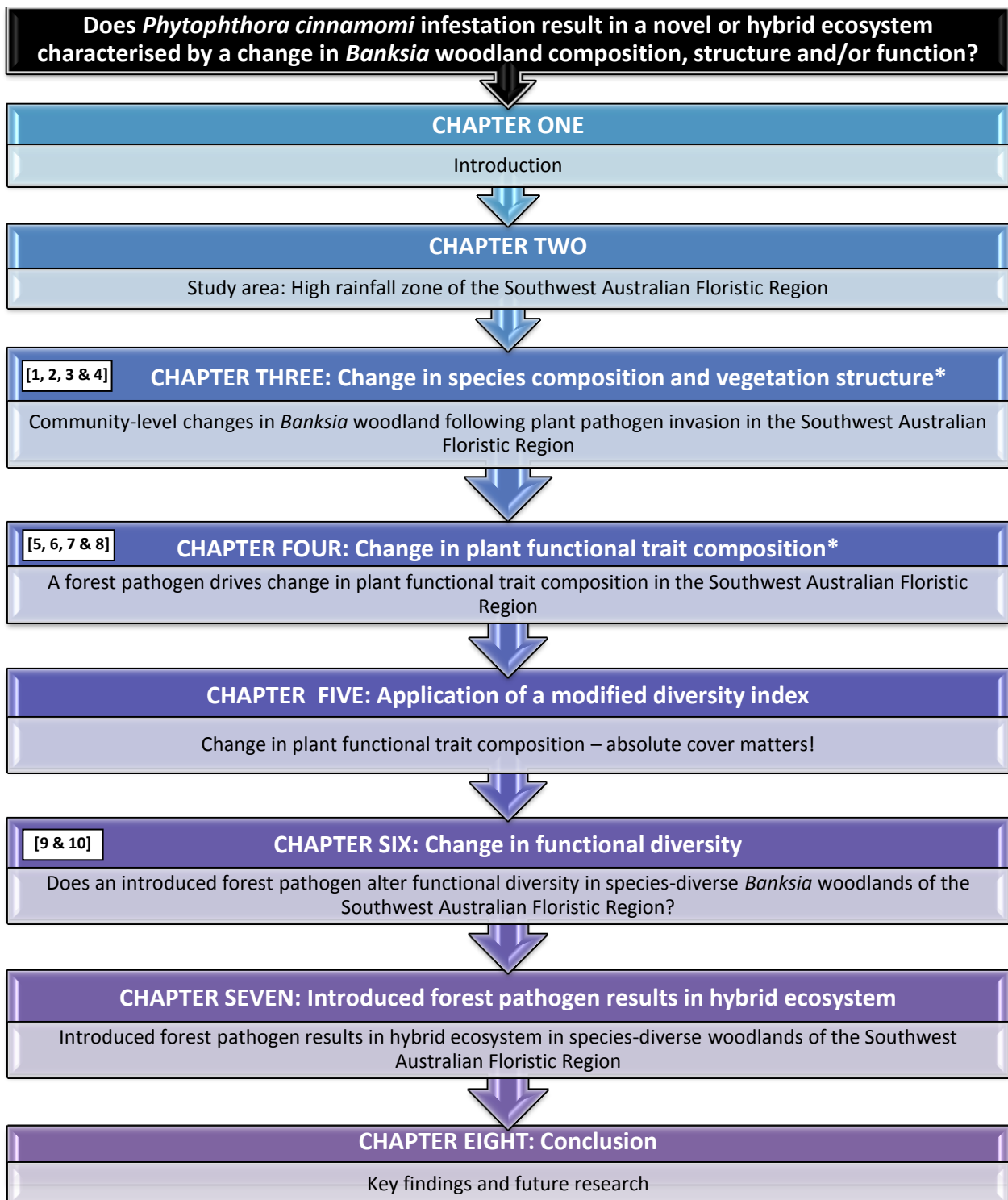


Figure 7: Thesis structure and chapter titles. Bracketed numbers refer to research questions addressed in data chapters. * signifies chapter published or in press.

Study design

Pathogen induced change was identified using comparative data from newly established chronosequence transects and re-sampling of historic quadrats. Chronosequence transects (space-for-time) consisting of 3 quadrats of different disease ages were replicated across the study area. Each transect was located in *Banksia attenuata* woodland on deep leached white/grey sands. Vegetation mapping completed by Havel & Mattiske (2002) was used as a preliminary guide for site placement and ground-truthed by field inspection.

Seventeen sites (transects) were selected across the study area at least 500 m apart. Sites were selected based on identification of key susceptible species identified by Department of Environment & Conservation dieback interpreters. Dieback interpreters assisted in site selection by identifying the presence of *Phytophthora cinnamomi* by visual assessment of susceptible species. Key susceptible species have been identified by Grehan (2005) as having a moderate to high susceptibility rating based on laboratory studies. Species used for site selection in this study included *Banksia attenuata*, *Adenanthos obovatus*, *Banksia ilicifolia* and *Xanthorrhoea preissii*. Laboratory analysis of soil samples provided verification of the pathogen presence.

Each site had one disease chronosequence (transect) consisting of three 20 x 20 m quadrats: (H) healthy vegetation with no disease expression; (F) early disease with susceptible species displaying leaf chlorosis in combination with dead and healthy susceptible species e.g. *Banksia attenuata*; and (D) long diseased vegetation infested for approximately 15 to 20 years, characterised by long dead *Banksia attenuata* (Figure 8).

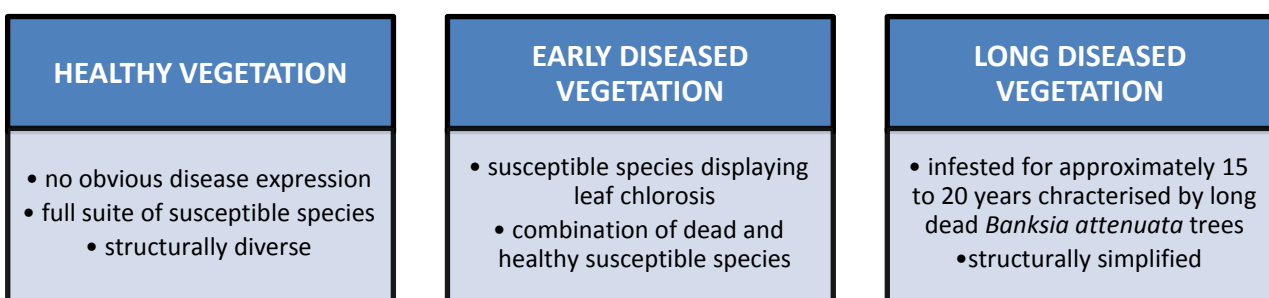


Figure 8: Disease chronosequence quadrat placement at each site. This design was replicated 17 times at random sites across the landscape.

The study area is topographically and edaphically similar to coastal sand-plains immediately to the south where rates of disease spread are approximately 1.5 m/year (Grant & Barrett 2003). Additional disease extension studies in *Banksia* woodland on comparable soil to the study area (also deep leached grey/white sands) have been done in the Perth vicinity (400 km north of the study site) by Shearer et al. (2004b). This study found disease extension in Perth *Banksia* woodlands ranged from 1.3 m/year \pm 0.1 up to 1.8 m/year \pm 0.2 – comparable to the southern plains study which found 1.5 m/year. Based on these studies and in absence of data for the immediate study area, the rate of 1.5m/year was used to guide placement of quadrats in long diseased vegetation relative to quadrats in early diseased vegetation. Quadrats in healthy vegetation were placed approximately 50 m from quadrats in vegetation expressing early disease symptoms. All quadrats were augered to a depth of 2 m to confirm soil type between sites and along chronosequence transects.

In addition to the disease chronosequence design, additional data was collected to validate the space-for-time transect data. Historic quadrats originally scored in 1990 for species cover-abundance were re-sampled in 2006 to provide a comparative data set. The historic quadrats had succumbed to infestation since establishment, but were unable to be directly incorporated in the chronosequence transects due to the lack of adjacent uninfested vegetation. Eight historic quadrats (20 x 20 m) were suitable for re-sampling, having analogous soil and vegetation types to the newly established chronosequence transects.

Historic quadrats had been permanently marked with aluminium droppers which allowed re-identification for sampling in the current study. Sampling of both chronosequence and historic quadrats used the same methods as the 1990 study to ensure consistency of the data collected. This was achieved through consultation with the botanists who completed the original 1990 surveys. The historic and chronosequence data sets form the basis of Chapter 3 on community-level vegetation change. As chronosequence data reflected the change identified in the historic quadrats, subsequent chapters include transect data only for clarity and brevity. Further details relevant to specific aspects of study design are described in subsequent chapters.

CHAPTER TWO: STUDY AREA

The high rainfall zone of the Southwest Australian Floristic Region (SWAFR)

The Southwest Australian Floristic Region (SWAFR) is one of the world's 5 regions of mediterranean climate, prone to hot dry summers and cool, moist winters (*sensu* Hopper & Gioia 2004) (Figure 9). The predominantly old infertile landscape is topographically subdued in comparison to other biodiversity hotspots and displays diversity and endemism usually associated with more mountainous regions (Hopper & Gioia 2004, Wardell-Johnson & Horwitz 2000).

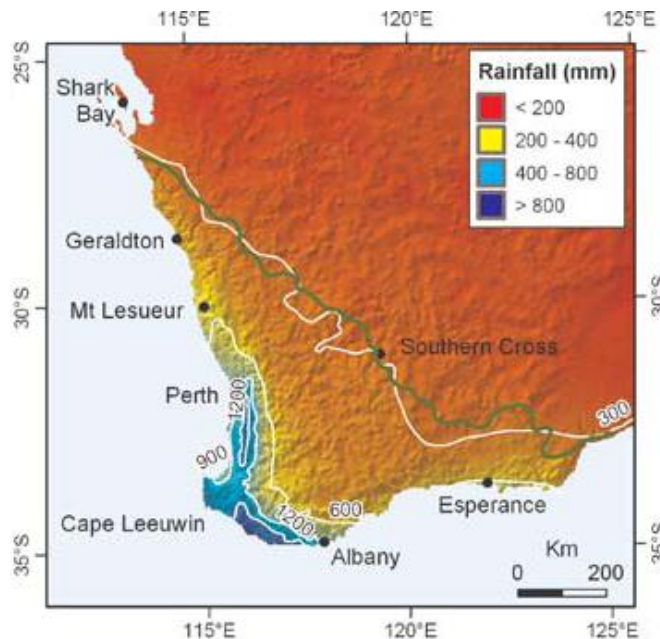


Figure 9: Location of the Southwest Australian Floristic Region (green line) with average annual rainfall isohyets (from Hopper & Gioia 2004).

The SWAFR lies within a Global Biodiversity Hotspot and contains a diversity of endemic flora and fauna with increasingly high levels of threat to such endemism (Bowman 2003, Myers et al. 2000). To date, approximately 7380 plant species have been described with approximately 50% endemic to the region and 2500 of conservation concern (Table 2) (Hopper & Gioia 2004).

Table 2: Diversity and endemism in the Southwest Australian Floristic Region (Bowman 2003).

TAXONOMIC GROUP	SPECIES	ENDEMIC SPECIES	PERCENT ENDEMICISM
Plants	7380	3616	49.0
Mammals	59	12	20.3
Birds	285	10	3.50
Reptiles	177	27	15.3
Amphibians	32	22	68.8
Freshwater Fishes	20	10	50.0

A distinct rainfall gradient exists across the SWAFR ranging from 1400 mm annual rainfall in the south to < 300 mm annual rainfall in the north-east (Hopper 1979) (Figure 10). Hopper (1979) broadly categorised the SWAFR into 3 zones based on annual rainfall isohyets with each zone loosely associated with broad vegetation types. On a gradient of increasing rainfall lies the:

- i. Arid Zone with < 300 mm annual rainfall dominated by *Eucalyptus* woodlands, *Acacia* shrublands, and *Triodia* hummock grassland;
- ii. Transitional Rainfall Zone with 300-800 mm annual rainfall dominated by woodlands, mallees and heathlands;
- iii. High Rainfall Zone with 800-1400 mm annual rainfall dominated by forests and woodlands of jarrah (*Eucalyptus marginata*), marri (*Corymbia calophylla*) and karri (*E. diversicolor*) (Hopper 1979).

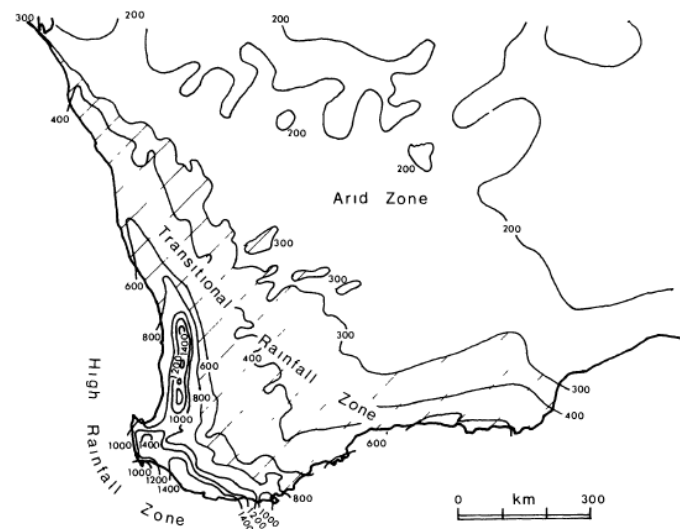


Figure 10: Rainfall isohyets and associated rainfall zones of the Southwest Australian Floristic Region (Hopper 1979).

The immediate study area lies within the high-rainfall zone in the south of the SWAFR and is locally known as the Walpole Wilderness Area (WWA). The WWA includes a number of contiguous national parks, nature reserves, state forests and timber reserves in the Walpole-Denmark region and covers approximately 325 000 ha (Department of Environment and Conservation 2008). The area is managed by the state government conservation agency, the Department of Environment and Conservation (DEC).

Conservation theory

Traditional conservation theory has been developed on northern hemisphere landscapes that although geologically old, are fertile due to relatively recent rejuvenation. Such rejuvenation results from landscape-level disturbance such as glacial grinding, volcanism, mountain building or altered sea levels (Hopper 2009). The application of this traditional theory to old and infertile landscapes has been dismissed by Hopper (2009) and explored further by Mucina & Wardell-Johnson (2011). Both propose new frameworks describing the geologically old and infertile landscapes such as the SWAFR. Hopper (2009) suggests recognition of Old Climatically Buffered Infertile Landscapes (OCBILs) in contrast to Young Often Disturbed Fertile Landscapes (YODFELs) – extremes on a timescale continuum. The concept of OCBILs and YODFELs is based on rates of landscape renewal and may provide a level of theoretical generalisation when considering evolutionary and conservation concepts.

Mucina & Wardell-Johnson (2011) suggest the Old Stable Landscapes scheme (OSLs) which builds upon Hopper's (2009) original paper through offering a modified framework. Mucina & Wardell-Johnson (2011) question the appropriateness of Hopper's (2009) original three dimensions (landscape age, climatic buffering and soil fertility) and propose a modified framework based on landscape age, fire regime predictability and climate stability. In essence, the OSLs scheme is a refinement of the OCBIL/YODFEL dichotomy with the added dimension of fire regime predictability for use in classification of landscapes.

Apart from clear differences in landscape age (including soil fertility), climate stability and fire regime predictability, both OCBILs and OSLs have fundamental biotic differences in comparison the young often disturbed landscapes that dominate the northern hemisphere. These differences have implications for disturbance and ecological change. Hopper (2009) has derived a number of predictions (testable hypotheses) that are anticipated to characterize OCBILs (Table 3).

Table 3: Predicted characteristics of Old Climatically Buffered Infertile Landscapes (OCBILs) (Hopper 2009).

Prediction	
1	Reduced dispersability, increased local endemism and common rarity
2	Accentuated persistence—old lineages (Gondwanan Heritage Hypothesis), old individuals (Ultimate Self Hypothesis)
3	The James Effect (pursuit of heterozygosity, e.g. bird pollination, genomic coalescence)
4	Prolonged speciation at the margins (Semiarid Cradle Hypothesis)
5	Adaptation to saline soils (only flat lands such as the Southwest Australian Floristic Region)
6	Nutritional and other biological specialisation
7	Special vulnerability (e.g. to soil removal) and enhanced resilience (e.g. to fragmentation)

Geology and soils

The study area is topographically subdued through substantial weathering of ancient Precambrian granitic rock which forms part of the Ravensthorpe Ramp. Comparative to other Biodiversity Hotspots, the SWAFR has few geographical barriers which allow *P. cinnamomi* to successfully spread across the landscape through overland water flow. The lateritic mantle overlays both granitic and sedimentary rocks with grey sands deposited in various locations (Commonwealth and Western Australian Regional Forest Agreement Steering Committee 1998). Three key landscape zones dominate the region including sharply delineated landforms such as low hills, ridges and slopes; swampy terrain and parabolic dune systems; and zones associated with drainage lines (Churchward et al. 1988, Department of Environment and Conservation 2008).

The diversity and endemism of plant species is driven by a combination of factors including climate, geology and soils with further heterogeneity resulting from fire regimes (Hopper 2009, Hopper & Gioia 2004). The region has an abundance of distinct soil types within a relatively small geographical area which typically track changes in vegetation. The soils of the SWAFR are nutrient poor (primarily in Nitrogen and Phosphorus) with plant species exhibiting various adaptive strategies for acquisition of scarce resources (Hopper 2009).

Climate

The study area and surrounds is characterised by a mediterranean-type climate with cool, wet winters and warm, dry summers. Located in the High Rainfall Zone of the SWAFR the study area is

one of the wettest and least seasonal parts of Western Australia, climatically buffered by the Indian Ocean (Hopper 2009). Annual rainfall is 1100mm, and average temperatures range from 5 to 15 °C in winter and 15 to 25 °C in summer (Figure 11).

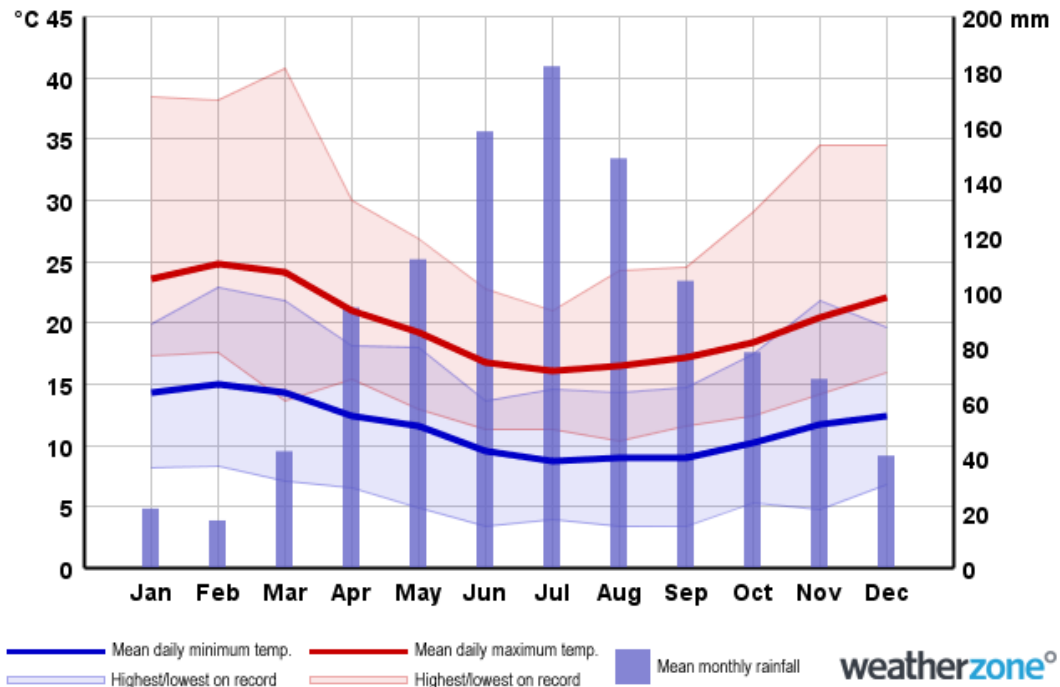


Figure 11: Temperature and rainfall averages for Walpole (Weatherzone 2011).

In addition to broad climatic patterns, specific microclimates within the landscape favour *Phytophthora cinnamomi* success. Niche refuges are characterised by optimal oxygen levels, sources of carbon & energy and favourable soil moisture & temperatures (Shearer et al. 2009b). Two types of niche refuge exist and can be either plant or pathogen-created. A plant-created refuge occurs when the water content around the base of plants is higher than the surrounding area due to preferential wetting from water channelling down the stems (Pressland 1976, Specht 1957). Shearer et al. (2009b) found higher inoculum levels at the base of *Banksia* trees (in a moisture refuge) comparative to areas further away from the tree base.

An example of a pathogen-created refuge are changes in soil temperature and moisture that result from the reduction in canopy cover in infested vegetation. Canopy cover reductions result in increased soil temperatures in autumn and spring, coupled with increased rainfall reaching the ground through reduced canopy cover for rainfall interception (Levia & Frost 2006, Shearer et al.

2009b). This combination of warmer soil temperatures with higher soil moisture extends the period of time suitable for pathogen sporulation and spread.

Vegetation

The high rainfall zone of the SWAFR contains a diversity of vegetation types that are floristically and structurally complex. Vegetation patterns reflect the diversity of fine-scale climatic conditions, soil types and landforms resulting in a complex mosaic of unique vegetation types across the landscape. The key families that dominate include the Proteaceae, Papilionaceae, Myrtaceae, Orchidaceae and Ericaceae families (Gole 2006, Wardell-Johnson & Williams 1996). The diversity of structural types ranges along a continuum from tall open forests, through to open woodlands & shrublands. The region is dominated by tall open forests and woodlands composed of eucalypt species in various combinations. These include the widespread Jarrah (*Eucalyptus marginata*) and Marri (*Corymbia calophylla*); localised patches of Karri (*E. diversicolor*) where rainfall is adequate; and the three endemic eucalypt species - Rates tingle (*E. brevistylis*), Yellow tingle (*E. guilfoylei*) and Red tingle (*E. jacksonii*).

The woodlands in this study are characterised by structurally dominant *Banksia attenuata* that form an open canopy; a dense and species-diverse woody shrub layer composed of sub-dominant species; and a herbaceous ground layer (Pate & Bell 1999) (Figure 12). These woodlands occur in a matrix of vegetation types and although not dominant in the landscape comparative to the diversity of tall open forests, they are widespread across the region and have a greater species richness than many other vegetation types (Wardell-Johnson & Williams 1996).

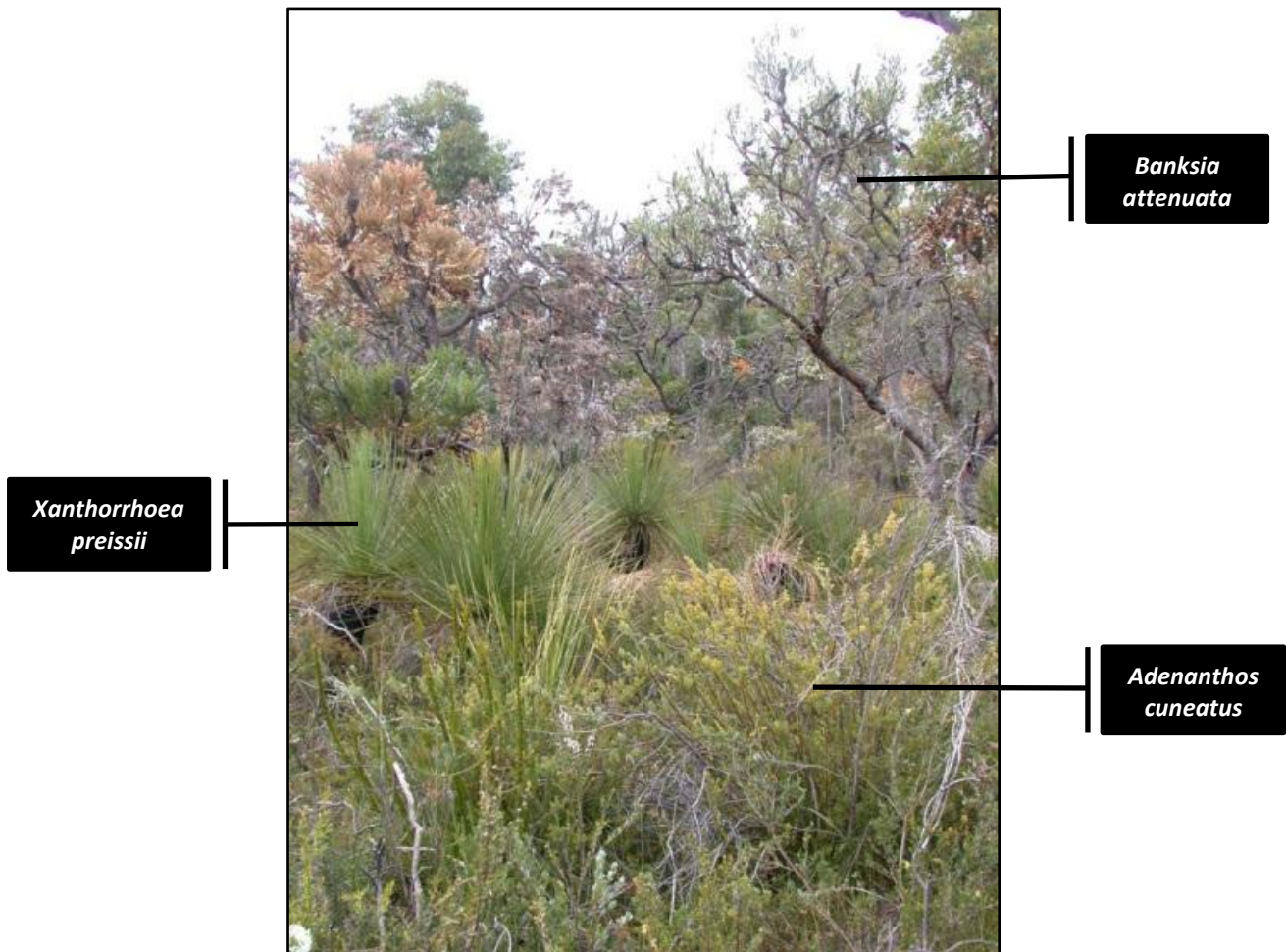


Figure 12: *Banksia attenuata* woodland in the high rainfall zone of the Southwest Australian Floristic Region. Key species susceptible to *Phytophthora cinnamomi* are indicated.

These *Banksia* woodlands are found in low-lying parts of the landscape on highly oligotrophic deep grey/white sands. The sands have an extremely low clay and organic matter content which limits nutrient acquisition and storage (Pate & Bell 1999). This has led to a number of adaptive plant strategies (trophic specialisations) that enhance nutrient uptake in these deficient soils. A range of acquisition strategies are utilised including proteoid roots (predominantly), mycorrhizal associations, parasitic associations, carnivorous adaptations, capillarioid roots and nitrogen fixation (Pate & Bell 1999).

Banksia woodlands are dominated by fire-adapted species that require fire for regeneration and maintenance of biodiversity (Abbott & Burrows 1999, Burrows & Wardell-Johnson 2003, McCaw & Hanstrum 2003). These fire-prone woodlands comprise both resprouter and obligate seeder species that proliferate post-fire due to a release of resources required for growth. Fire

substantially reduces standing biomass and results in an abundance of light, moisture and previously limiting nutrients to stimulate new growth (Pate & Bell 1999).

Disturbance

The plant communities of the study area are impacted by multiple agents of disturbance including landscape fragmentation from clearing, prescribed burning and wildfire, introduced plant pathogens, weeds, introduced fauna, salinity and climate change (Department of Environment and Conservation 2008).

Key disturbances that influence ecosystem dynamics in the high rainfall zone of the SWAFR are the introduced plant pathogen *Phytophthora cinnamomi* and altered fire regimes (Department of Environment and Conservation 2008). Additionally, global climate change scenarios are predicted to cause additional stress on SW Australian ecosystems, with the potential to exacerbate other ecological changes (Burdon et al. 2006).

Introduced plant pathogen: Phytophthora cinnamomi

Phytophthora cinnamomi is recognised both internationally and nationally for its destructive impact upon native plant communities and has been recorded in Australia, Europe, North America, and South Africa (National biological information infrastructure & IUCN/SSC invasive species specialist group 2005). It is the only pathogenic taxon specifically cited in 1996 strategy for Conservation of Australian Biodiversity and is also recognised as one of the Key Threatening Processes to the environment under the Commonwealth *Environment Protection and Biodiversity Conservation Act 1999* (Dawson 2005, Environment Australia 2001).

Native forests across Australia have yielded at least 20 different species of the *Phytophthora* pathogen (Irwin et al. 1995). However, recent advances in DNA analysis have revealed that morphological differences alone have failed to recognise a number of previously undocumented species (Stukely pers. comm. 2007). In addition to this, more species are likely to be identified simply through sampling in unstudied vegetation types (Dunne pers. comm. 2011).

Thought to have originated in Papua New Guinea or South East Asia, *P. cinnamomi* is negatively impacting a wide range of plant communities not only in Western Australia, but also Queensland, Tasmania, Victoria, South Australia and New South Wales (Garkaklis et al. 2004). The pathogen is

of particular concern in the SWAFR as the number of known native plant species susceptible to *P. cinnamomi* is approximately 40% of which 14% are listed as highly susceptible (> 80% plants of a species killed) (Shearer et al. 2004a).

Although the origins of *P. cinnamomi* are unclear, it was initially spread throughout the forests of the SWAFR from infected soil during post-war road building for forestry (Shearer & Tippett 1989). *Phytophthora cinnamomi* was first identified as the agent responsible for Jarrah dieback (*Eucalyptus marginata*) in the 1960's in Western Australia, however unexplained Jarrah deaths were observed as early as 1920 (Shearer 1990).

The pathogen is a water mould that requires warm moist conditions for survival, sporulation and dispersal (Shearer 1990). It can be spread throughout the landscape passively via water flow or actively when the motile zoospores move through soil. The fastest rate of spread is caused by humans when infected soil is transferred throughout the landscape on vehicle tyres or other mechanical means (Garkaklis et al. 2004, Shearer & Tippett 1989). The pathogen has proliferated in the SWAFR due to ideal climatic conditions and a wide availability of host plants across numerous plant families. Plant species with a network of fine roots (an adaptation to maximise resource acquisition) are particularly vulnerable to infection (Shearer & Tippett 1989).

A range of direct impacts of been observed and loosely documented with the indirect impacts hypothesized (Figure 13). Most visible are the direct impacts of increased mortality and decreased canopy cover of susceptible plant species.

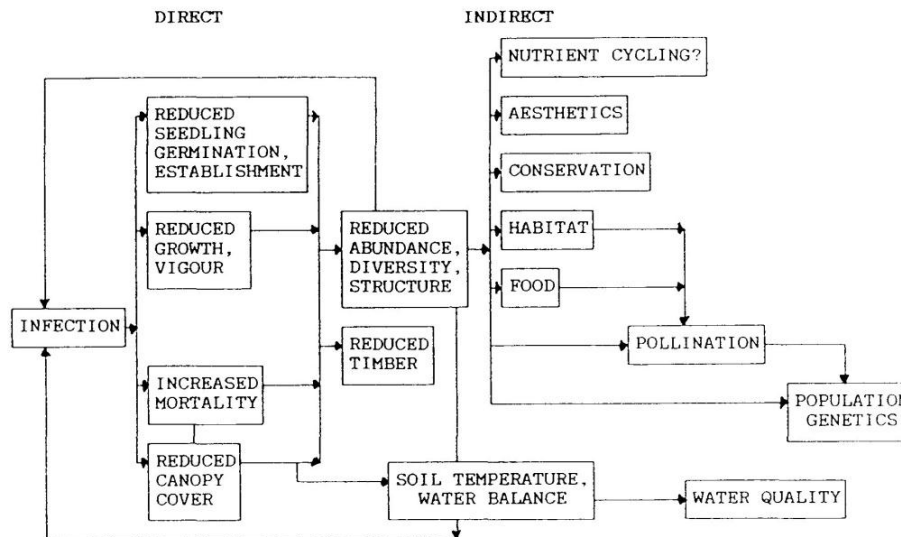


Figure 13: Direct and potential indirect effects of *Phytophthora cinnamomi* on susceptible plant communities (Shearer & Smith 2000).

In addition to the environmental impacts of *P. cinnamomi*, there are associated social and economic implications. In 2005, the Department of Environment and Heritage commissioned a review into the progress of invasive species (Dawson 2005). The report describes the current impacts, distribution and abundance of invasive species and current prevention, containment, eradication and control mechanisms. The ecological impacts of *P. cinnamomi* are sparsely documented and the review highlights the need to consider the economic impacts that invasive species may have regarding natural ecosystems (Dawson 2005). The economic impact is particularly relevant as tourism in the high rainfall zone of the SWAFR contributes 13% to the Western Australian economy (Department of Environment and Conservation 2008). Ecotourism features prominently in the SWAFR with numerous nature-based private enterprises as well as government interpretive experiences.

Fire

In addition to the main drivers of vegetation patterns, climate and geology, fire plays a key role in creating further heterogeneity across the landscape. Prior to both Aboriginal and European settlement, wildfire from lightning strike was an evolutionary force that played a major role in shaping the diverse mosaic of fire-prone plant communities (Abbott 2003, Hassell & Dodson 2003). Charcoal evidence has been found in a Pliocene lake deposit indicating frequent fires in the south-west since at least 2.5 million years ago and possibly 15 million years ago, long before human habitation (Dodson & Lu 2000, Dodson & Ramrath 2001, Hassell & Dodson 2003). The

arrival of Aboriginal people (approx. 50 000 years ago) (Turney et al. 2001) added further fire pressure to native vegetation through Indigenous burning used to facilitate hunting and gathering. The frequency and intensity of Indigenous lit fires are not known, but based on accounts by early European settlers, some Indigenous fires were lit in summer every 3 to 5 years, often burning hundreds of hectares of bushland (Abbott 2003).

Natural wildfire in combination with Indigenous fire practices have further shaped vegetation patterns of the SWAFR (Abbott 2003, Hassell & Dodson 2003). More recently, summer wildfires occurred in the study area in 1937 and 1954 from which the impact is still evident with an extensive distribution of large dead trees (Department of Environment and Conservation 2008). Small scale attempts at prescribed burning began in 1954, followed by more widespread prescriptions in 1965 using aerial ignition. From the 1960's low intensity prescribed burns have occurred at 5 to 10 year intervals across the landscape creating a mosaic of different burn ages (Department of Environment and Conservation 2008).

A diversity of fire regimes across the landscape maintains biodiversity and ecosystem function in the high rainfall zone of the SWAFR (Abbott & Burrows 1999, Burrows & Wardell-Johnson 2003, McCaw & Hanstrum 2003). Due to the influence of fire on the Australian landscape for at least 2.5 million years, plant communities in the SWAFR are not only tolerant of recurrent fire but adapted and somewhat dependent on particular fire regimes for maintenance of floristic and structural diversity (Burrows & Wardell-Johnson 2003). The products of fire (smoke, gases and heat) are required for the optimal germination and flowering of many species. However inter-fire recruitment does occur in some species at a reduced intensity, but the highest rates of seed release and recruitment occur following fire (Dixon & Barrett 2003). This has been documented for the structurally dominant species *Banksia attenuata* where a small proportion of seed is released in the inter-fire period evident from seedling recruitment in the absence of fire (Dixon & Barrett 2003, Enright et al. 1998).

There is increasing evidence that a diverse fire regime benefits biodiversity and is an important driver of floristic compositional and structural complexity (Price et al. 2005, Russell-Smith et al. 2002, Wardell-Johnson et al. 2006). A single fire regime will not be optimal for all species and determining adequate regimes remains a challenge. This is due to the complexity of biodiversity

through space and time and incomplete knowledge (Abbott & Burrows 2003, Bradstock et al. 2002, Burrows & Wardell-Johnson 2003, Huston 2003). Determining appropriate ecological fire regimes to conserve biodiversity while reducing the threat that wildfire presents to life and community assets is a challenging task. One method of achieving conservation outcomes is to base fire regimes on plant attributes such as the juvenile period of the slowest maturing fire sensitive understorey species. This ensures such species have adequate time between fires to produce viable seed for regeneration (Burrows 2008, Burrows & Abbott 2003, Department of Environment and Conservation 2008).

The *Banksia* woodlands in this study had similar long-term fire histories and time since previous fire ranged from approximately 8 to 15 years. Time since previous fire was incorporated into data analysis to determine any interactions between fire and disease and the impact on vegetation patterns.

Interaction between disease and fire

The interaction between fire and *P. cinnamomi* has yet to be explored. However, links have been hypothesized between disease, fire and logging. Exploitation practices (logging, road building) may increase susceptibility of some forest stands to disease by manipulating plant species composition, light intensity and water tables (see Burrows & Wardell-Johnson 2003, Stack & Brown 2003). It has also been suggested that fire may temporarily alter the soil micro-climate to favour the activity of *P. cinnamomi*, through a rise in water table and increase in soil temperatures through removal of vegetation and presence of a dark ash bed (pers. comm. Wardell Johnson 2007).

Such interactions require further investigation and may be further exacerbated by the anticipated warming from global climate change.

**CHAPTER THREE: COMMUNITY-LEVEL CHANGES
IN BANKSIA WOODLAND FOLLOWING PLANT
PATHOGEN INVASION**

Abstract

Question: Does the introduced pathogen *Phytophthora cinnamomi* change *Banksia* woodland α or β diversity and what are the implications for species re-colonisation?

Location: High rainfall zone of the Southwest Australian Floristic Region (SWAFR)

Methods: Pathogen induced floristic change was measured along a disease chronosequence, and historic quadrats re-sampled in *Banksia attenuata* woodlands of the SWAFR. The chronosequence represents three disease stages: (1) healthy vegetation with no disease expression, (2) the active disease front, and (3) diseased vegetation infested for at least 15 years. Comparative data were obtained by resampling diseased plots that were historically disease-free when established in 1990.

Results: Beta diversity differed substantially for both chronosequence and historic data while α diversity was maintained, as measured by plot species richness and Simpson's reciprocal index. Species of known pathogen susceptibility were significantly reduced in cover-abundance including the structurally dominant species; *Banksia attenuata*, *B. ilicifolia* and *Allocasuarina fraseriana*. Although these species remained present on diseased sites, there were overall reductions in canopy closure, leaf litter and basal area. These declines were coupled with an increase of species with unknown susceptibility suggesting potential resistance and capacity to take advantage of altered site conditions.

Conclusions: This study highlights the ability of an introduced plant pathogen to alter community floristics and associated stand variables. Species cover-abundances are unlikely to recover due to a reduced seed source, altered site conditions and pathogen persistence at the landscape level. However, maintenance of α diversity suggests continued biological significance of *Phytophthora* affected sites and the formation of novel ecosystems, themselves worthy of conservation.

Keywords: Beta Diversity; Disturbance; Multivariate analysis; *Phytophthora cinnamomi*; Vegetation Change.

Abbreviations: CAP = Canonical Analysis of Principal Coordinates; PERMANOVA = Permutational Manova; SWAFR = Southwest Australian Floristic Region.

Nomenclature: Paczkowska & Chapman(2000)

Introduction

Plant pathogens are increasingly recognised as powerful agents of ecological change with an ability to transform plant community composition, structure and function (Burdon et al. 2006, Hansen 1999). Although recognition of plant pathogen impacts has expanded from species to community-level change, documentation remains critically limited when compared with more conspicuous agents of disturbance such as grazing, fire and weed invasion (Brown & Allen-Diaz 2009, Burdon et al. 2006). The impact of forest pathogens has been traditionally assessed by focussing on changes in individual species and associated shifts in canopy or basal area. Classic examples of introduced pathogens include the aerially dispersed chestnut blight (*Cryphonectria parasitica*) and sudden oak death (*Phytophthora ramorum*); and soil-borne Jarrah dieback (*Phytophthora cinnamomi*). These diseases alter vegetation structure considerably by reducing the dominant canopy species which are susceptible to the pathogen (Castello et al. 1995, Gilbert 2002). Despite substantial structural changes following pathogen invasion, community-level floristic changes are poorly documented as information on pre-pathogen vegetation composition is limited (Brown & Allen-Diaz 2009, Gilbert 2002).

Despite *P. cinnamomi* introduction to Australia in the early 20th century (Shearer & Tippett 1989), associated studies using univariate approaches and un-standardised species richness dominate the literature (e.g. Shearer & Dillon 1996a, Shearer & Dillon 1995, Weste 2003). The exception is Laidlaw & Wilson's (2003) study which explored change in species cover using a multivariate approach in south-eastern Australian forests. Species richness is generally found to decrease following disease infestation which is associated with the impact on susceptible species (Shearer & Dillon 1996a, Shearer & Dillon 1995, Weste 2003). However, in two separate studies species richness did not reduce significantly and on some sites actually increased following disease infestation (Laidlaw & Wilson 2003, McDougall et al. 2002). Consistent across all studies were shifts in species dominance, broadly linked to the susceptibility or resistance of individual species (e.g. Laidlaw & Wilson 2003, McDougall et al. 2002, Shearer & Dillon 1996a, Shearer & Dillon 1995, Weste 2003).

Banksia woodlands of the high rainfall zone of the Southwest Australian Floristic Region (SWAFR) are vulnerable to *P. cinnamomi*, occurring in a zone of warm, moist soil conditions ideal for pathogen sporulation and spread (Shearer & Tippett 1989). In addition to optimal abiotic

conditions, there is a predominance of pathogen-susceptible species in this region. Approximately 40% of SWAFR flora are listed as susceptible to *P. cinnamomi*, with 14% listed as highly susceptible (> 80% plants of a species killed) (Shearer et al. 2004a). The combination of abundant susceptible species together with optimal soil and climatic conditions has resulted in extensive pathogen impact (Shearer et al. 2007, Shearer & Dillon 1996a, Shearer & Dillon 1996b).

This study was conducted in a region of conservation significance with exceptionally high levels of diversity and endemism (Hopper 2009, Hopper & Gioia 2004). The south-western Australian *Banksia attenuata* woodlands are threatened by the combined impacts of *Phytophthora cinnamomi*, altered fire regimes and global climate change (Shearer et al. 2007, Wardell-Johnson & Nichols 1991). Determining pathogen-induced floristic change is fundamental to identifying interactions between disease and other agents of disturbance. Exploring changes in both α and β diversity following pathogen invasion also enables assessment of the re-colonisation potential of affected *Banksia* woodlands. This study uses both univariate and multivariate analyses to explore the community-level impact of *P. cinnamomi*. Chronosequence transects and historic data were used to quantify changes in α and β diversity and dependant stand variables.

Methods and materials

Study area

The study area is located in the high rainfall zone of the SWAFR ca. 400 km SSE of Perth, Western Australia (34° 49'S, 117° 9' E). The region is climatically buffered by the Indian Ocean and experiences a mediterranean-type climate with warm, dry summers and mild wet winters with an average annual rainfall of 1000 mm. The region is topographically subdued but contains high levels of species diversity and endemism more typically associated with mountainous regions (Hopper & Gioia 2004, Wardell-Johnson & Horwitz 2000). Dominant over-storey vegetation includes eucalypt forests and woodlands in pure stands or combinations of karri (*Eucalyptus diversicolor*, Myrtaceae), jarrah (*E. marginata*, Myrtaceae) and marri (*Corymbia calophylla*, Myrtaceae). *Banksia* (*B. attenuata*, Proteaceae) and Sheoak (*Allocasuarina fraseriana*, Casuarinaceae) woodlands are found in low-lying areas adjacent to sedge lands and swamps or in upland saddles. The various vegetation types are compositionally and structurally diverse, and typically track changes in soil type (Mattiske & Havel 1998). Conspicuous edaphic variation is associated with diverse vegetation types uncharacteristic for a topographically subdued landscape (Hopper 2009,

Wardell-Johnson & Horwitz 2000). Poor dispersal capabilities dominate SWAFR flora in response to a highly heterogeneous environment that favours species able to efficiently exploit scarce resources within their localised patch (Hopper 2009).

Study design and data collection

Site selection

Surveys were undertaken in *Banksia attenuata* woodlands on deep leached sands and replicated across the study area in analogous vegetation complexes (equivalent soil type, vegetation type and position within the landscape) (Havel & Mattiske 2000). Sites had similar long-term fire histories and time since previous burn ranged from approximately 8 to 15 years. Vegetation change was assessed using a chronosequence of quadrats crossing the disease gradient, and by re-sampling historically disease-free quadrats established in 1990 (Wardell-Johnson & Williams 1996). All quadrats were augered to a depth of 2 m to confirm soil type between sites and along chronosequence transects. The historic quadrats had succumbed to infestation since establishment, but were unable to be directly incorporated in the chronosequence transects due to the lack of adjacent uninfested vegetation. Eight historic quadrats (20 x 20 m) were suitable for re-sampling, having analogous soil and vegetation to the newly established chronosequence transects.

Transect locations were chosen based on vegetation complexes, and spatial autocorrelation was overcome by placement of only one transect per vegetation complex polygon. Effectively, each of the 17 transects was separated by different vegetation complexes across the landscape. Transects were positioned at least 20 m from road verges to avoid other edge effects. Each chronosequence consisted of three 20 x 20 m quadrats: (H) healthy vegetation with no disease expression; (F) the disease front with susceptible species displaying chlorotic leaves; and (D) diseased vegetation infested for approximately 15 to 20 years, dominated by dead susceptible species. The study site was topographically and edaphically similar to coastal sand-plains to the south of the study area where rates of disease spread are approximately 1.5 m/year (Grant & Barrett 2003). This rate was used to guide placement of quadrats in diseased vegetation relative to disease fronts.

Data collection

A species list was compiled for both historic quadrats and the transects with species scored using the Braun-Blanquet (1932) cover-abundance scale to allow comparison with the original survey data (Wardell-Johnson & Williams 1996). Adult plants of all growth forms were included in the survey. Additional data including leaf litter, basal area and canopy closure was collected along the chronosequence transects to identify changes in stand variables related to vegetation change. Five leaf litter samples were taken in each quadrat using a 20 x 20 cm frame with samples taken from each quadrant of the quadrat and one from the centre. Samples were air-dried before being oven dried for 12 hours at 80 °C. Quadrat basal area was determined by the sum of the sectional areas ($\pi r^2/400$) of all trees greater than 10 cm in diameter and expressed on a per hectare basis. Percentage canopy closure was measured using hemispherical digital photographs following Crane & Shearer (2007) and processed using Gap Light Analyser software (Frazer et al. 1999). *Banksia* woodland canopy closure varies little with season due to the evergreen nature of the dominant species. However, assessment was carried out in spring to ensure thorough floristic assessment and to match historical survey protocols.

Phytophthora cinnamomi activity was confirmed by laboratory analysis using the *Eucalyptus sieberi* isolation technique (Greenhalgh 1978, Marks & Kassaby 1974). Six soil and root samples were taken from susceptible species within each quadrat. Each soil/root sample was flooded to a 1:4 soil/water ratio upon which approximately ten *E. sieberi* cotyledons were floated. Samples were stored at 22 °C for optimal pathogen growth and checked on day five for evidence of cotyledon colour change indicative of *P. cinnamomi* presence (purple to yellow/green). Potentially infected cotyledons were plated onto *Phytophthora*-selective agar and stored for three days at 22°C. Plates were then inspected for characteristic hyphal swellings and mycelial growth patterns indicative of *P. cinnamomi* presence.

Data analysis

Community-level changes

Species richness (S) and Simpson's diversity index (SD) were calculated using the DIVERSE routine in PRIMER (Clarke & Gorley 2008). Simpson's reciprocal index (1/D) was also calculated as, unlike raw diversity indices, 1/D presents an actual species number allowing intuitive interpretation (Jost 2006).

Community analyses of the historic and transect data were performed using the PRIMER and PERMANOVA+ package (Clarke & Gorley 2008). The Bray-Curtis coefficient was used to determine dissimilarities between sampling units as it is particularly suited to ecological data (Clarke & Warwick 2001). Changes in β diversity were assessed using permutational multivariate analysis of variance (PERMANOVA, Anderson 2001, Anderson et al. 2008). PERMANOVA and similar procedures (e.g. Pillar & Orloci 1996) partition the sum of squares of both uni-variate or multivariate data and test hypotheses using permutation techniques (Anderson 2001). Interactions between the main effects of 'disease status' and 'time since previous fire' were tested for with a two-way crossed PERMANOVA prior to analysis of disease effect alone.

Results were displayed using Canonical Analysis of Principal coordinates (CAP), a constrained ordination method suited to *a priori* groups that can be used on any dissimilarity measure (Anderson & Willis 2003). CAP uses a Principal Coordinate Analysis (PCO) followed by a Canonical Discriminant Analysis (CDA) which finds an axis through the data cloud that maximises differences among the predefined groups (Anderson & Willis 2003). Canonical eigenvalues are derived for each axis with higher values indicating greater separation between groups.

Change in stand variables (canopy closure, basal area and leaf litter) along the chronosequence was determined using a repeated-measure ANOVA. Stand variable data was displayed on the CAP graph as a vector overlay and Pearson's correlations with the 1st CAP axis were generated. Pearson's correlation tests were also used to determine relationships between each of the variables.

The multivariate exploratory SIMPER routine has been used to determine species that discriminate between diseased and healthy vegetation in response to pathogen infestation. The SIMPER routine determines individual species contributions to the average species dissimilarity between groups by disaggregating the Bray-Curtis dissimilarities between samples (Clarke & Warwick 2001). Species were listed in order of greatest contribution to dissimilarity between healthy and diseased vegetation and graphically represented in stacked dot plots after Warton (2008).

Species-level changes

Changes in single species cover-abundances were identified using Mann-Whitney U tests (2 samples) for the historic data and Kruskal-Wallis tests (3 samples) with multiple pair-wise comparisons for the transect data (Kassi N' Dja & Decocq 2008). Uni-variate tests were carried out using the XL STAT program (Addinsoft 2006).

Results

Community-level changes

The 17 transects (51 quadrats) included 178 native plant species, compared to 154 species recorded from the 8 historic quadrats. *Phytophthora cinnamomi* was isolated from 95% of chronosequence transects and 12% of historic quadrats. Despite the low pathogen detection rate for historic quadrats, a reduction of susceptible species indicates previous *P. cinnamomi* infestation (Table 4).

Table 4: Mean (\pm standard error) cover-abundance of species that changed significantly following infestation for chronosequence and historic data in *Banksia* woodland of the Southwest Australian Floristic Region. * $p < 0.05$; ** $p < 0.01$; * $p < 0.001$.**

	Healthy vegetation	Disease Front	Diseased vegetation	Susceptibility to pathogen	1990	2006
SPECIES THAT DECREASED						
<i>Banksia attenuata</i>	55.1 \pm 5.0	45.7 \pm 6.1***	20.3 \pm 3.8***	High	22.1 \pm 7.7	4.2 \pm 1.6*
<i>Banksia ilicifolia</i>	1.9 \pm 0.3	0.9 \pm 0.3	0.2 \pm 0.1*	High	8.8 \pm 4.7	0.9 \pm 0.5
<i>Daviesia flexuosa</i>	1.8 \pm 0.4	0.8 \pm 0.2	0.7 \pm 0.2*	Unknown	25.9 \pm 9.7	1.4 \pm 0.5*
<i>Eucalyptus marginata</i>	2.0 \pm 1.1	0.8 \pm 0.8	1.3 \pm 0.8	Moderate	18.8 \pm 4.5	6.4 \pm 2.5*
<i>Gompholobium capitatum</i>	2.3 \pm 0.8	1.0 \pm 0.3	0.5 \pm 0.2*	High	0.13 \pm 0.1	0.5 \pm 0.4
<i>Hibbertia commutata</i>	3.0 \pm 0.0	2.3 \pm 0.3	1.3 \pm 0.4**	High	1.9 \pm 1.8	0.25 \pm 0.1
<i>Lyginia barbata</i>	-	-	-	Unknown	2.1 \pm 0.5	0.7 \pm 0.3*
<i>Phlebocarya ciliata</i>	-	-	-	Unknown	1.1 \pm 0.5	0.3 \pm 0.1
<i>Pimelea longifolia</i>	10.9 \pm 2.1	8.7 \pm 2.2	4.0 \pm 0.9**	Unknown	2.1 \pm 0.5	0.3 \pm 0.1**
SPECIES THAT INCREASED						
<i>Anarthria prolifera</i>	23.3 \pm 3.3	30.2 \pm 3.0	34.4 \pm 3.6**	Unknown	3.6 \pm 1.7	15.8 \pm 5.2*
<i>Lyginia barbata</i>	3.3 \pm 1.1	8.2 \pm 1.7	7.3 \pm 1.5*	Unknown	-	-
<i>Phlebocarya ciliata</i>	2.3 \pm 0.8	2.7 \pm 0.8	5.4 \pm 2.0*	Unknown	-	-
<i>Xanthosia huegelii</i>	0.2 \pm 0.2	0.3 \pm 0.2	2.0 \pm 0.8*	Unknown	0.5 \pm 0.3	0.06 \pm 0.06

Native species richness and Simpson's reciprocal index were not significantly different following pathogen invasion for both data sets (species richness: historic $p = 0.49$; chronosequence $p = 0.52$ and Simpson's reciprocal index: historic $p = 0.23$; chronosequence $p = 0.73$). Historic species richness ranged from 37 to 38 species over time while the chronosequence data averaged 46 to 47

species per quadrat despite disease status. Dataset differences are due likely to a combination of varied sampling effort, different fire histories and year of data collection. Simpson's reciprocal index varied little, from healthy vegetation (38.1), disease front (37.7) and diseased vegetation (37.2), a pattern also reflected in the historic data.

In contrast to the univariate indices, multivariate analysis revealed significantly altered β diversity following pathogen invasion for both data sets (historic $p < 0.017$; chronosequence $p = 0.001$). The clear distinction between chronosequence quadrats was also comparable to β diversity changes in the historic data (Figure 14). Beta diversity also varied with the time since previous fire, but there was no interaction between the main effects (Disease Status or Year x Previous Fire) ($p = 0.981$). The first canonical axis discriminated groups based on disease status, showing that species abundances were significantly different following pathogen infestation ($\delta^2_1 = 0.798$ - Figure 14). The proportion of points that were classified correctly (allocation success) was 66.7% for the three disease groups, greater than the 33.3% expected by chance alone.

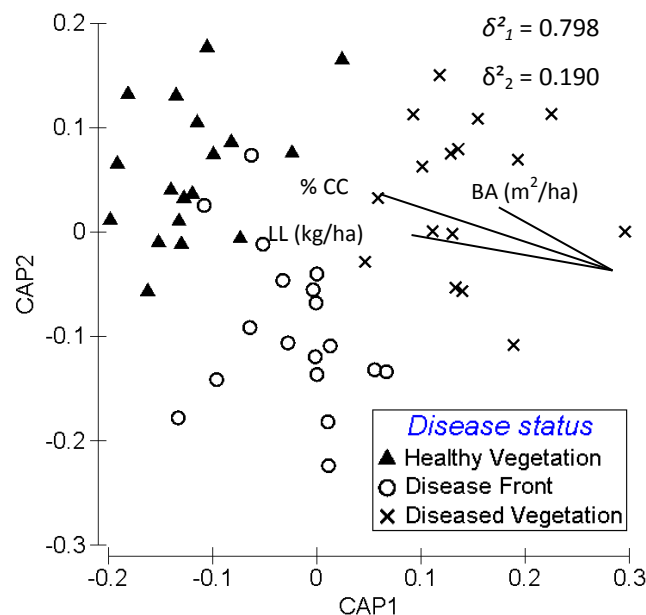


Figure 14: Constrained ordination of species cover-abundance across disease chronosequence in *Banksia* woodland of the Southwest Australian Floristic Region ($p=0.001$) with vector overlay of stand variables CC = canopy closure, BA = basal area, LL = leaf litter.

Change in stand variables – chronosequence data only

All stand variables changed significantly following disease infestation (Table 5). Canopy closure and leaf litter were reduced by approximately 75% ($p = 0.001$) and 50% ($p = 0.001$) respectively;

both with strong positive correlations with the first canonical axis (Figure 14). Basal area was reduced by 50% on diseased sites but relatively weakly correlated with the first axis ($\rho = 0.028$; $\delta^2_1 = 0.33$). As with species cover-abundances changes, the greatest differences between all stand variables were observed between diseased and healthy sites, with disease fronts being more similar to healthy vegetation. All stand variables were significantly correlated with one another ($\rho < 0.01$).

Table 5: Vegetation dependant stand variables (mean \pm standard error) in relation to chronosequence disease status in *Banksia* woodland of the Southwest Australian Floristic Region.

Variable	Healthy Vegetation	Disease front	Diseased vegetation	Transect p value	1st CAP axis correlation
Canopy closure (%)	19.9 \pm 1.4	10.4 \pm 1.3***	3.9 \pm 0.7***	0.001	0.72
Basal area (m ² /ha)	22.0 \pm 3.0	16.3 \pm 2.9	10.7 \pm 2.9*	0.028	0.33
Leaf litter (kg/ha)	85.9 \pm 9.9	58.8 \pm 6.5***	37.6 \pm 3.7***	0.001	0.59

Species-level changes

Eleven species changed significantly in cover-abundance following disease infestation, with 5 of these species changes common to both datasets (Table 4, Figure 15 & 16). Structurally dominant *B. attenuata* reduced significantly both across the chronosequence ($p < 0.001$) and in historic data ($p < 0.05$), as did the shrub species *Daviesia flexuosa* (Papilionaceae, historic and chronosequence $p < 0.05$). The moderately susceptible tree species *Eucalyptus marginata* reduced significantly in cover-abundance in historic quadrats ($p < 0.05$), reducing by approximately 30% from 1990 to 2006. The sedge-like species *Anarthria prolifera* (Anarthriaceae) has unknown susceptibility but increased in cover-abundance for both data sets (historic $p < 0.05$; chronosequence $p < 0.01$). Highly susceptible *B. ilicifolia* and *Hibbertia commutata* (Dilleniaceae) significantly decreased in cover-abundances along the disease transect. These trends were reflected in the historic data, however changes were not significant. Several species known to be highly susceptible did not significantly reduce in cover abundance. These included *Adenanthos cuneatus*, *A. obovatus*, *Petrophile acicularis* (Proteaceae), *Andersonia caerulea* (Ericaceae), *Hypocalymma strictum* (Myrtaceae) and *Pultenea reticulata* (Papilionaceae).

The exploratory SIMPER analysis revealed *A. scabra*, *A. fraseriana* and *Taxandria parviceps* (Myrtaceae) contributed most to dissimilarity between 1990 and 2006 (Figure 15). Several

susceptible species including the dominant *B. attenuata*, not only reduced over time, but featured in the top 40% of species contributing to dissimilarity between 1990 and 2006. A range of species currently of unknown susceptibility displayed variable responses over time which may provide an indication of potential susceptibilities.

Similar trends were revealed from the chronosequence data regarding reduced cover-abundance of susceptible species and an increase in species of unknown susceptibility (Figure 16). Similar to the historic data, susceptible proteaceous species declined in cover-abundance with reduced *B. ilicifolia*, *B. quercifolia*, *B. attenuata* and *A. cuneatus*. A range of species of unknown susceptibility displayed variable cover-abundance shifts. Additional congruence between data sets was the reduction in the moderately susceptible tree species *A. fraseriana*.

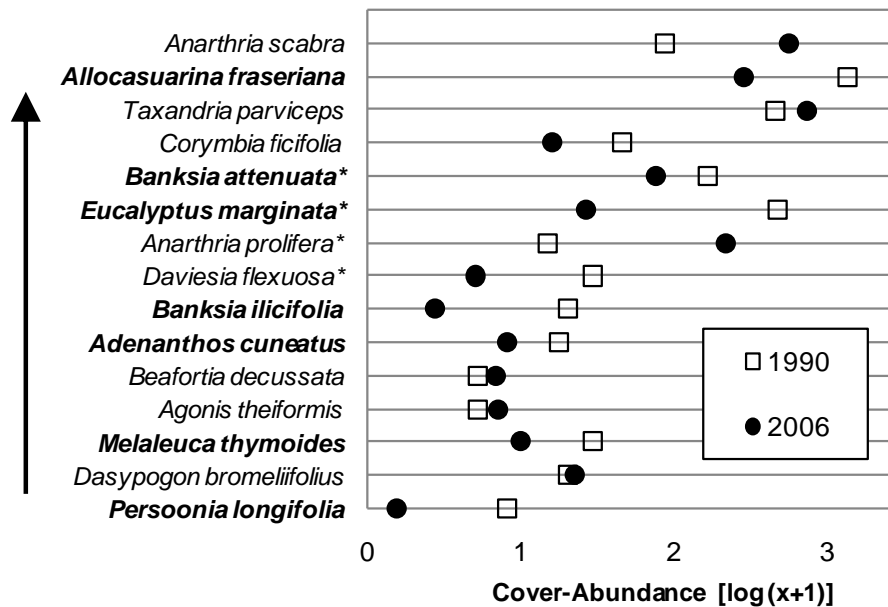


Figure 15: Historic (1990 v 2006) dot plot of changes in species cover-abundance following pathogen infestation in *Banksia* woodland of south-western Australia. Species means are plotted in order of greatest contribution to dissimilarity between healthy and diseased vegetation as derived from the SIMPER routine in PRIMER. Species listed are the top 40% of species contributing to site dissimilarity. Species susceptible to the pathogen are printed in bold. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

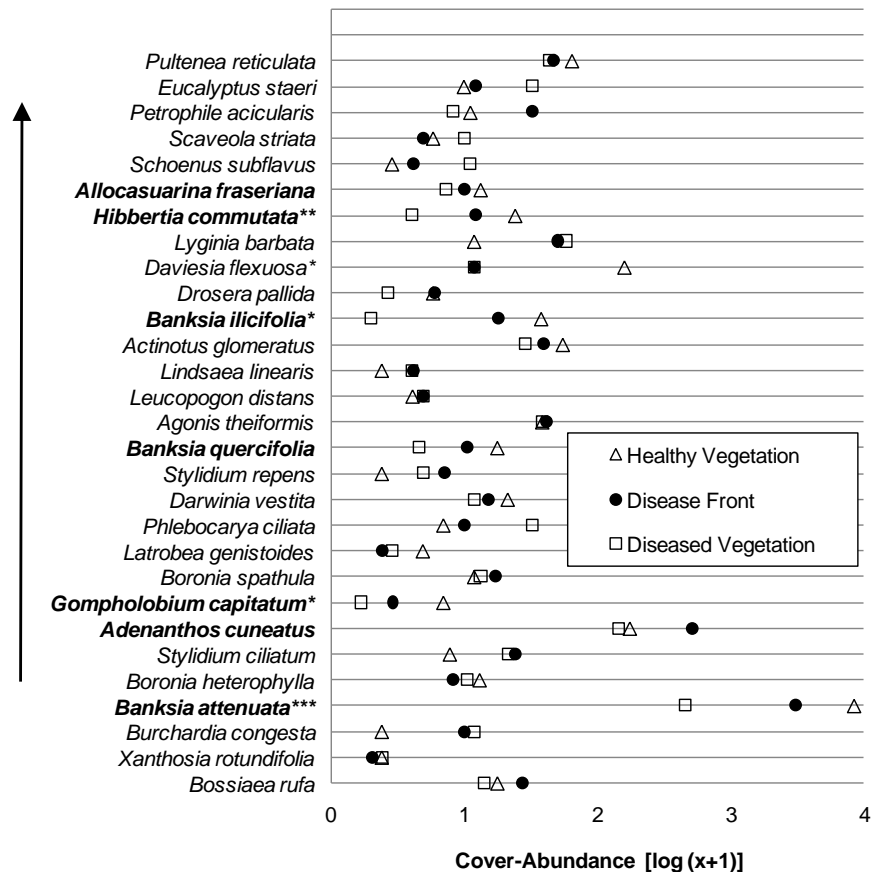


Figure 16: Disease chronosequence dot plot of changes in species cover-abundance following pathogen infestation in *Banksia* woodland of south-western Australia. Species means are plotted in order of greatest contribution to dissimilarity between healthy and diseased vegetation as derived from the SIMPER routine in PRIMER. Species listed are the top 40% of species contributing to site dissimilarity. Species susceptible to the pathogen are printed in bold. ** $p < 0.05$; * $p < 0.01$; *** $p < 0.001$.

Discussion

Community-level changes

The invasion of plant pathogen *P. cinnamomi* has led to substantial shifts in *Banksia* woodland β diversity, primarily due to the reduction of structurally dominant but pathogen susceptible species. Despite altered β diversity, species richness did not vary regardless of disease presence, which contrasts the majority of comparable studies (e.g. Shearer & Dillon 1996a, Shearer & Dillon 1995, Weste 2003). However, maintenance of α diversity following *P. cinnamomi* infestation has been found elsewhere in Australia (Laidlaw & Wilson 2003, McDougall et al. 2002), suggesting variable vegetation responses to pathogen presence. The inconsistent impact of *P. cinnamomi* on α diversity demonstrates regional differences and variable patterns of pathogen impact across different vegetation types. Differences may also reflect variation in the time since initial

infestation, initial species composition and idiosyncratic site conditions being either suppressive or conducive to disease expression. Additionally, irregularities may be attributed to diverse disturbance histories, particularly logging and fire regimes.

Despite clear compositional change for both the chronosequence and historic data, total vegetation cover remained unchanged, also found in *Banksia* woodlands in the Swan Coastal Plain Bioregion outside the study area (Shearer et al. 2009a). This is attributed to the cumulative effect of individual species increases and decreases based on pathogen susceptibility and altered site conditions. Indeed several species did decrease significantly in cover, but this was coupled with increases in other species sufficient to maintain total vegetation cover following infestation.

In conjunction with direct effects on β diversity, indirect pathogen effects have been anticipated to be of greater concern than initial changes in site floristics (Hansen 1999, Shearer et al. 2007). Substantial reductions in variables basal area, canopy closure and leaf litter are the product of direct pathogen impact on canopy species *B. attenuata*, *B. ilicifolia* and *A. fraseriana*. Changes in site microclimate from increased canopy gaps and reduced litter may promote a novel re-colonisation pattern. This could be related to individual species germination and growth requirements, coupled with species susceptibility to the pathogen. Although seed of affected species may be present, germination conditions may be unfavourable due to changes in canopy closure and litter cover (Dupuy & Chazdon 2008, Prescott 2002).

Species that prefer conditions with reduced canopy closure and litter may have a competitive advantage on *P. cinnamomi* affected sites. These effects have been documented for invasive plant pathogens Chestnut blight (*Cryphonectria parasitica*) and Sudden oak death (*P. ramorum*) in the United States. A reduction in dominant susceptible species has generated a decrease in basal area and canopy closure resulting in recruitment and dominance of previously less abundant species (Brown & Allen-Diaz 2009, Rizzo & Garbelotto 2003, Vandermast & Van Lear 2002). Dominance shifts and reductions in basal area and canopy closure have also been found in preliminary investigations of *P. ramorum* in the mixed evergreen and redwood forests from California to Oregon (Brown & Allen-Diaz 2009, Rizzo & Garbelotto 2003). Alternatively, the pathogen effect may potentially be greatest on germination and seedling survival in the post-fire environment due to altered fire conditions linked to reductions in available material to burn from pathogen reduced

basal area and canopy closure. This is likely as *Banksia* woodlands contain a dominance of fire-adapted species which require the products of fire (heat & smoke) for seed release and germination. However the aspects of post-pathogen recruitment and seedling survival require further investigation to clarify pathogen impact.

Reduced re-colonisation potential of *P. cinnamomi* susceptible species may be compounded by the poor dispersal capabilities that characterize SWAFR flora based on seed morphology and the high levels of genetic structuring in plant populations (Hopper & Gioia 2004, Wardell-Johnson & Williams 1996). Seeds of SWAFR species are predominantly small, and most lack obvious aids for long distance wind or animal dispersal (Hopper 2009, Sweedman & Merritt 2006). Patches of unaffected vegetation and individuals that indiscriminately avoid infestation are important sources of seed for re-colonisation of infested areas. However, isolated patches may prove ineffectual due to the characteristic limited dispersal abilities of SWAFR flora (Hopper & Gioia 2004). *Banksia* woodlands in upland saddles which are generally unaffected due to their position in the landscape are also available as a seed sources. Although potentially important for seed, distance from the saddle may limit re-colonisation success of affected lowland *Banksia* woodlands.

Although commonly accepted that SWAFR flora are poor dispersers, emerging literature exists to the contrary, having implications for re-colonisation of pathogen infested *Banksia* woodlands (He et al. 2004, Higgins et al. 2003). Higgins et al. (2003) conclude that the relationship between morphologically defined dispersal syndromes and long-distance dispersal is poor, and multiple processes may generate long distance seed dispersal. In a genetic study of *Banksia hookeriana* (a fire killed shrub) long distance dispersal was greater than anticipated with distances of some individuals ranging from (1.6 to > 2.5 km) from the parent plants (He et al. 2004). The potential mechanisms of long distance dispersal were wind vortexes that commonly follow fire; reduced resistance from other vegetation following fire – allowing for longer distance wind dispersal; and removal of cones by cockatoos (He et al. 2004). If like *B. hookeriana*, *B. attenuata* and other pathogen affected species had long distance seed dispersal, positive implications for re-colonisation would result. This warrants further research to determine if long distance seed dispersal is more prevalent in SWAFR flora than previously anticipated.

Observed beta diversity shifts and related reductions in canopy closure, leaf litter and basal area have important implications for *Banksia* woodland dynamics. Pathogen-mediated community level changes have wide ranging implications for nutrient cycling, light levels, soil temperatures and soil water dynamics, and form a basis for further investigation (Burdon et al. 2006, Shearer et al. 2009a).

Species-level changes

Following infestation, substantial cover changes of several species was evident from both chronosequence and historic data. Of the species that changed significantly, only 40% were known to be directly susceptible to the pathogen with the remainder having unknown susceptibility. Several susceptible species did not reduce as anticipated which may be attributed to inherent genetic resistance, effective re-colonisation strategies or mere escape from pathogen spread. Differential susceptibility due to genetic resistance of individual plants or populations has been documented in *E. marginata* (Stukely & Crane 1994) and other species (Harris et al. 1985, Shearer et al. 2004a). Although selective genetic resistance is likely to extend to *Banksia* woodland species, this has yet to be investigated beyond informal observation (Shearer & Dillon 1995). Susceptible species persistence may also be attributed to effective re-colonisation abilities. Species able to disperse widely or that have an abundance of stored seed may be favoured following *P. cinnamomi* infestation, provided conditions are conducive to regeneration (McDougall 1997, Rockel et al. 1982). This has been documented for *B. sessilis*, a susceptible species that seeds prolifically and germinates easily, making it an aggressive coloniser in *P. cinnamomi* affected areas (Rockel et al. 1982).

Escape from infection has also been suggested as a possible explanation for persistence of susceptible species (McDougall et al. 2002). Although sites were suitably replicated at a fine scale, inoculum is spatially irregular at the quadrat level allowing local escapes to occur (Shearer et al. 2009b). Patchiness of disease effect was also observed at a landscape level due to irregular spread and areas with suppressive site conditions (i.e. soil type, antagonist microflora and/or inadequate temperature & moisture levels) (Shearer & Dillon 1995).

Interacting agents of disturbance

In addition to the inherent susceptibility of *Banksia* woodlands, inappropriate fire regimes and global climate change are anticipated to exacerbate pathogen impact (Chakraborty et al. 1998,

Podger & Brown 1989). The effect of fire on vegetation dynamics is currently being explored with experimental fire regimes, but hypothesized links between fire regimes and *P. cinnamomi* suggest that frequent fires generate an immediate though short-term water table rise and warmer soil temperatures, causing enhanced pathogen activity (Cahill et al. 2008, Podger et al. 1990). Additionally, reduced activity of microbial antagonists has been associated with burnt sites, which would further promote pathogen spread (Malajczuk 1988, Nesbitt et al. 1979a).

A preliminary study investigating the interaction between *P. cinnamomi* and fire, found that recently burned (1 to 2 years) diseased sites had lower α diversity than comparable longer unburnt sites (Moore et al. 2007). Long unburnt pathogen-free sites were not measured. It is likely that reduction of the shrub and herb layer by fire generates immediate and temporarily enhanced conditions for *P. cinnamomi* sporulation and spread. The dark ash bed is likely to increase soil temperature, and coupled with a rise in water table provides optimal conditions for pathogen success (Abbott & Burrows 2003). There was no interaction between time since previous burn and disease status, as the study focussed on a plant community in which none of the quadrats had been burnt for at least 8 years.

In addition to pathogen-fire interactions, predicted climate change may further enhance pathogen impact. Significant declines in autumn and early winter rainfall (10-20%) has occurred in the SWAFR since the 1970's and has been partly attributed to global climate change (Bates et al. 2008). The slight increase in summer rainfall coupled with predicted temperature rises may enhance conditions for *P. cinnamomi* spread by providing moist conditions in typically dryer periods. The interactions between *P. cinnamomi*, fire and climate change are inherently complex. However, modification of fire regimes to alter pathogen impact may enhance desired biodiversity outcomes.

This study demonstrates the formation of a novel but diverse ecosystem following infestation by an introduced plant pathogen. Altered β diversity will hinder re-colonisation and persistence of susceptible species due to altered site conditions and reduced seed production as inferred from a reduction in cover values. In addition, the pathogen persists where suitable climatic conditions and host material exist, having continued impact on susceptible plant communities (Nesbitt et al. 1979b, Shearer & Shea 1987, Weste & Vithanage 1979). Although the consequences of *P.*

cinnamomi invasion are profound, maintenance of α diversity indicates the continuation of significant biodiversity values in a region recognised internationally for its exceptionally high levels of diversity and endemism (Hopper 2009, Myers et al. 2000).

Acknowledgements

I thank B. Shearer, L. Duarte and an anonymous referee for valuable comments on earlier versions of the manuscript. Thank you also to B. Ward, R. Cranfield & R. Davis for their assistance with floristic surveys. This study was supported by a University of Queensland APAI scholarship and Australian Research Council Linkage Project LP0560809, "*Towards a landscape conservation culture – broadening the spatio-temporal scope of ecological studies to anticipate change in Australian forested ecosystems*". Field work was supported by the Western Australian Department of Environment and Conservation. All experiments and analyses in this manuscript comply with Australian federal and Western Australian state laws and codes of practice.

**CHAPTER FOUR: A FOREST PATHOGEN
DRIVES CHANGE IN PLANT FUNCTIONAL
TRAIT COMPOSITION IN THE SOUTHWEST
AUSTRALIAN FLORISTIC REGION**

Abstract

Plant functional traits weighted by cover-abundance have been used to measure change across a wide range of temperature, moisture and grazing gradients. This approach was used along a chronosequence of disease infestation (*Phytophthora cinnamomi*) in the species-diverse *Banksia* woodlands of the Southwest Australian Floristic Region (SWAFR). Absolute (community-weighted totals – CWT) and relative cover data (community-weighted means – CWM) were compared to demonstrate the importance of total cover change in reference to the Mass Ratio Hypothesis.

Plant species cover-abundance was recorded along a space-for-time disease chronosequence, and functional trait data collected for the 48 dominant species from healthy vegetation. Six traits with deduced links to key ecosystem functions were measured for each species and values for two indices (CWT and CWM) compared along the disease chronosequence. Trait data was collected on plant height, growth form, specific leaf area, leaf dry matter content, root pattern and carbohydrate storage.

Despite substantial shifts in individual species cover and a reduction in total species cover, the majority of CWM values did not change significantly following disease infestation. The use of relative cover-abundance data disregards important changes in total species cover, apparent from comparative analysis. In contrast to CWMs, all CWT values were reduced following disease infestation, suggesting a potential reduction in productivity, reduced capacity as a carbon sink and altered site water balance. Verification of these potential changes in ecosystem functions is required using fine-scale quantitative techniques. The CWT index is complementary to traditional CWMs and useful when analysing changes in plant trait data where total species cover changes have been detected. In relation to *P. cinnamomi* infestation, shifts in CWT trait values indicate the ability of an introduced plant pathogen to have substantial indirect impacts beyond substantial floristic change.

Keywords: community-weighted means; disease; mass ratio hypothesis; *Phytophthora cinnamomi*.

Abbreviations: CAP = Canonical Analysis of Principal Coordinates; CWM = Community-weighted mean; CWT = Community-weighted total; LDMC = Leaf Dry Matter Content; SLA = Specific Leaf Area.

Nomenclature: Paczkowska & Chapman(2000)

Introduction

Beyond direct alteration of vegetation composition and structure, forest pathogens are thought to initiate local level changes in productivity, nutrient cycling and water resources; and to generate larger scale functional change (Hooper et al. 2005, Vitousek 1990, Vitousek et al. 1996). Pathogen-induced change in ecosystem function is frequently assumed (Burdon et al. 2006, Hansen 1999, Lovett et al. 2006, Shearer et al. 2009a), but the study of plant pathogen impact is limited to changes in composition and structure.

The introduced plant pathogen *Phytophthora cinnamomi*, causes substantial floristic change, yet documentation of its impact on plant community composition, structure and ecosystem function is limited, and no long-term studies exist (Shearer et al. 2007, Shearer et al. 2009a). Vegetation in the Southwest Australian Floristic Region (SWAFR) are inherently vulnerable to *P. cinnamomi*, occurring in a zone of warm, moist soil conditions ideal for pathogen sporulation and spread (Hopper & Gioia 2004, Shea et al. 1983, Shearer & Tippett 1989). In addition to ideal abiotic conditions, there is a predominance of pathogen-susceptible species in the region. Approximately 40% of SWAFR flora are listed as susceptible to *P. cinnamomi*, with 14% listed as highly susceptible (> 80% plants of a species killed) (Shearer et al. 2004a). The combination of abundant susceptible species together with optimal soil and climatic conditions has resulted in extensive pathogen impact (Shearer & Dillon 1996a, Shearer & Dillon 1996b).

A preliminary investigation by Shearer et al. (2009a) suggests pathogen-induced changes in ecosystem function, with associations between canopy closure, species cover changes and other species variables. Exploring pathogen impact on ecosystem function requires definition of the relevant functions to be investigated combined with a community-level investigation that integrates plant traits and species cover changes. This approach explores community-level shifts in functional diversity which has greater relevance than taxonomic diversity when explaining local-scale ecosystem functioning and responses along environmental or disturbance gradients (Diaz et al. 2007, Hooper et al. 2005).

Analysis of plant functional traits is an efficient method of investigating potential functional change across gradients through deduced links between traits and ecosystem functions (Diaz & Cabido 1997, Díaz et al. 1999, Lavorel & Garnier 2002). Plant traits can be considered as “effect” or

“response” traits based on whether they effect ecosystem functions (effect traits) or drive community assembly along gradients of change (response traits) (Lavorel & Garnier 2002). Analysis of effect trait values can test and generate hypotheses regarding changes in ecosystem function. However, direct measurement using traditional techniques is necessary for clarification and verification. Both the type and abundance of plant traits provides insight into the functional organisation and characteristics of a plant community.

Changes in ecosystem function using plant traits is based on the premise that, through these traits, plant species exert different influences on ecosystem function, and hence trait changes may indicate ecosystem effects (Cornelissen et al. 2003, Eviner & Chapin III 2003, Garnier et al. 2004). In addition to changes in species composition, significant changes in species abundance can also initiate shifts in function (Suding et al. 2008). This encapsulates the Mass Ratio Hypothesis suggesting that abundant species generally dominate ecosystem function due to greater plant biomass (Bormann & Likens 1979, Grime 1998, Huston 1997). The Mass Ratio Hypothesis has been quantitatively represented by the community-weighted means index (CWM), which is the aggregation of trait data weighted by relative species abundance (Garnier et al. 2004, Quetier et al. 2007).

Trait analysis allows for preliminary investigation of functional change, without the requirement of excessive expenditure to quantitatively measure ecosystem functions using traditional time-intensive techniques. For example, conventional measurement of specific annual net primary productivity (SANPP) involves harvesting, sorting, drying and weighing standing biomass at replicated sites. Garnier *et al.* (2004) have demonstrated a relationship between traditionally collected SANPP values and the relatively easily collected leaf trait values for specific leaf area, dry matter content and nitrogen concentration. Strong correlations were revealed between SANPP and these leaf traits which demonstrates the ability to use plant traits as surrogates to identify change in productivity (Lavorel et al. 2007).

Shifts were identified in *Banksia* woodland effect plant traits from the introduced plant pathogen, *P. cinnamomi*, in the SWAFR (Hopper & Gioia 2004). Shifts in six functional traits were explored, weighted by relative (community-weighted means – CWM) and absolute cover-abundance (community-weighted totals – CWT) to investigate the potential impact of disease on trait values.

Data was collected on plant height, growth form, specific leaf area, leaf dry matter content, root pattern and carbohydrate storage for dominant species. Based on deduced links with plant effect traits (Table 6), substantial shifts in ecosystem function are anticipated due to shifts in species dominance coupled with a reduction in canopy cover, leaf litter and basal area (Bishop et al. 2010, Shearer et al. 2009a).

Specifically I explore the impact of *Phytophthora cinnamomi* by asking:

1. Are there changes in site productivity traits (Specific Leaf Area & Leaf Dry Matter Content)?
2. Does the pathogen alter nutrient cycling rates?
3. Does pathogen introduction alter *Banksia* woodlands capacity for carbon immobilisation?
4. a) Does the dominance of particular root patterns change following disease infestation?
b) What are the potential implications regarding hydraulic lift and site water balance?

Additionally I compare the use of relative and absolute cover data in the generation of trait values and introduce a modification of the traditional community-weighted mean index (CWM). The modified index, community-weighted total (CWT), is applied to demonstrate the importance of absolute cover changes in relation to altered trait composition and the Mass Ratio Hypothesis (Grime 1998).

Material and methods

Study area

The study area is located in the high rainfall zone of the SWAFR ca. 400 km SSE of Perth, Western Australia (34° 49` S, 117° 9` E). The region is climatically buffered by the Indian Ocean and experiences a mediterranean-type climate with warm, dry summers and mild wet winters with an average annual rainfall of 1000 mm. The study site and surrounds is topographically subdued but contains high levels of species diversity and endemism more typically associated with mountainous regions (Hopper 1979, Hopper 1992, Hopper & Gioia 2004, Wardell-Johnson & Horwitz 2000).

The SWAFR lies within a global biodiversity hotspot (Myers et al. 2000) with 7380 native plants including 3616 endemic taxa (Hopper & Gioia 2004). Among these is a prevalence of species with

lignotubers that serve as a regenerative and storage organ as an adaptation in fire-prone mediterranean-type ecosystems (James 1984, Pate & Beard 1984). The *Banksia* woodlands under investigation are dominated by a *Banksia attenuata* (Proteaceae) over-storey and a sclerophyllous tall shrub layer (up to 2 m) dominated by *Taxandria parviceps* and *Melaleuca thymoides* (both Myrtaceae). The lower stratum below 1 m is dominated by herbs, sedges and sedge-like species, including *Anarthria scabra*, *A. prolifera* (Anarthriaceae) and *Dasypogon bromeliifolius* (Dasypogonaceae) (Bishop et al. 2010). These *Banksia*-dominated woodlands occur in a complex mosaic of vegetation types and are found in both low-lying areas adjacent to sedge lands and swamps, and in upland saddles on highly oligotrophic soils (Churchward et al. 1988, Pate & Bell 1999).

Site selection

Surveys were undertaken on 17 *B. attenuata* woodland sites on deep oligotrophic sands, with replication in analogous vegetation complexes (equivalent soil type, vegetation type and position within the landscape) (Havel & Mattiske 2002). Sites were randomly located across the landscape due to the patchy nature of *P. cinnamomi* infestation and disease spread.

Sites had similar long-term fire histories, and time since previous fire ranged from 8 – 15 years. Changes were assessed along space-for-time transects in a randomized block design. Each disease centre had one chronosequence (block) consisting of three 20 x 20 m quadrats: (H) healthy vegetation with no disease expression; (F) early disease with susceptible species displaying leaf chlorosis in combination with dead and healthy susceptible species e.g. *B. attenuata*; and (D) long diseased vegetation infested for approximately 15 to 20 years, characterised by long dead *B. attenuata*.

Spatial autocorrelation was minimised by placement of transects in separate (but homogenous) vegetation complex polygons. Effectively, transects were separated by different vegetation complexes across the landscape and were at least 500 m apart. Transects were positioned at least 20 m from road verges to avoid other edge effects.

The study site is topographically and edaphically similar to coastal sand-plains immediately to the south where rates of disease spread are approximately 1.5 m/year (Grant & Barrett 2003). This

rate was used to guide placement of quadrats in long diseased vegetation relative to those with early disease symptoms. Quadrats in healthy vegetation were placed approximately 50 m from quadrats showing early disease. All quadrats were augered to a depth of 2 m to confirm soil type between sites and along chronosequence transects.

Trait measurement

Cover-abundance of dominant species was scored using the Braun-Blanquet (1932) scale, with adult plants of all growth forms included. The dominant species for which trait data could be accessed (desktop and laboratory measurement) were selected for analysis. The dominant 48 species were identified across all healthy quadrats and trait measurements taken on uninfected adult specimens growing in optimal conditions (Cornelissen et al. 2003).

Six traits (plant height, growth form, specific leaf area, leaf dry matter content, root pattern and carbohydrate storage) were selected for measurement. These traits relate to plant strategies with potential links to ecosystem functions of interest. Within the constraints of the project, traits requiring more intensive collection and analysis methods such as the distribution of rooting depth and leaf N and P concentration could not be considered. Deduced links exist between the selected traits and productivity, nutrient cycling, carbon immobilisation & storage and hydraulic lift – (Table 6) (Cornelissen et al. 2003, Diaz & Cabido 1997). Trait data was obtained by a desktop study from region specific databases (Western Australian Herbarium 2010, Wheeler et al. 2002), and organised into trait relevant classes using Diaz and Cabido (1997) and Walker and Langridge (2002) for guidance. Specific leaf area and leaf dry matter content were measured on a minimum of 10 fresh specimens from each of the 48 species following procedures outlined in Cornelissen *et al.*, (2003). SLA and LDMC data were collected and analysed as continuous data but presented in classes to clearly show changes comparative to other trait data (Table 6).

Table 6: Plant functional traits measured with deduced links to ecosystem function.

Trait	Functional significance	Trait classes
<i>Plant height</i>	Net amount of carbon fixed and stored per year; maximum carbon storage. Broadly correlates with above ground biomass (Cornelissen et al. 2003).	<0.5; 0.5-1; 1-2; 2-5, >5 (metres)
<i>Growth form</i>	Determines carbon immobilisation rates which are a function of the ability of a species to invest carbon in plant support tissues (xylem & bark) which is not broken down for use in further biosynthesis. Positively correlated with sink strength for carbon (Diaz & Cabido 1997)	herbaceous monocots; herbaceous eudicots; semi-woody eudicots; woody eudicots with trunk and bark
<i>Specific leaf area (SLA)</i>	Positively correlated with potential relative growth rate and linked to above ground productivity (Cornelissen et al. 2003, Garnier et al. 2004, Westoby 1998)	< 3 or aphyllous; 3 to 3.9; 4 to 4.9; 5 to 5.9; 6 to 6.9; >7 (mm ² .mg ⁻¹)
<i>Leaf dry matter content (LDMC)</i>	Community aggregated LDMC is an approximate measure of leaf tissue density linked with nutrient cycling (litter quality, rate of decomposition and release of C and N) (Poorter & Garnier 1999, Quested et al. 2007). Also linked to above ground productivity (Garnier et al. 2004)	<200 or aphyllous; 200 to 300; 301 to 400; 401 to 500; 501 to 600; >601 (mg.g ⁻¹)
<i>Root pattern</i>	Root pattern is used as surrogate for potential water uptake and access to water table (Dodd et al. 1984, Pate & Bell 1999, Walker & Langridge 2002)	<1m with no obvious main root, shallow laterals; 1-2m with shallow single main root, shallow laterals; >2m deep tap root with or without laterals
<i>Carbohydrate storage</i>	Capacity to store carbohydrate that can be broken down and allocated to new growth (thickened roots and stems, bulbs and rhizomes). Positively correlated with sink strength for carbon (Cornelissen et al. 2003, Diaz & Cabido 1997)	presence/absence of specialised carbohydrate storage organs such as lignotubers

Pathogen activity

To ensure potential changes are from *P. cinnamomi* activity and not from other forest pathogens or simply drought, *P. cinnamomi* presence was confirmed by laboratory isolation (Greenhalgh 1978, Marks & Kassaby 1974). Different susceptible species displaying disease symptoms were targeted for root sampling within quadrats in early diseased and long diseased vegetation. Six samples were taken within each quadrat and pooled into 3 samples to increase pathogen recovery rates.

Samples were flooded to a 1:4 soil/water ratio upon which 10 *E. sieberi* cotyledons were floated. Samples were stored at 22 °C for optimal pathogen growth and checked on day 5 for evidence of cotyledon colour change indicative of *P. cinnamomi* presence (purple to yellow/green). Potentially infected cotyledons were plated onto *Phytophthora*-selective agar and stored for 3 days at 22°C. Plates were then inspected for characteristic hyphal swellings and mycelial growth patterns indicative of *P. cinnamomi* presence.

Data analysis

Matrices of species cover and plant traits were used to generate aggregated trait values and assess change across the disease gradient (Diaz & Cabido 1997, Meers et al. 2008, Pakeman et al. 2009). Total cover was obtained by taking midpoints from the Braun-Blanquet data, and summed across species for each disease state.

The trait values matrix was multiplied by the cover matrix resulting in the weighted trait matrix. Relative species cover was used to generate community-weighted means (CWM) (Garnier et al. 2004) and absolute species cover data used to calculate community-weighted totals (CWT). For the trait by cover matrix, midpoints were multiplied by respective trait values to generate continuous-like data suitable for analysis by two-way ANOVA.

Weighted trait data were partitioned by disease treatment and time since previous fire; and multivariate analysis performed using the PERMANOVA routine in PRIMER (Clarke & Gorley 2008). Interactions between the main effects of “disease status” and “time since previous fire” were tested for in addition to disease effect alone. The Bray-Curtis coefficient was used and results displayed using a Canonical Analysis of Principal Coordinates (CAP). CAP is a constrained ordination method suited to a priori groups that can be used on many dissimilarity measures (Anderson & Willis 2003). CAP uses a Principal Coordinate Analysis (PCO) followed by a Canonical Discriminant Analysis (CDA), which finds an axis through the data cloud that maximizes differences among the predefined groups (Anderson & Willis 2003). Canonical eigenvalues are derived for each axis, with higher values indicating greater separation between groups. For comparative purposes, results were also displayed in an unconstrained PCO. A PCO was chosen as distances are calculated on actual dissimilarities, consistent with the PERMANOVA analysis.

Differences in individual plant traits (CWMs and CWTs) and total species cover were analysed using two-way ANOVAs in S-plus (TIBCO Spotfire 2007). As for the multivariate analysis main effects and interactions were tested for between disease status and time since previous fire. Pair-wise comparisons using the Dunnett method were used to compare disease treatments. Although analysis was run on continuous SLA and LDMC data, results are presented in classes to succinctly demonstrate changes in trait values and cover consistent with the other traits. For completeness, analysis was also performed on SLA and LDMC class data with results consistent with that of the continuous data.

Results

Total species cover changed significantly across the disease gradient ($p = 0.019$), with no interaction with time since previous fire ($p = 0.540$). Total vegetation cover was 60.7% in healthy vegetation, 44.8% in early disease 36.7% in long diseased vegetation. Cover reduction was greatest between long diseased and healthy treatments (40% decline) with the least difference between long diseased vegetation and early disease (13%) (Table 7).

Table 7: Change in total species cover across the disease chronosequence by two-way ANOVA with multiple pair-wise comparisons.

Source	F statistic	p-value	cover change (%)
Disease gradient	4.52	0.02	-
Healthy v long diseased	–	<0.05	-40
Early disease v long diseased	–	>0.05	-13
Healthy v early disease	–	>0.05	-26
Time since previous fire	2.63	0.12	-
Disease*Fire	0.63	0.54	-

Change in community-weighted means (CWM)

Multivariate analysis of CWM trait values revealed an overall significant change following disease infestation (PERMANOVA $p = 0.04$). Traits varied with time since previous burn, however, there was no interaction between the main effects ($p = 0.764$).

There was no interaction between fire and disease status for any individual trait (results not shown). Of the six traits measured, plant height ($p = 0.011$) and SLA ($p = 0.034$) changed significantly following disease infestation (Table 9). Plant height reduced following infestation,

shifting from a dominance of > 5 m species in healthy vegetation to long diseased vegetation dominated by species 1–2 m in height. There was a 44% reduction in relative cover of species > 5 m following disease infestation. Despite the very narrow SLA range, higher trait values dominated long diseased vegetation. Healthy vegetation was dominated by species with SLA values of 3 – 3.9 mm².mg⁻¹, whereas both early disease and long diseased vegetation were dominated by slightly higher values (5 – 5.9 mm².mg⁻¹). Relative cover increased for this trait class by 47% in long diseased vegetation.

Change in community-weighted totals (CWT)

Multivariate analysis of CWT trait values revealed significant differences along the disease chronosequence (PERMANOVA $p = 0.03$). As for CWM, traits also varied with time since previous fire however, there was no interaction between the main effects ($p = 0.878$). Pair-wise tests revealed that the greatest difference was between long diseased and healthy vegetation ($p = 0.024$) with no overall significant difference between the healthy vegetation and early disease ($p = 0.176$). Both the PCO and CAP show a similar separation of groups based on disease status to reflect results from the PERMANOVA test (Figure 17 & 18). However, the distinction is enhanced in the constrained ordination and the first canonical axis discriminated groups based on disease status with an eigenvalue of $\delta^2_1 = 0.69$ (Figure 18). Allocation success was 57% for the three disease groups, greater than the 33% expected by chance alone.

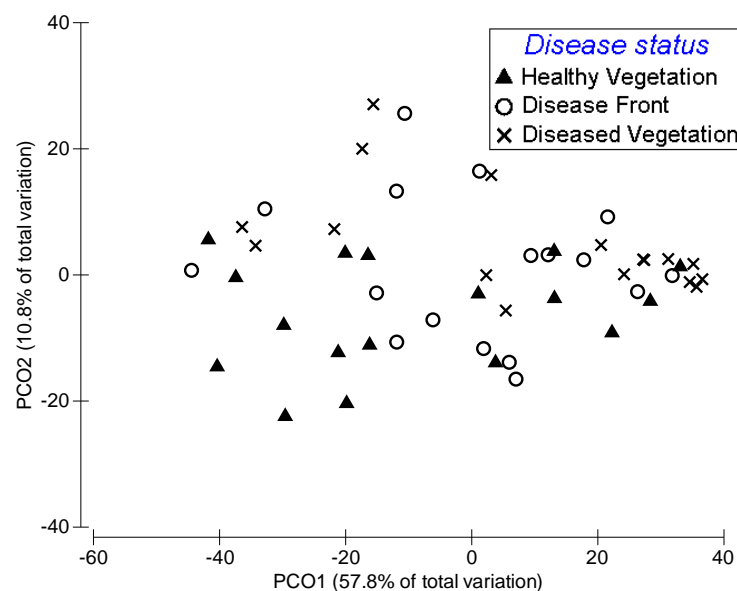


Figure 17: Change in community-weighted total trait values following disease infestation in *Banksia* woodland of south-western Australia ($p=0.03$) - Unconstrained ordination: Principal Coordinate Analysis.

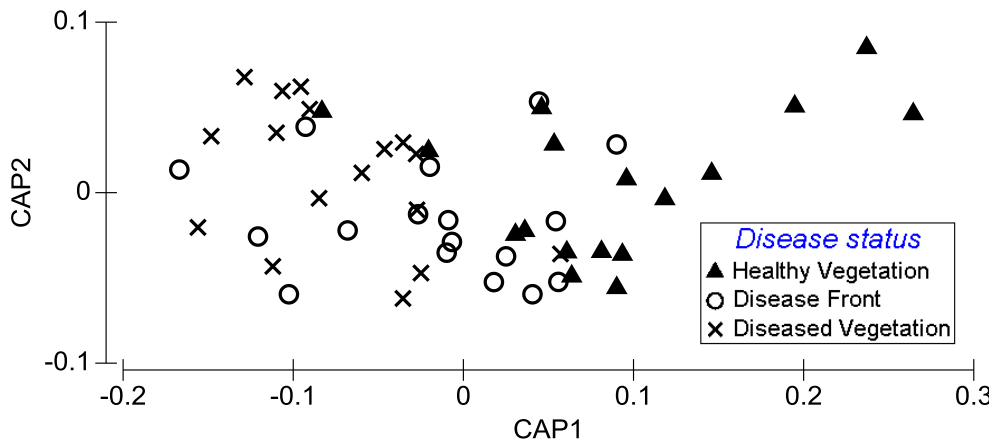


Figure 18: Change in community-weighted total trait values following disease infestation in *Banksia* woodland of south-western Australia ($p=0.03$) - Constrained ordination: Canonical Analysis of Principal coordinates.

All traits were positively correlated with both the first PCO and CAP axes and are displayed in Table 8 due to overcrowding in bi-plots. Healthy sites had high values for all traits.

Table 8: Pearson's correlations with first & second PCO and CAP axes.

Trait	PCO 1	PCO 2	CAP 1	CAP 2
Plant height	-0.907	-0.203	0.555	0.118
Growth form	-0.919	-0.155	0.514	0.094
Specific Leaf Area	-0.922	0.071	0.390	0.090
Leaf dry matter content	-0.935	-0.075	0.458	0.092
Root pattern	-0.931	-0.066	0.484	0.105
Carbohydrate storage	-0.895	-0.169	0.503	0.065

For all individual CWTs, there was no interaction between fire and disease status for any trait (results not shown). In contrast to the CWM analysis, five of the six CWT values changed significantly across the disease chronosequence (Table 9). Of these, two resulted in clear changes in trait class (plant height & growth form) with the remaining 3 traits showing significant changes in species cover with no change in trait class dominance (LDMC; root pattern; carbohydrate storage). In contrast to the CWM analysis, SLA did not change significantly across the disease chronosequence. However, inspection of pair-wise comparisons between long diseased and healthy vegetation revealed a marginally significant difference of $p = 0.052$. The pattern of SLA change matched that of CWM, with a shift in dominance to species with relatively higher SLA values following disease infestation. As for the CWMs, healthy vegetation was dominated by lower SLA values of $3 - 3.9 \text{ mm}^2.\text{mg}^{-1}$ with a shift to higher SLA values at infested sites ($5 - 5.9 \text{ mm}^2.\text{mg}^{-1}$).

Healthy vegetation was dominated by species > 5 m in height with a reduction in absolute cover of 65% following disease infestation ($p = 0.017$). This was coupled with a dominance shift in long diseased vegetation to species 1 – 2 m in height which also reduced in absolute cover by 14%. Associated with plant height, growth form CWT values also decreased significantly following disease infestation ($p = 0.033$), with a shift from woody eudicot dominance (trees) in healthy vegetation to semi-woody eudicots (shrubs) in long diseased vegetation. High leaf dry matter content values ($> 600 \text{ mg.g}^{-1}$) dominated each disease treatment with a significant change in CWT ($p = 0.045$) reflected in a cover reduction of 37% across the chronosequence. Although species with deep tap-roots dominated each disease treatment, there was a significant cover reduction of 43% following pathogen infestation ($p = 0.045$). Species lacking specialised carbohydrate storage organs also remained dominant for each disease treatment, but cover decreased by 15% following disease infestation.

Table 9: Variation in community-weighted means (CWM) and community-weighted totals (CWT) across the disease chronosequence with dominant trait classes printed in bold.

	RELATIVE COVER-ABUNDANCE (community-weighted means)						ABSOLUTE COVER-ABUNDANCE (community-weighted totals)					
	Healthy		Early Disease		Long Diseased		Healthy		Early Disease		Long Diseased	
	% cover	sd	% cover	sd	% cover	sd	% cover	sd	% cover	sd	% cover	sd
Plant height (CWM: $p = 0.01$, $f = 5.29$)												
<0.5m	7.13	5.36	7.74	4.49	13.2	7.29	3.12	1.46	2.59	0.69	3.47	1.28
0.5 to 1m	21.5	15.6	29.0	11.6	25.9	10.8	13.5	17.9	12.4	7.25	8.79	6.91
1 to 2m	27.1	14.5	31.7	18.2	34.4	17.0	17.1	15.5	15.7	17.0	14.7	14.5
2 to 5m	3.35	2.31	2.88	2.07	3.66	2.41	1.71	1.45	0.97	0.48	0.88	0.33
>5m	41.0	18.7	28.7	17.8	22.8	12.5	25.3	20.1	13.2	12.6	8.85	9.66
Growth form (CWM: $p = 0.13$, $f = 2.20$)												
herbaceous monocots	17.2	16.0	18.4	12.5	23.1	8.92	12.7	18.9	8.41	7.39	8.09	6.61
herbaceous eudicots	9.58	14.4	6.19	4.62	8.00	5.80	4.85	9.03	2.06	1.03	1.94	0.90
semi-woody eudicots	31.6	14.7	46.6	17.4	45.8	14.1	17.5	13.5	21.0	16.45	17.7	14.7
woody eudicots	41.6	18.1	28.9	17.8	23.1	12.7	25.6	19.9	13.3	12.62	8.94	9.69
SLA ($\text{mm}^2.\text{mg}^{-1}$) (CWM: $p = 0.04$, $f = 3.52$)												
< 3 or aphyllous	26.0	17.6	24.8	13.8	30.4	15.1	14.7	16.1	10.5	6.65	11.1	9.74
3 to 3.9	36.6	21.2	24.2	16.1	13.9	10.6	24.0	20.8	11.7	12.7	5.03	5.52
4 to 4.9	3.55	7.22	1.40	1.03	1.69	1.74	2.94	9.04	0.53	0.37	0.44	0.35
5 to 5.9	17.4	11.6	28.1	18.6	32.7	16.9	11.0	13.2	14.6	17.3	14.4	14.4
6 to 6.9	4.48	3.61	4.57	4.14	7.31	6.46	2.44	2.36	1.68	1.10	2.09	1.55
>7	12.1	6.57	16.9	13.7	14.0	8.56	5.59	2.33	5.82	4.72	3.59	1.41
LDMC (mg.g^{-1}) (CWM: $p = 0.70$, $f = 0.41$)												
>601	43.9	21.8	48.1	15.8	47.0	17.1	30.1	26.2	22.8	18.1	19.0	18.4
501 to 600	16.6	14.4	12.2	6.65	14.6	13.2	7.47	7.54	6.50	9.02	5.74	8.31
401 to 500	25.8	21.5	21.9	13.4	16.6	8.74	16.6	20.4	9.03	6.25	5.97	5.73
301 to 400	9.22	5.70	11.9	8.21	11.8	5.88	4.68	2.53	4.56	3.64	3.53	2.44
200 to 300	0.61	0.88	0.75	0.95	2.17	3.35	0.24	0.26	0.24	0.26	0.47	0.70
<200 or aphyllous	3.85	3.02	5.24	3.27	7.83	4.30	1.62	0.76	1.74	0.56	1.94	0.30
Root pattern (CWM: $p = 0.38$, $f = 1.0$)												
shallow laterals <1m	18.6	14.8	20.9	11.2	22.6	8.3	13.3	18.8	9.09	6.37	7.79	6.22
shallow single main root 1 to 2m	13.2	8.00	13.0	5.99	19.5	10.2	5.88	2.23	4.76	1.49	5.24	2.81
deep tap root laterals >2m	68.1	16.3	66.2	13.2	57.9	14.5	41.5	25.3	31.0	25.6	23.7	21.7
Carbohydrate storage (CWM: $p = 0.12$, $f = 2.31$)												
No specialised storage organs	58.5	22.3	62.7	17.1	71.1	9.1	31.2	16.5	28.8	24.1	26.5	19.6
Specialised storage organs present	41.5	22.3	37.3	17.1	28.9	9.1	29.5	26.9	16.0	9.71	10.2	7.48

Pathogen activity

P. cinnamomi was isolated from 95% of chronosequence transects. Failure to recover the pathogen from all transects may be a function of inadequate soil sample or low pathogen load. Additionally the site may simply have been free of the pathogen despite the decline of known susceptible species. However, this seems unlikely.

Discussion**Community weighted means (CWM) vs. Community-weighted totals (CWT)**

Infestation by the plant pathogen *P. cinnamomi* has generated shifts in CWTs linked to substantial shifts in total vegetation cover. The traditional community-weighted mean index (CWM) was compared with the modified community-weighted total index (CWT) with important differences found. These differences result from the use of relative versus absolute cover data. In light of the changes identified using CWTs, the failure of some CWM values to shift indicates the importance of absolute cover changes which are concealed when relative cover data are used. This is relevant to the Mass Ratio Hypothesis (Grime 1998) which suggests that ecosystem functions are largely influenced by the traits of the dominant species and are relatively insensitive to the traits of subordinate or transient species. With this in mind, it may be more suitable to identify shifts in absolute data as a reflection of biomass changes (Ricotta 2003). The metric demonstrated, incorporates such changes to reflect net changes in cover/biomass. The CWT metric complements CWMs and the indices should be used comparatively to disentangle trait and total cover changes relevant to ecosystem function.

Community-weighted mean values (except plant height & SLA) failed to change substantially across the disease chronosequence, suggesting a generally resilient system able to maintain functional diversity following disease infestation. However, there was a substantial reduction (40%) in total species cover not detected by the CWM index. In contrast with CWMs, the majority of traits changed when using the CWT index which was driven by the substantial reduction in total species cover. This, in conjunction with reductions in canopy cover, basal area and leaf litter, may indicate altered ecosystem function in *Banksia* woodlands following infestation with *P. cinnamomi* (Bishop et al. 2010, Shearer et al. 2009a). It is recognised that the links between changes in trait values and ecosystem function are deduced. However, it is anticipated that these broad links

translate across to this vegetation type and recognise the need for quantitative assessment and verification.

Shifts in trait values

Specific leaf area is a positive correlate of net assimilation rate and plant relative growth rate (Cornelissen et al. 2003, Reich et al. 1997, Reich et al. 1992). Although the CWT value remains unchanged following disease infestation, a net decrease in site productivity is anticipated. This is due to the substantial decrease in total species cover following infestation coupled with the dominance shift from trees > 5 m in healthy vegetation (predominantly *B. attenuata*) to shrubs following pathogen infestation (Bishop et al. 2010). Furthermore, basal area reduction following infestation (Bishop et al. 2010, Shearer et al. 2009a) and reduction in LDMC values supports reduced site productivity. From this it can be concluded that SLA may not be an appropriate trait for the pathogen-driven changes in this community type.

Although high LDMC values (> 600 mg.g⁻¹) remained dominant across disease treatments, there was a substantial reduction in CWT following infestation. The dominance of high LDMC values suggests litter quality remains unchanged, with quantity substantially reduced. Litter quality and decomposition rates are determined by fibre concentration, C:N and lignin:N ratios, which correlate with both LDMC and SLA (Garnier et al. 2004, Quested et al. 2007). Based on these links, Garnier *et al.* (2004) demonstrated that communities composed of low SLA and leaf nitrogen contents coupled with high LDMC had poor litter quality and slow decomposition rates. *Banksia* woodlands also exhibit these characteristics having low SLA - high LDMC species, indicative of high lignin and fibre contents and poor quality litter (Quested et al. 2007).

As the rate of litter decomposition determines the rate of release of both carbon and nitrogen (Quested et al. 2007, Walker et al. 1999), it is anticipated that nutrient cycling rates will remain constant due to unchanged litter quality. However, although litter quality is the key determinant of decomposition rates (Aerts 1997, Lavelle et al. 1993, Quested et al. 2007), plant driven changes in microbial loads, soil temperature, moisture and oxygen concentrations also influence decomposition rates (Eviner & Chapin III 2003). A strong correlation has been found between LDMC and soil carbon and nitrogen stocks as well as organic matter (Garnier et al. 2004). Unchanged soil nutrients following *P. cinnamomi* infestation has been found elsewhere using

traditional quantitative techniques, in which soil nutrients remained constant across space-for-time disease transects (Shearer et al. 2009a).

Pathogen-initiated changes of soil nutrients are unlikely to occur even over a longer time period due to the highly oligotrophic nature of *Banksia* woodland soils. In resource rich regions, the impact of plant pathogens on plant communities is more likely to influence nutrient dynamics. Limited data exist, but temporary shifts in nutrient cycling rates have been found for Mountain Hemlock stands (*Tsuga mertensiana*) infested with plant pathogen *Phellinus weirii*. Infested stands of Mountain Hemlock had increased nitrogen mineralisation and availability in the short-term, before returning to pre-infestation levels over time (Matson & Boone 1984).

Carbon immobilisation rates are a function of the ability of a species to invest carbon in plant support tissues (xylem & bark) which is not broken down for use in further biosynthesis (Diaz & Cabido 1997). A reduction in carbon immobilisation rates was anticipated due to substantial reductions in basal area following infestation (Bishop et al. 2010). This was reflected in CWT trait values, with reductions in plant height, growth form and carbohydrate storage. These substantial reductions may be linked to a reduced capacity for carbon storage however further investigations are required for confirmation. These traits are positively correlated with the sink strength for carbon, with plant height and growth form closely linked to the ability of a species to store carbon not used in further biosynthesis (Cornelissen et al. 2003, Diaz & Cabido 1997).

Although there may be seasonal increases in fine-scale soil moisture from reduced canopy cover (Kinal 1993, Shearer et al. 2009b), it's anticipated the substantial reduction of deep-rooted species cover would lower potential hydraulic lift. This would have wide ranging implications for the site water balance and plant-plant interactions (Burgess et al. 1998, Caldwell et al. 1998, Dawson 1993). Deep-rooted species remained dominant following disease infestation, however there was a substantial reduction of deep-rooted species cover by approximately 50%. This total cover change is reflected in the CWT but not for CWM. Deep-rooted species hydraulically lift water to redistribute it from the lower soil profile to the drier upper soil profile at night when transpiration has ceased (Caldwell et al. 1998, Richards & Caldwell 1987). The deep-rooted and dominant canopy species *B. attenuata* performs this function by drying out the lower soil profile and lowering the water table over summer following winter rains (Groom 2004, Pate & Bell 1999).

Redistribution of ground water over summer is an important function of deep-rooted species due to the extremely low water holding capacity of *Banksia* woodland soils (Dodd & Bell 1993, Pate & Bell 1999). Hydraulic lift facilitates survival of shallower rooted understorey species (roots < 2 m) by providing sustained moisture over the dry summer months (Caldwell et al. 1998, Groom 2004).

In conjunction with sustaining understorey species through hydraulic lift, deep-rooted species also moderate water table changes from seasonal rainfall (Pate & Bell 1999). Each quadrat was augered to a depth of 2 m to confirm soil type and identify water table depth, but the water table was not reached even on long diseased sites. Although a water table rise is expected from the reduction of deep-rooted species (Pate & Bell 1999), it's anticipated that the rise will be insufficient for the majority of understorey species to access. As a consequence, implications arise for species that rely on *B. attenuata* hydraulic lift for moisture over the dry summer period. However, the persistence of deeper rooted understorey species such as *T. parviceps*, *M. thymoides* & *A. cuneatus* may partially compensate for the decline of deep-rooted species (Bishop et al. 2010).

Additional impact on site water balance may result from the significant reduction of leaf litter on long diseased sites (Bishop et al. 2010). Litter reduction may lead to increased evapotranspiration on diseased sites which would enhance soil moisture loss from the upper soil profile (Evans & Young 1970). Additionally, soil temperature has been found to increase on diseased sites in conjunction with reductions in canopy cover and leaf litter to further alter site micro conditions (Kinal 1993).

The reduction in litter cover may have long-term effects on other aspects of the soil environment, beyond site hydrology. Reduced litter cover has implications for soil temperature and moisture levels and is a key determinant of antagonistic microbe loads (Nesbitt et al. 1979a). The positive correlation between soil organic matter and antagonistic microbial load is well documented, with sites conducive to pathogen activity having comparatively lower levels of both organic matter and antagonistic microbes (Broadbent & Baker 1974, Malajczuk 1983, Tippett & Malajczuk 1979).

Notes on using community-weighted totals (CWT)

Community-weighted totals should be used to complement traditional CWMs, to disentangle trait and total cover changes. The proposed CWT index is best suited to continuous data, although interval data can also be used to generate interpretable results. Additionally, many quantitative measures are re-coded on an ordinal scale and the CWTs in these cases must be interpreted carefully with due consideration of the scale of the measurement. Such ranked ordinal data can only provide an indication of directional change, requiring further inquiry and quantitative assessment. CWTs using nominal data do not have any ecological meaning.

Conclusion

This study demonstrates the ability of an introduced plant pathogen to alter community-level trait composition, in addition to substantial shifts in vegetation structure and composition (Bishop et al. 2010, Shearer et al. 2009a). Altered community-level plant traits may indicate pathogen-driven changes in productivity, carbon storage, and hydrology over an ecologically brief time period. However, these links are deduced requiring further inquiry and clarification using traditional techniques. Investigations targeted at specific functions are now required to obtain a comprehensive and quantitative description of pathogen-induced functional change. Although the pathogen will persist in the landscape, maintenance of species diversity may allow some regeneration of key species (and hence function) through persistence of susceptible species tolerant or more resistant to the pathogen (e.g. Stukely & Crane 1994, Stukely et al. 2007). However, pathogen-infested *Banksia* woodlands are unlikely to regain the functional properties characteristic of uninfested vegetation due to the substantial reduction in species cover and associated structural and compositional changes.

Acknowledgements

Thanks are extended to the anonymous referees for providing comments on earlier versions of the manuscript. This paper is a component of a PhD project of the senior author and was supported by a University of Queensland APAI scholarship and Australian Research Council Linkage Project Grant LP0560809, "*Towards a landscape conservation culture – broadening the spatio-temporal scope of ecological studies to anticipate change in Australian forested ecosystems*". Field work was supported by the Western Australian Department of Environment and Conservation. All experiments and analyses in this manuscript comply with Australian federal and Western Australian state laws and codes of practice.

CHAPTER FIVE: CHANGE IN ABSOLUTE COVER MATTERS!

Abstract

Incorporating species cover or abundance into trait-based classifications is a parsimonious method to test hypotheses regarding effects on ecosystem function across environmental and disturbance gradients. The community-weighted mean trait index (CWM) is commonly used to identify shifts in trait means, weighted by the relative cover or abundance of each species. However, this method doesn't incorporate changes in total species cover, which has important implications for ecosystem function. Here a modification of the traditional CWM index is applied – the Community-weighted Total trait index (CWT) – that incorporates changes in absolute cover or abundance. This index provides a more appropriate and ecologically intuitive measure to identify shifts in functional traits that may indicate altered ecosystem function. The outcome of applying CWT and CWM is compared using 6 plants traits across a gradient of pathogen infestation. Analysis identified changes across the disease gradient in CWT values but not for traditional CWMs. This demonstrates that the incorporation of absolute cover alters the outcome of trait-based analysis with important implications for data interpretation regarding shifts in ecosystem function.

Keywords: community-weighted means; ecosystem function; mass ratio hypothesis; plant disease; vegetation change

Introduction

Trait-based classifications are increasingly being used to link changes in characteristic plant traits, such as specific leaf area, leaf dry matter content or plant height, to shifts in particular ecosystem process (Díaz et al. 1999, Garnier et al. 2004, Suding et al. 2008, Swenson & Weiser 2010). The range and distribution of traits across species reflects the functional diversity of the community, and there is substantial evidence that the combination and abundance of functional traits influences ecosystem functioning (Diaz & Cabido 2001, Grime 1998, Loreau et al. 2001, Petchey & Gaston 2002). This represents the Mass Ratio Hypothesis, which suggests that ecosystem functions are largely influenced by the traits of the dominant species and are relatively insensitive to the traits of subordinate or transient species (Grime 1998). Typically, this is quantitatively represented by the community-weighted mean index (CWM) which reflects the average trait value of a species in a community and can be used to test hypotheses regarding shifts in ecosystem function (Garnier et al. 2004, Quetier et al. 2007, Suding et al. 2008). However, the use of CWM

values conceals absolute changes in species cover which are intrinsically linked to ecosystem function through the Mass Ratio Hypothesis.

The CWM index uses relative cover, abundance or biomass data (hereafter referred to as ‘cover’ for convenience) to generate aggregated mean values of selected traits (Garnier et al. 2004). Relative cover data is traditionally used to derive various indices of biological diversity (Magurran 2004, Ricotta 2003). However, in regards to ecosystem function, it may be more appropriate to identify shifts in absolute data as a reflection of biomass changes (Ricotta 2003). A modified index is applied, the community-weighted total (CWT), which incorporates changes in total cover to better reflect changes in quantitative plant traits linked to potential shifts in ecosystem function. This index has been formulated previously but has not, to our knowledge, been used to explore hypotheses regarding trait changes (see Suding et al. 2008 - equation 3).

Derivation of the index

To incorporate changes in total species cover to measure trait shifts, absolute cover data was used to generate community-weighted totals (CWTs). Calculation of CWTs (equation 1) uses the same logic as for CWMs (equation 2), with aggregate values for each functional trait calculated as follows:

Equation One

$$CWT_i = \sum_{j=1}^S C_j T_{ij}$$

Equation Two

$$CWM_i = \sum_{j=1}^S R_j T_{ij}$$

CWT_i is the community-weighted total value of trait i , and C_j and T_{ij} are the absolute cover and functional trait value of species j ($j = 1, 2, \dots, S$), respectively. This is similar for CWMs, with relative cover (R_j) replacing absolute cover (C_j). Values of the CWTs are thus equal to the CWMs multiplied by total cover, so have the property of producing identical patterns of change if total cover remains constant across treatments. The value and interpretation of the CWT index is illustrated below using an example.

Testing the index

The CWM and CWT indexes were used to identify changes in trait values following disease infestation in species-diverse *Banksia* woodlands of the Southwest Australia Floristic Region (SWAFR). These woodlands are inherently vulnerable to *Phytophthora cinnamomi*, occurring in a zone of warm, moist soil conditions ideal for pathogen sporulation and spread (Shearer & Tippett 1989). In addition to ideal abiotic conditions, there is a predominance of pathogen-susceptible species in the region. Approximately 40% of SWAFR flora are listed as susceptible to *P. cinnamomi*, with 14% listed as highly susceptible (> 80% plants of a species killed) (Shearer et al. 2004a). The combination of abundant susceptible species together with optimal soil and climatic conditions has resulted in extensive pathogen impact. The aim was to identify changes in plant trait values with proposed links to key ecosystem functions, including hydraulic lift, productivity and carbon immobilisation. Changes in functional traits were examined across a chronosequence of disease infestation.

Transformation of trait data was not required as class data was analysed and each trait had a similar number of classes. Analysis of CWMs, the standard method of assessing such change, showed that some trait values did not change following disease despite a substantial and statistically significant decline in total species cover (40%, $p = 0.019$; Table 10). This demonstrates that the pathogen reduced total cover without any selective removal of particular functional traits. The substantial reduction in total species cover intuitively suggests a potential impact on ecosystem function in line with the Mass Ratio Hypothesis (Grime 1998). As the CWM index requires cover to be rescaled to 100%, gross changes in species cover are not reflected in the results.

Of the six traits measured, there was no change in the CWM for growth form, leaf dry matter content (LDMC) and root pattern ($p > 0.05$) following disease infestation, indicating little change in relative species cover. In contrast, there was a significant change in the CWTs for each of these traits ($p < 0.05$) due to substantial reductions in total species cover following disease. These changes are effectively concealed when using relative cover data, i.e. when using CWMs. The remaining three traits (plant height, specific leaf area and carbohydrate storage) changed significantly for both CWM and CWT ($p < 0.05$). Interestingly, specific leaf area changed

significantly for CWM, but for CWT was only marginally significant, however potentially ecologically important.

Table 10: Changes in relative (community-weighted means: CWM) and absolute (community-weighted totals: CWT) trait values across the disease chronosequence in species-rich *Banksia* woodland, southwest Australia. Changes in CWMs and CWTs were measured for six traits at 17 sites, and analysed using analysis of variance; full details of the study are presented elsewhere (Bishop et al. 2011).

	Community-weighted means <i>p</i> -values & % change	Community-weighted totals <i>p</i> -values & % change
Plant height	0.011 (-15.1%)	0.017 (-47.4%)
Growth form	0.129 (-9.63%)	0.033 (-43.2%)
Specific Leaf Area	0.042 (+9.64%)	0.076 (-33.0%)
Leaf dry matter content	0.670 (-3.52%)	0.040 (+40.1%)
Root pattern	0.380 (-5.68%)	0.045 (-40.4%)
Carbohydrate storage	0.117 (-8.88%)	0.001 (-48.1%)

This example (Table 10) demonstrates how the CWT index detected changes in trait values driven by absolute vegetation cover, which were not detected when using the traditional CWM index. The associated shifts in CWT provide a preliminary indication of altered ecosystem functions in species-diverse *Banksia* woodlands following disease infestation. Such shifts indicate potential reductions in productivity, reduced capacity for carbon immobilisation and altered site water balance through reduced hydraulic lift (Bishop et al. 2011). However, accurate quantification of these changes requires direct assessment of ecosystem functions using traditional quantitative techniques.

The CWT index can provide an appropriate indication of potential functional change in ecosystems experiencing a shift in total cover or biomass. However, CWTs and CWMs should be used in a comparative and exploratory capacity to identify the effect of using relative and absolute cover data. Community-weighted means reflect aggregated trait means using relative cover data for the dominant species (Garnier et al. 2004). The CWM index cannot detect shifts if trait cover changes are proportional across a gradient of change. The CWT index also reflects aggregated trait means but in contrast to CWM, it can detect absolute trait changes across a gradient through using absolute cover data. For this reason, CWTs are inherently better at indicating potential changes in ecosystem functions in the presence of absolute cover or biomass shifts.

The use of absolute cover data in aggregated trait analysis is limited to particular data types. Often, functional traits are quantified in specific, continuous units (e.g. leaf dry matter content may be measured in mg.g⁻¹) and such data produces CWTs with corresponding and easily interpretable units. Although this index is best suited to quantitative data, interval data could also be used to generate interpretable results. Additionally, many quantitative measures are re-coded on an ordinal scale and the CWTs in these cases must be interpreted carefully, with due consideration of the scale of the measurement. Such ranked ordinal data can only provide an indication of directional change, requiring further inquiry and quantitative assessment. CWTs using nominal data do not have any ecological meaning.

Conclusion

The ecological significance of shifts in absolute cover or abundance is widely recognised in the literature (Chapin 2003, Ricotta 2003, Suding et al. 2008) and application of the CWT index captures this cover change in relation to plant functional traits shifts. Constraints can be minimised by suitable data selection and perceptive interpretation. The CWT index incorporates ecologically important changes in total vegetation cover and can be used to assess climatic or disturbance-driven trait changes in plant communities. Findings from trait-based analysis may drive more detailed inquiry into specific aspects of ecosystem function using traditional quantitative laboratory techniques.

**CHAPTER SIX: DOES AN INTRODUCED
FOREST PATHOGEN ALTER FUNCTIONAL
DIVERSITY?**

Abstract

Question: Does the introduced plant pathogen *Phytophthora cinnamomi* change *Banksia* woodland functional diversity? To what extent do *Banksia attenuata* woodlands exhibit functional redundancy as characterised by the presence of functionally similar species?

Location: High rainfall zone of the Southwest Australian Floristic Region (SWAFR).

Methods: Rao's index of functional diversity (RIFD) was used to document shifts in functional diversity from the introduced forest pathogen *Phytophthora cinnamomi*. Functional diversity was measured along 17 disease chronosequences of varying fire histories in species-diverse *Banksia* woodlands of the SWAFR. Each chronosequence represents three disease stages: (1) healthy vegetation with no disease expression; (2) early disease onset; and (3) long diseased vegetation infested for at least 15 years. Floristic surveys were carried out across sites with cover-abundance scored for the dominant species. Plant traits relating to key ecosystem functions and regeneration were measured to capture shifts in functional diversity. Rao's index of functional diversity was calculated for each quadrat and shifts explored both along the disease chronosequence and between fire ages. An interaction between disease and fire was tested for. Functional redundancy was examined through determining if a relationship existed between functional diversity and species richness & diversity.

Results: There was no significant change in RIFD (trait variance), either along the disease chronosequences, or across fire histories. Despite a substantial reduction in species cover by the pathogen, *P. cinnamomi* did not affect trait variance due to the persistence of dominant species and the maintenance of species richness. There was no relationship between RIFD and species richness.

Conclusions: This study shows that despite substantial pathogen-induced shifts in species cover and functional trait composition, functional diversity has remained constant. Maintenance of functional diversity indicates that *P. cinnamomi* is not selecting out particular plant traits, and hence there is no evidence for trait convergence or divergence following disease infestation. However, there may be a lag in functional diversity shifts due a combination of an inherently slow system (linked to relatively slow growth rates and nutrient cycling) and potential interactions between disease and climate change. Additionally, as there was no relationship between RIFD and species richness, this indicates that functional redundancy is low or absent in these *Banksia* woodlands. This supports the notion that taxonomic diversity is a poor indicator of functional

diversity. These findings demonstrate that multiple diversity indices in conjunction with species & plant trait composition data are necessary to comprehensively describe impact of an introduced forest pathogen.

Keywords: disease; disturbance; fire; functional traits; *Phytophthora cinnamomi*; Rao's index of functional diversity.

Nomenclature: Paczkowska & Chapman(2000)

Abbreviations: CWM = Community-Weighted Mean; LDMC = Leaf Dry Matter Content; RIFD = Rao's index of functional diversity; SLA = Specific Leaf Area; SWAFR = Southwest Australian Floristic Region.

Introduction

Quantifying functional diversity provides insight into trait convergence or divergence in response to disturbance or environmental gradients (de Bello et al. 2009). Functional diversity has been defined as the extent of functional differences among species in a community and incorporates functional traits of individual species (Petchey & Gaston 2002, Tilman 2001). Recent interest in functional diversity has generated several alternative measures, with the choice of measure dependent on the questions being examined (Petchey & Gaston 2006, Reiss et al. 2009). Trait convergence or divergence is one aspect of functional diversity that measures shifts in trait variances generated by changes in species abundance and/or composition. Of increasing interest are shifts in plant traits driven by changes in species composition and abundance both within and between communities, akin to Whittaker's (1975) classical concepts of alpha and beta species diversity (de Bello et al. 2009, Ricotta 2005). This can also be translated across disturbance or environmental gradients by applying Rao's index of functional diversity (RIFD) (Lepš et al. 2006). The index generates abundance-weighted trait variances to indicate convergence or divergence along a gradient. Rao's index of functional diversity estimates the extent of trait complementarities among species and is a generalisation of Simpson's diversity index (Lepš et al. 2006). The dissimilarity between species is weighted by species relative abundance and determines the probability that two species selected from a community at random are functionally dissimilar (Lepš et al. 2006, Rao 1982, Ricotta 2005).

Relationships between functional and traditional diversity measures such as species richness can be evaluated to determine functional redundancy (de Bello et al. 2006, de Bello et al. 2009,

Pavoine & Doledec 2005). Functional redundancy is presence of taxonomically distinct species that exhibit similar ecological functions (Walker et al. 1999). Systems with high levels of functional redundancy have increased resilience to disturbance due to the ability to substitute functionally similar species (Walker 1995). The amount of functional redundancy within a system will determine the direction and strength of the relationship between taxonomic and functional diversity (Lawton & Brown 1993, Micheli & Halpern 2005, Naeem 1998, Walker 1995). For example, de Bello *et al.* (2006) found functional diversity to remain unchanged despite an increase in species richness along both grazing and moisture gradients. This indicates the presence of functionally redundant species in the system and also demonstrates that different components of diversity can vary independently of each other (de Bello et al. 2006, Magurran 2004). An example of a system with low functional redundancy was described by Micheli & Halpern (2005). The authors identified a strong positive relationship between fish species diversity and functional diversity. In this example, reduced species diversity as a result of selective removal of fish by angling, had the effect of removing entire functional groups. This led to reduced functional diversity as a result of the assemblage having inherently low functional redundancy.

This study examines if the introduced forest pathogen, *Phytophthora cinnamomi*, generates shifts in trait variance indicative of functional convergence (homogenisation) or divergence in species-diverse *Banksia* woodlands in the Southwest Australian Floristic Region (SWAFR). Pathogen-induced shifts in trait means has previously been explored (Bishop et al. 2011), and application of RIFD will complement this study. While the pathogen generated substantial shifts in trait dominance, no insight was provided into trait variances and whether disturbance is homogenising functional diversity (Bishop et al. 2011). Rao's index of functional diversity will be used to determine if disease can generate trait convergence or divergence along space-for-time transects (de Bello et al. 2006, Petchey & Gaston 2002). Additionally, to determine functional redundancy in the system the relationships between functional diversity and species richness/diversity are explored.

Changes in functional diversity patterns driven by forest pathogens have yet to be explored, with pathogen literature predominantly focused on changes in species abundance and richness (e.g. McDougall et al. 2002, Shearer & Dillon 1995). More conspicuous forms of disturbance dominate

functional diversity literature, with no studies examining forest pathogen impact (Brown & Allen-Diaz 2009, Burdon et al. 2006, Castello et al. 1995). Specific questions to be explored are:

- Does the introduced pathogen *Phytophthora cinnamomi* alter functional diversity of species-diverse *Banksia* woodlands?
- Do *Banksia attenuata* woodlands exhibit functional redundancy as characterised by the presence of functionally similar species.

Methods

Study area

The study area is located in the high rainfall zone of the SWAFR ca. 400 km SSE of Perth, Western Australia (34° 49'S, 117° 9' E). The region is climatically buffered by the Indian Ocean and experiences a mediterranean-type climate with warm, dry summers and mild wet winters with an average annual rainfall of 1000 mm. The study site and surrounds is topographically subdued but contains high levels of species diversity and endemism more typically associated with mountainous regions (Hopper & Gioia 2004, Wardell-Johnson & Horwitz 2000). Such diversity and endemism has led the region to be recognised as an international biodiversity hotspot (Myers et al. 2000). The SWAFR has approximately 7500 native plant species including 3616 endemic taxa (Hopper & Gioia 2004). Dominant over-storey vegetation includes eucalypt forests and woodlands in pure stands or combinations of karri (*Eucalyptus diversicolor*, Myrtaceae), jarrah (*E. marginata*, Myrtaceae) and marri (*Corymbia calophylla*, Myrtaceae). *Banksia attenuata* woodlands (Proteaceae) and Sheoak woodlands (*Allocasuarina fraseriana*, Casuarinaceae) occur in low-lying areas adjacent to sedge lands and swamps or in upland saddles.

The various vegetation types are compositionally and structurally diverse, and typically track changes in soil type (Wardell-Johnson & Williams 1996). Conspicuous edaphic variation is associated with diverse vegetation types uncharacteristic for a topographically subdued landscape (Hopper 2009, Wardell-Johnson & Horwitz 2000). Poor dispersal capabilities dominate SWAFR flora, in response to a highly heterogeneous environment that favours species able to efficiently exploit scarce resources within their localised patch (Hopper 2009).

Site selection

Surveys were undertaken in 17 *Banksia attenuata* woodland sites on deep oligotrophic sands, with replication across the study area in analogous vegetation complexes (equivalent soil type, vegetation type and position within the landscape) (Havel & Mattiske 2002).

Disease centres were randomly located across the landscape due to the patchy nature of *P. cinnamomi* infestation and disease spread. Sites had similar long-term fire histories, and time since previous fire ranged from 8 – 15 years. Changes were assessed along space-for-time transects in a randomized block design with disease centres identified across the landscape. Each disease centre had one chronosequence (block) consisting of three 20 x 20 m quadrats: (H) healthy vegetation with no disease expression; (F) early stage disease onset with susceptible species displaying leaf chlorosis in combination with both dead and healthy individuals of susceptible species (e.g. *Banksia attenuata*); and (D) long diseased vegetation infested for approximately 15 to 20 years, characterised by long dead susceptible species.

Spatial autocorrelation was minimised by placement of transects in separate (but homogenous) vegetation complex polygons across the study area. Effectively, transects were separated by different vegetation complexes across the landscape and were at least 500 m apart. Each transect was positioned at least 20 m from road verges to minimise other edge effects.

The study site is topographically and edaphically similar to coastal sand-plains immediately to the south where rates of disease spread are approximately 1.5 m/year (Grant & Barrett 2003). This rate was used to guide placement of quadrats in long diseased vegetation relative to quadrats in early diseased vegetation. Quadrats in healthy vegetation were placed approximately 50 m from quadrats in vegetation expressing early disease symptoms. All quadrats were augered to a depth of 2 m to confirm soil type between sites and along chronosequence transects.

Data collection

A species list was compiled with species scored using the Braun-Blanquet (1932) cover-abundance scale. Adult plants of all growth forms were included in the survey. The dominant species, for which trait data could be obtained (via both desktop and laboratory measurement), were selected for analysis. The dominant 48 species were identified across all quadrats in healthy vegetation and

trait measurements taken on uninfected specimens. Ten plant traits linked to key ecosystem processes and associated with regeneration were selected for analysis (Table 11). Specific leaf area and leaf dry matter content were collected following Cornelissen *et al.* (2003) and data for the remaining traits collected by desktop study from region specific databases (Western Australian Herbarium 2010, Wheeler *et al.* 2002). Data for these traits were organised into relevant trait classes using Diaz and Cabido (1997) and Walker and Langridge (2002) as guidance.

Table 11: Plant traits used in calculation of Rao's index of functional diversity.

Trait	Categories
Plant height	<0.5; 0.5-1; 1-2; 2-5, 5+ (metres)
Life form	herbaceous monocots; herbaceous eudicots; semi-woody eudicots; woody eudicots with trunk and bark
Specific leaf area (SLA)	< 3 or aphyllous; 3 to 3.9; 4 to 4.9; 5 to 5.9; 6 to 6.9; >7 (mm ² .mg ⁻¹)
Leaf dry matter content (LDMC)	<200 or aphyllous; 200 to 300; 301 to 400; 401 to 500; 501 to 600; <601 (mg.g ⁻¹)
Root type	no obvious main root, shallow laterals; shallow single main root, shallow laterals; deep tap root with or without laterals
Carbohydrate storage	presence/absence of specialised storage organs
Growth form	herbaceous monocot, herbaceous eudicot, semi-woody eudicot or wood eudicot with trunk and bark
Mycorrhizal association type	non-mycorrhizal, ectomycorrhizal; ericoid; vesicular-arbuscular mycorrhiza
Seed dispersal mode	unassisted, myrmecochory, Internal or external animal transport or anemochory
Seed storage	bradysporous or geosporous

Presence of *P. cinnamomi* was confirmed by laboratory analysis using standard techniques (Greenhalgh 1978, Marks & Kassaby 1974). Six soil and root samples were taken from susceptible species within each quadrat. Each sample was flooded to a 1:4 soil/water ratio upon which approximately ten *Eucalyptus sieberi* cotyledons were floated. Samples were stored at 22 °C for optimal pathogen growth and checked on day five for evidence of cotyledon colour change indicative of *P. cinnamomi* presence. Potentially infected cotyledons were plated onto *Phytophthora*-selective agar and stored for three days at 22 °C. Plates were then inspected for diagnostic hyphal swellings and mycelial growth patterns indicative of *P. cinnamomi* presence.

Data analysis

Three diversity indices were calculated across the disease gradient: Rao's index of functional diversity (RIFD) (Lepš *et al.* 2006); species richness (S); and Simpson's diversity index (SD).

Rao's index of functional diversity was calculated for individual traits using the excel macro available at <http://botanika.bf.jcu.cz/suspa/FunctDiv.php>. (see Lepš et al. 2006). This index of functional diversity was suited to the study as it estimates changes in trait variance to indicate shifts in trait ranges along a gradient of change. Rao trait values were analysed collectively using a crossed PERMANOVA design in PRIMER/PERMANOVA v6 (Clarke & Gorley 2008). Data transformation was not required as analysis was on class data and each trait had a similar number of classes. Euclidean distance was used to test firstly for an interaction between terms ("disease status" and "time since previous fire") and then each term tested individually.

Additional to the multivariate analysis, two-way ANOVAs were used on each individual trait to identify changes in RIFD values. As for the multivariate analysis, an interaction between disease and fire was tested for in addition to each term alone. Two-way ANOVAs were also performed on species richness and Simpson's diversity index along the disease chronosequence using the same design.

The RELATE routine in PRIMER was used to test for a relationship between RIFD (all 10 traits) and both species richness and Simpson's diversity index. This routine generates rank correlations and compares this with results of randomly permuted samples (Clarke & Gorley 2008). Two correlation routines were run. Firstly, the species richness matrix was compared with the RIFD trait matrix. This was followed by comparison of the Simpson's diversity index matrix with the RIFD trait matrix. The RELATE routine generates the sample statistic *Rho* in addition to a significance level.

Results

There was no significant difference in the compound RIFD (all traits) along the disease gradient (Table 12). There was also no difference in the RIFD for time since previous fire and no interaction between the two terms. Both species richness and Simpson's diversity index did not shift significantly across the disease chronosequence.

Table 12: Results of 2-way ANOVA for species richness and Simpson's diversity index; and PERMANOVA for Rao's index of functional diversity using all traits.

	DF	Species richness (S)		Simpson's diversity index (SD)		RIFD - all traits	
		F	<i>p</i>	F	<i>p</i>	pseudo F	<i>P</i>
Disease status	2	1.70	0.20	1.46	0.25	0.95	0.42
Time since previous fire	1	0.50	0.49	1.75	0.20	0.31	0.87
Disease status *	2	0.11	0.90	0.170	0.85	0.49	0.83
Time since previous fire							

Of the 10 traits, only the RIFD for LDMC changed significantly, with a mean increase from 0.17 to 0.23 following disease infestation ($p < 0.001$; Table 13).

Table 13: Change in Rao's index of functional diversity across the disease chronosequence and time since previous fire with *p*-values.

Trait	Disease	Time since previous fire	Disease x Previous fire
Life form	0.71	0.53	0.34
Plant height	0.33	0.74	0.76
Carbon immobilisation	0.46	0.90	0.84
Root depth	0.15	0.79	0.89
Mycorrhizal association type	0.89	0.43	0.54
Seed dispersal mode	0.70	0.96	0.66
Carbohydrate storage	0.75	0.80	0.35
Specific Leaf Area (SLA)	0.61	0.86	0.73
Leaf Dry Matter Content (LDMC)	<0.001	0.06	0.16
Seed storage	0.43	0.18	0.86

Using all 10 traits, the RELATE routine revealed no relationship between RIFD and species richness ($p = 0.943$). There was a strong correlation between RIFD and Simpson's diversity index ($p = 0.001$) (Figure 19).

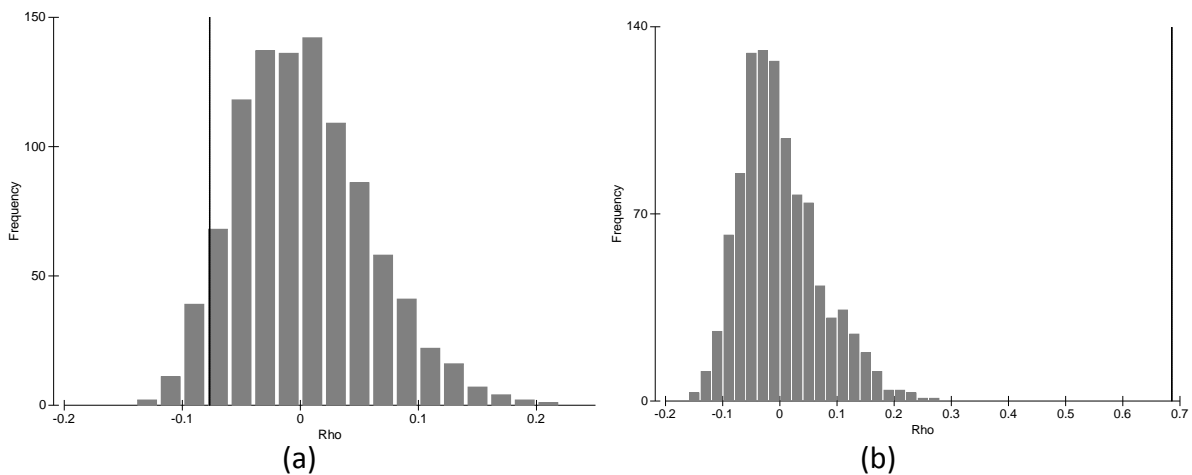


Figure 19: Relationship between Rao's index of functional diversity (10 traits) and (a) species richness and (b) Simpson's diversity index.

Discussion

Following pathogen infestation, there was no observable shift in Rao's index of functional diversity in species-diverse *Banksia* woodlands of the SWAFR. This is reflected through no discernible shift in trait variance and indicates the pathogen is not removing or selecting for particular plant traits. This apparent stability of functional diversity is linked to the persistence of susceptible species and hence species richness following pathogen infestation (Bishop et al. 2010). Susceptible species, most notably the dominant canopy species *Banksia attenuata*, had substantial reductions in cover on diseased sites but was still present following infestation. Despite the potential for some recovery, cover-abundances are unlikely to return to pre-infestation levels due to a reduced seed source, altered site conditions and pathogen persistence at the landscape level (Bishop et al. 2010).

When viewed in isolation, the persistence of functional diversity may indicate resilience of ecosystem function. However, maintenance of functional diversity through application of RIFD doesn't take into account the changes in total species cover. Such shifts in total species cover and hence biomass, are linked to altered ecosystem function through Grime's (1998) Mass Ratio Hypothesis. Grime's (1998) hypothesis suggests changes in ecosystem function is linked to shifts in traits associated with species dominant by biomass. Although RIFD did not change significantly, previous work has found substantial shifts in trait abundances linked to substantial reductions in total vegetation cover (Bishop et al. 2011). Although functional diversity shifts were not observed, previously found shifts in trait abundances may indicate change in ecosystem function. These links between changes in trait values and ecosystem function are deduced. However, it is anticipated

that these broad links translate across to this vegetation type and acknowledge the need for quantitative verification.

There was no relationship between species richness and RIFD, consistent with the notion that taxonomic diversity is a poor indicator of functional diversity (de Bello et al. 2006). This additionally indicates that functional redundancy is absent or low in the ecosystem. This suggests that taxonomically distinct species exhibit no substantial overlap in regards to their ecological function. Where functional redundancy is low, this can indicate an inherently reduced resilience to disturbance comparative to an ecosystem that has species with overlapping ecological functions (i.e. high functional redundancy). Low functional redundancy results in an inability to substitute functionally similar species if species are removed or reduced from disturbance.

There was a substantial correlation between species and functional diversity; not unexpected, as RIFD is a generalisation of Simpson's diversity index. The correlation shows that species diversity does capture functional diversity. However, the relationship is more meaningful if weakly or not correlated at all. This was found by de Bellow *et al.* (2006) where a weak correlation was found between RIFD and species diversity indicating species diversity to be a poor indicator of functional diversity. This in conjunction with the findings regarding species richness further highlights the importance of utilising a range of diversity indices to describe community-level pathogen impact.

Petchey & Gaston (2006) caution that non-significant results need to be carefully considered before being disregarded. Although *P. cinnamomi* did not generate a significant shift in functional diversity, this may not necessarily be the case if a different set of traits were chosen. Results depend on trait choice and although a range of traits of ecological importance and relevance were measured inclusion of further fine scale physiological traits may potentially alter the results. However, due to the overwhelming non-significant results of nine of the 10 selected traits, the results suggest little or no pathogen impact on functional diversity.

Time since initial disease infestation may influence future functional diversity. Over time, long term infestation from the continued presence of *Phytophthora cinnamomi* and its interactions with both fire and climate change may alter functional diversity. Although no interaction between disease and fire was found, other pervasive ecosystem changes such as climate change may

generate interactions which could be identified through re-sample of sites over time. The quadrats used in this study have been permanently marked providing the opportunity for re-sampling to identify long-term assemblage changes.

In conjunction with disturbance interactions, functional diversity may be further altered by re-colonisation of pathogen infested sites. Although the pathogen will persist in the landscape, there is potential for some site re-colonisation by both pathogen resistant species and susceptible species (Rockel et al. 1982, Weste 2003). Furthermore, there may be a lag in functional diversity shifts due an inherently slow system linked primarily to low rates of nutrient cycling that creates conditions predominantly suitable for slow growing, long lived plant species (Hopper 2009, Mucina & Wardell-Johnson 2011). Long-term studies are required in infertile landscapes as changes are anticipated to lag in comparison to more fertile “faster” systems. The combination of disturbance interactions and altered site floristics through species re-colonisation may alter functional diversity in the future. In the short-term at least, there has been no detectable change in functional diversity from *P. cinnamomi* infestation, through use of RFID.

This study has shown that the introduction of forest pathogen *P. cinnamomi* has not generated an observable shift in *Banksia* woodland functional diversity. The findings further demonstrate that a range of diversity indices should be utilised when measuring change across a gradient to ensure a comprehensive description of change is obtained (de Bello et al. 2006). Although there was no shift in trait variance, previous investigations have found substantial shifts in beta diversity and functional trait composition (Bishop et al. 2010, Bishop et al. 2011). The combination of these diversity indices in association with other stand variables provides a novel depiction of the impact of an introduced plant pathogen in species-diverse *Banksia* woodlands.

**CHAPTER SEVEN: INTRODUCED FOREST
PATHOGEN RESULTS IN HYBRID
ECOSYSTEM IN SPECIES-DIVERSE
WOODLANDS**

Abstract

Novel and hybrid ecosystems are becoming increasingly evident through rapid transformation of vegetation over ecologically brief periods of time. Although frequently reported in the literature, empirical measurement is dominated by non-manipulative approaches with potentially ambiguous interpretation. I propose that Holling's (1973) resilience theory can be used as criteria to determine if a novel, hybrid or resilient (unchanged) ecosystem results following disturbance. Resilience is the ability of a system to absorb a disturbance by maintaining structure, function and composition. If these components are altered by disturbance a regime shift has occurred to result in either a novel or hybrid ecosystem. Where the altered ecosystem lies on the novel-hybrid continuum will depend on the extent of change comparable to the pre-disturbance state.

Using an introduced forest pathogen as a case study, I demonstrate the quantitative application of resilience theory to describe the type of ecosystem that results following disturbance. *Banksia* woodlands infested with *Phytophthora cinnamomi* underwent a regime shift to identify as a hybrid ecosystem. An irreversible regime shift has occurred with substantial shifts in species abundance, vegetation structure and functional trait composition. However, the maintenance of species richness, species diversity and functional diversity suggests the system does not identify as novel, as some pre-disturbance characteristics were preserved. Additionally, weed species did not colonise after pathogen infestation, despite substantial reductions in canopy cover and leaf litter. As the system is not novel, this implies a degree of resilience to the pathogen. Despite substantial changes over an ecologically brief period of time, the resultant hybrid ecosystem is equally speciose though structurally and functionally altered.

Although susceptible species persisted on diseased sites and species richness maintained, infested *Banksia* woodlands are unlikely to return to a pre-disease state. This is due to the combination of direct and indirect pathogen effects that has generated altered site conditions (changes in local hydrology, canopy cover and leaf litter) and a reduced seed source. Additionally the pathogen will persist in the landscape leading to potential re-infestation in the future. The potential interactive effects between *P. cinnamomi*, fire and climate change may further compound existing changes and requires further investigation.

The impact of the introduced pathogen on *Banksia* woodlands demonstrates how resilience theory can be used as criteria to systematically describe and determine if a novel, hybrid or resilient (unchanged) ecosystem results following disturbance.

Keywords: disease, disturbance, ecosystem function, novel ecosystem, regime shift, resilience.

Nomenclature: Paczkowska & Chapman (2000)

Introduction

The transformation of ecosystems by human-induced disturbances is increasingly being observed and documented across a wide range of terrestrial and marine ecosystems (Folke et al. 2004, Hobbs et al. 2006, Scheffer et al. 2001). Various terms have been suggested to describe systems that have undergone relatively rapid and often irreversible change, including novel, emerging and transformed (Chapin & Starfield 1997, Hobbs et al. 2006, Hobbs et al. 2009, Seastedt et al. 2008, Suding & Hobbs 2009). These terms describe ecosystems that have undergone a fundamental change in identity often with new species combinations and abundances (often non-native) and altered function beyond what is historically known (Hobbs et al. 2006, Hobbs et al. 2009). Such ecosystems, collectively described here as 'novel', have crossed a threshold and undergone fundamental changes in identity driven by a range of disturbances such as grazing, fire, over-fishing and pollution (Hobbs et al. 2006, Hobbs et al. 2009, Lindenmayer et al. 2008). Although novel ecosystems are formed by deliberate or inadvertent human action, their maintenance isn't dependent on continued human intervention (Hobbs et al. 2006).

In contrast to a novel ecosystem, a system that retains some pre-disturbance characteristics but has undergone substantial shifts in function and/or composition, can be described as a hybrid ecosystem (Hobbs et al. 2009 - Figure 20). In most circumstances, hybrid ecosystems can return to a pre-disturbance state through restoration efforts, however, this is yet to be documented (Hobbs et al. 2009). Although such generalisations have been suggested, the point at which an ecosystem is considered hybrid or novel is context dependent and somewhat arbitrary (Hobbs et al. 2009).

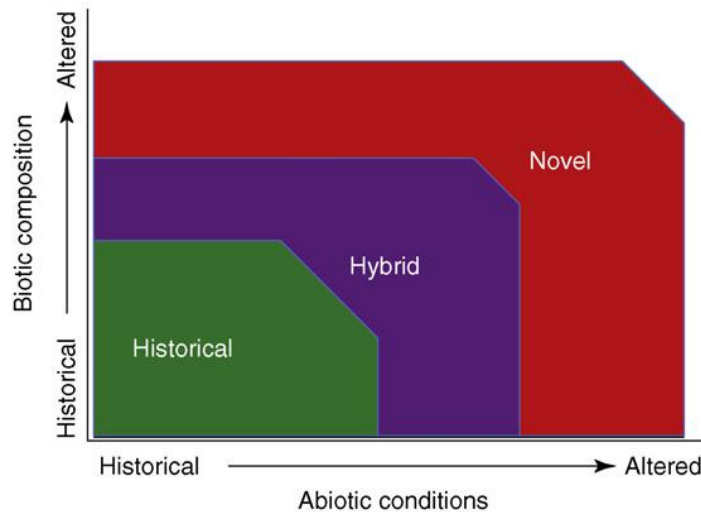


Figure 20: Shifts from historical biotic composition and/or abiotic conditions that result in hybrid or novel ecosystems (from Hobbs et al. 2009).

The rapid formation of novel or hybrid plant communities is traditionally associated with climate change, agriculture and invasive species (Folke et al. 2004, Hobbs et al. 2009). However, biotic disturbance from forest pathogens also have the ability to fundamentally change ecosystem identity through substantial changes in forest composition, structure and function. Although forest pathogens are increasingly recognised as powerful agents of ecological change, few quantitative studies have documented changes beyond composition and structure. Traditional assessments of forest pathogen impact focuses on individual species and associated shifts in canopy or basal area. This has been the case with prominent forest pathogens including the aerially dispersed chestnut blight (*Cryphonectria parasitica*) (Vandermast & Van Lear 2002) and sudden oak death (*Phytophthora ramorum*) (Brown & Allen-Diaz 2009, Rizzo & Garbelotto 2003); and soil-borne Jarrah dieback (*P. cinnamomi*) (Shearer et al. 2009a, Shearer & Dillon 1996a).

Accepting and managing novel ecosystems challenges traditional conservation and restoration theory, and initial instincts may deem this pessimistic (Fox 2007, Hobbs et al. 2006). In many circumstances an ecosystem change is irreversible and efforts to conserve or return to a 'natural' state are not possible or require substantial input of scarce resources. When ecosystem identity is changed beyond recognition, an alternate management approach is required to achieve revised conservation outcomes. Whether a novel/hybrid ecosystem is acceptable is an inherently complex and subjective judgement (Hobbs et al. 2006).

Although novel ecosystems are frequently discussed in the literature, examples of empirical and systematic measurement and documentation are few. Of the studies that do exist (see Folke et al. 2004) the majority use non-manipulative approaches with potential for ambiguous results (Schroder et al. 2005). Using the impact of a forest pathogen as a case study, I demonstrate how the foundations of Holling's (1973) resilience theory can be used to systematically describe change in regards to novel/hybrid ecosystem theory. Resilience theory provides a framework that can be used as criteria to determine if post-disturbance ecosystems are novel, hybrid or unchanged (resilient to disturbance).

Holling (1973) describes resilience as the ability of an ecosystem to retain essentially the same basic structure, function, identity and feedbacks when disturbed. This differs from 'engineering resilience' which is the speed at which a system returns to a single steady or cyclic state after disturbance (Holling 1996). Once a system can no longer absorb a disturbance, a threshold is crossed and the system has experienced a *regime shift* (Folke et al. 2004, Holling 1973). The capacity of an ecosystem to absorb a disturbance and not undergo a regime shift forms the basis of ecosystem resilience.

In contrast to a regime shift, an ecosystem may absorb a disturbance without crossing an irreversible threshold. When a disturbance is absorbed, the system moves through phases in the adaptive cycle. The key aspect of the adaptive cycle concept is that reversible changes occur and the system retains its basic function and structure (Walker & Salt 2006). In an adaptive cycle, a disturbance can move the ecosystem through a series of alternative phases. However, the system has the capacity to return to the pre-disturbance state (Gunderson et al. 1995, Holling & Gunderson 2002).

The forest pathogen case study I use here to demonstrate the integration of resilience and novel ecosystems theory, is in itself an extension beyond current pathogen literature. *Phytophthora cinnamomi* is an introduced forest pathogen that has been impacting forests of the Southwest Australian Floristic Region (SWAFR) since the early 1920's (Shearer 1990). The pathogen is of particular concern in the SWAFR as the number of known native plant species susceptible to *P. cinnamomi* is approximately 40% (~2 280 species) of which 14% (~800 species) are listed as highly susceptible (> 80% plants of a species killed) (Shearer et al. 2004a). Despite recognition of

substantial compositional and structural change, functional shifts are poorly documented for forest pathogens (Brown & Allen-Diaz 2009, Castello et al. 1995, Gilbert 2002). Specifically for *P. cinnamomi*, studies using species-level uni-variate approaches and un-standardised diversity indices dominate the literature (e.g. Shearer & Dillon 1996a, Shearer & Dillon 1995, Weste 2003). *Phytophthora cinnamomi* has been consistently found to shift species dominance based on plant susceptibility or resistance (e.g. Laidlaw & Wilson 2003, McDougall et al. 2002, Shearer & Dillon 1996a, Shearer & Dillon 1995, Weste 2003). Studies have predominantly found species richness to decrease, however a minority have found the opposite with an increase in species richness following disease infestation (see Laidlaw & Wilson 2003, McDougall et al. 2002). Forest pathogen studies that explore beyond species-level changes are required for the comprehensive assessment of pathogen impact.

I use Holling's (1973) resilience theory as criteria to determine if pathogen infestation in *Banksia* woodlands results in a novel, hybrid or unchanged (resilient) ecosystem. Specifically I ask: Does *P. cinnamomi* infestation result in a novel ecosystem characterised by a change in *Banksia* woodland species composition, structure and function (regime shift)?

Methods

Study area

The study area is located in the high rainfall zone of the SWAFR ca. 400 km SSE of Perth, Western Australia (34° 49' S, 117° 9' E). The region is climatically buffered by the Indian Ocean and experiences a mediterranean-type climate with warm, dry summers and mild wet winters with an average annual rainfall of 1000 mm. The SWAFR lies within a global biodiversity hotspot (Myers et al. 2000) and has approximately 7500 native plant species including 3616 endemic taxa (Hopper & Gioia 2004). Key threats to biodiversity in this region include plant pathogen *Phytophthora cinnamomi*, altered fire regimes and global climate change (Shearer et al. 2007, Wardell-Johnson & Nichols 1991).

Banksia attenuata woodlands in the high rainfall zone of the SWAFR are particularly vulnerable to *P. cinnamomi*. This is due to optimal climatic conditions for sporulation and spread combined with abundant plant species of varying susceptibility (Shearer et al. 2007, Shearer & Dillon 1996a,

Shearer & Dillon 1996b). These woodlands are dominated by a *B. attenuata* (Proteaceae) overstorey and a sclerophyllous tall shrub layer (up to 2 m) dominated by *Taxandria parviceps* and *Melaleuca thymoides* (both Myrtaceae). The lower stratum below 1 m is dominated by herbs, sedges and sedge-like species, including *Anarthria scabra*, *A. prolifera* (Anarthriaceae) and *Dasyogon bromeliifolius* (Dasyogonaceae) (Bishop et al. 2010). These *Banksia*-dominated woodlands occur in a complex mosaic of vegetation types and are found in both low-lying areas adjacent to sedge lands and swamps, and in upland saddles on highly oligotrophic soils (Churchward et al. 1988, Pate & Bell 1999).

Study design

Surveys were undertaken on 17 *B. attenuata* woodland sites on deep leached sands, with replication in analogous vegetation complexes (equivalent soil type, vegetation type and position within the landscape) (Havel & Mattiske 2002). Disease centres were randomly located across the landscape due to the patchy nature of *P. cinnamomi* infestation and disease spread. Sites had similar long-term fire histories, and time since previous fire ranged from 8 – 15 years. Changes were assessed along space-for-time transects in a randomized block design. Each disease centre had one chronosequence (block) consisting of three 20 x 20 m quadrats: (H) healthy vegetation with no disease expression; (F) early disease with susceptible species displaying leaf chlorosis in combination with dead and healthy susceptible species e.g. *B. attenuata*; and (D) long diseased vegetation infested for approximately 15 to 20 years, characterised by long dead *B. attenuata*. Spatial autocorrelation was minimised by placement of transects in separate (but homogenous) vegetation complex polygons. Effectively, transects were separated by different vegetation complexes across the landscape and were at least 500 m apart. Transects were positioned at least 20 m from road verges to minimise other edge effects.

The study site is topographically and edaphically similar to coastal sand-plains immediately to the south where rates of disease spread are approximately 1.5 m/year (Grant & Barrett 2003). This rate was used to guide placement of quadrats in long diseased vegetation relative to quadrats in early diseased vegetation. Quadrats in healthy vegetation were placed approximately 50 m from the quadrats in early diseased vegetation. All quadrats were augered to a depth of two metres to confirm soil type between sites and along chronosequence transects.

To detect a potential regime shift I used resilience theory components (composition, structure and function) as criteria for change. A range of plant community components specific to woodland/forest communities was measured across the disease chronosequence. This included measures of plant community composition (alpha & beta diversity, species diversity and species abundance), vegetation structure (canopy closure, basal area & leaf litter) and ecosystem function surrogates (functional trait composition & trait functional diversity) (Figure 21). Detailed explanations of methodology and data analysis can be found in Bishop *et al.* (2010) for species richness, beta diversity and vegetation structure; and Bishop *et al.* (2011) for plant functional trait composition. Shifts in functional trait composition was measured using community-weighted means (CWMs) and community-weighted totals (CWTs) which incorporate changes in relative and absolute species cover respectively. The implications of this are explained in Bishop *et al.* (2011). Chapter six of this thesis outlines aspects relating to functional diversity through use of Rao's index of functional diversity (RIFD) (Lepš *et al.* 2006).

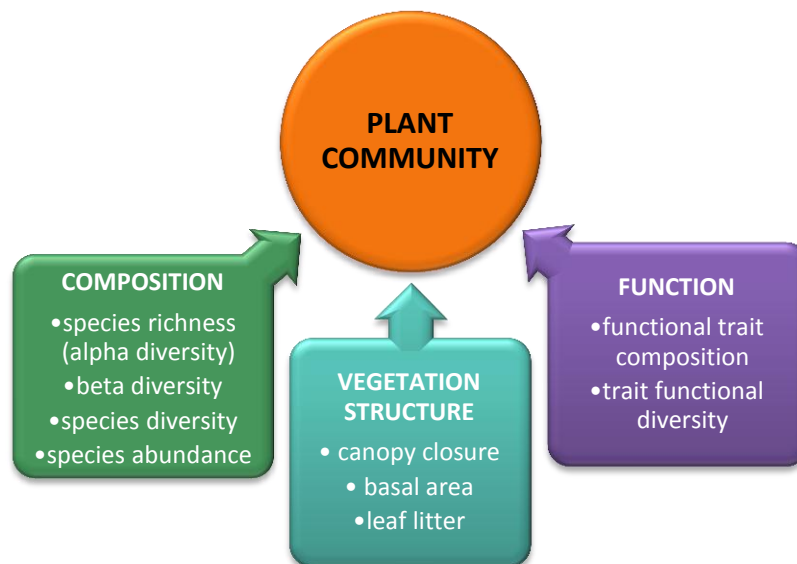


Figure 21: Resilience theory components (composition, structure & function) used as criteria in *Banksia* woodland to detect potential regime shift and determine and describe subsequent novel, hybrid or resilient ecosystem.

To ensure observed changes were from *P. cinnamomi* and not other forest pathogens, drought, or other disturbances, *P. cinnamomi* presence was confirmed by laboratory isolation (Greenhalgh 1978, Marks & Kassaby 1974). Different susceptible species displaying early disease symptoms were targeted for root and soil sampling from quadrats within both early diseased and long diseased vegetation. Six samples were taken within each quadrat and pooled into three samples to increase pathogen recovery rates.

Samples were flooded to a 1:4 soil/water ratio upon which 10 *E. sieberi* cotyledons were floated. Samples were stored at 22 °C for optimal pathogen growth and checked on day five for evidence of cotyledon colour change indicative of *P. cinnamomi* presence (purple to yellow/green). Potentially infected cotyledons were plated onto *Phytophthora*-selective agar and stored for three days at 22 °C. Plates were then inspected for characteristic hyphal swellings and mycelial growth patterns indicative of *P. cinnamomi* presence.

Results

Change in species composition and vegetation structure

Native species richness and Simpson's reciprocal index were not significantly different following pathogen invasion (Table 14). Species richness ranged from 47.2 in healthy vegetation to 45.8 in long diseased vegetation. Simpson's reciprocal index varied little, with healthy vegetation (38.1), early disease (37.7) and long diseased vegetation (37.2). Multivariate analysis of beta diversity revealed a significant change following disease presence driven by substantial shifts in species abundances ($p = 0.001$). Weed species were not present in either uninfested vegetation or infested vegetation. Following disease, canopy closure reduced by 75% ($p = 0.001$), and both basal area and leaf litter reduced by 50% ($p = 0.028$ and $p = 0.001$ respectively). For detailed results and explanation see Bishop et al. (2010).

Table 14: Diversity indices and stand variables (mean \pm standard error) in relation to disease status in *Banksia* woodland of southwest Australia (see Bishop et al. 2010).

Index or variable	Healthy vegetation	Early disease	Long diseased vegetation	Transect p value
Species richness	47.2 \pm 2.51	46.8 \pm 2.21	45.8 \pm 1.49	0.52
Simpson's reciprocal index	38.1 \pm 1.89	37.7 \pm 1.72	37.2 \pm 1.01	0.73
Beta diversity	NA	NA	NA	0.001
Canopy closure (%)	19.9 \pm 1.4	10.4 \pm 1.3***	3.9 \pm 0.7***	0.001
Basal area (m ² /ha)	22.0 \pm 3	16.3 \pm 2.9	10.7 \pm 2.9*	0.028
Leaf litter (kg/ha)	85.9 \pm 9.9	58.8 \pm 6.5***	37.6 \pm 3.7***	0.001

There was no interaction between disease status and time since previous fire for any indices or stand variables.

Change in plant functional trait composition

Trait abundances (community-weighted totals) shifted substantially while there was no observable change in trait means (community-weighted means) (Table 15). For detailed results and explanation see Bishop et al. (2011).

Table 15: Changes in relative (community-weighted means: CWM) and absolute (community-weighted totals: CWT) trait values across a disease chronosequence in species-rich *Banksia* woodland, southwest Australia. Changes in CWMs and CWTs were measured for six traits at 17 sites, and analysed using analysis of variance (see Bishop et al. 2011).

	Community-weighted means <i>p</i> -values & % change	Community-weighted totals <i>p</i> -values & % change
Plant height	0.011(-15.1%)	0.017 (-47.4%)
Growth form	0.129 (-9.63%)	0.033 (-43.2%)
Specific Leaf Area	0.042 (+9.64%)	0.076 (-33.0%)
Leaf dry matter content	0.670 (-3.52%)	0.040 (+40.1%)
Root pattern	0.380 (-5.68%)	0.045 (-40.4%)
Carbohydrate storage	0.117 (-8.88%)	0.001 (-48.1%)

No observable change was found for Rao's index of functional diversity following disease infestation for all traits measured except LDMC, which had a mean increase following disease.

Phytophthora cinnamomi was isolated from 95% of chronosequence transects.

Discussion

Hybrid or novel ecosystem?

The introduced forest pathogen *Phytophthora cinnamomi* has generated a regime shift and subsequent hybrid ecosystem in species-diverse *Banksia* woodlands of the SWA FR. The regime shift is characterised by substantial changes in species abundances, vegetation structure and plant functional trait composition in diseased vegetation (Figure 22). A hybrid ecosystem differs from a novel ecosystem through maintenance of some pre-disturbance characteristics (Hobbs et al. 2009). Although *P. cinnamomi* has altered species abundances, vegetation structure and plant functional trait composition, a number of key pre-disturbance features remain in diseased vegetation. These include maintenance of species diversity, and hence species richness coupled with preservation of functional diversity (Figure 22). Although the woodlands have been altered structurally and functionally following disease, the resultant hybrid ecosystem displays some resilience to the pathogen through continuation of species and functional diversity.

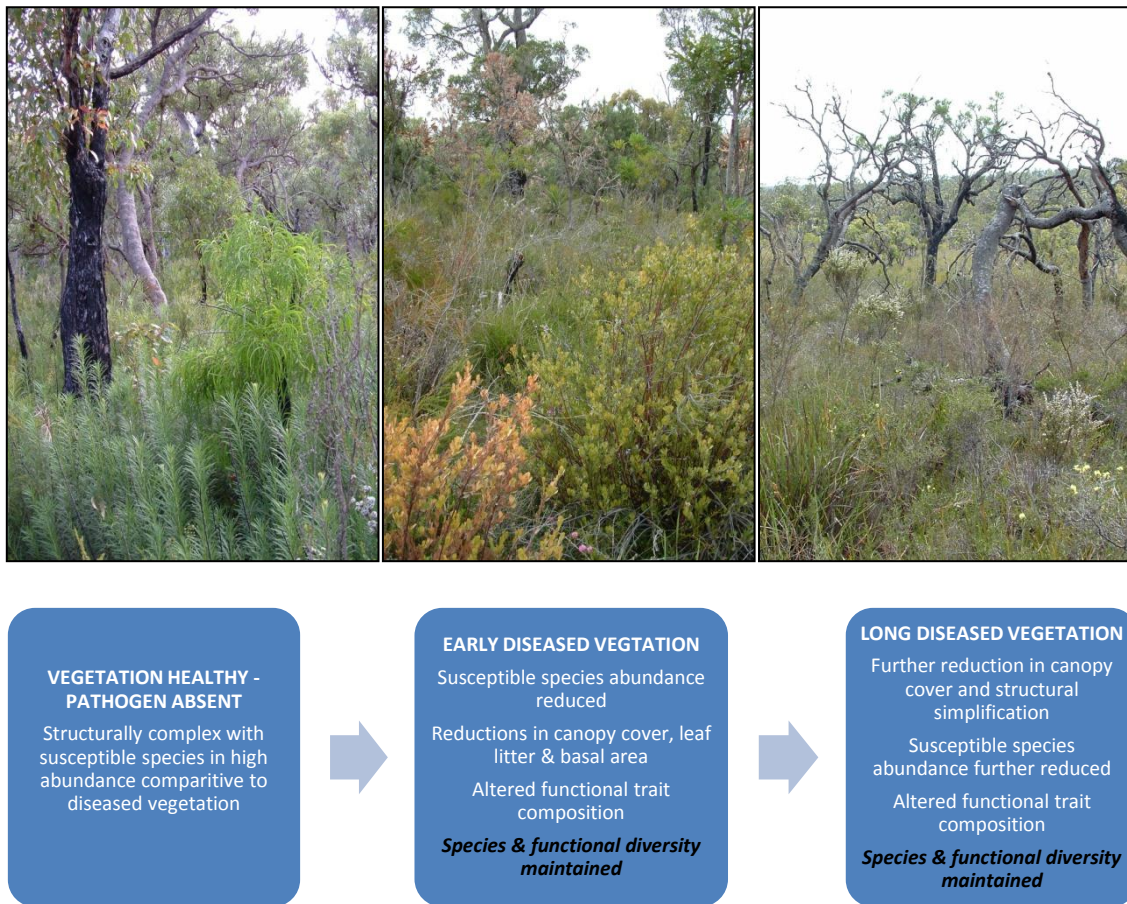


Figure 22: Disease chronosequence with changes listed in white text below corresponding quadrats. Characteristics that were maintained despite disease infestation are listed in black italic text. Chronosequence runs from healthy vegetation through to infested vegetation and was replicated 17 times in spatially separate polygons of *Banksia* woodland.

Hobbs (2009) states that the point at which a system becomes hybrid or novel is context dependant and somewhat arbitrary. To further clarify why I identify pathogen-infested *Banksia* woodlands as hybrid ecosystems, I summarise below the changes in composition, structure and functional trait composition that combine to describe a regime shift. This systematic approach underpinned by resilience theory provides a suitable framework for assessing the impact of disturbance at a plant community or ecosystem level.

Change in vegetation structure and species composition

Shifts in species dominance following pathogen infestation, has driven changes in *Banksia* woodland structure. Vegetation structure has changed substantially following disease with reductions in canopy closure and basal area. Structural change is also evident from a dominance shift from tree species > 5 m to shrubs 1 – 2 m following disease infestation (Bishop et al. 2011). These shifts are associated with the substantial declines in the dominant and pathogen-

susceptible canopy species *Banksia attenuata* following *P. cinnamomi* introduction (Bishop et al. 2010). Although species richness was maintained on diseased sites, *P. cinnamomi* will act as a selection pressure favouring pathogen-tolerant taxa or individuals over time. While the abundance of susceptible species reduced substantially following disease, complete removal was not seen due to the patchy nature of inoculum spread (Shearer et al. 2009b) and/or the presence of genetically tolerant individuals (Harris et al. 1985, Shearer et al. 2004a, Stukely & Crane 1994).

Maintenance of species richness coupled with shifts in species abundances has also been found in the Northern Jarrah Forests to the north of the study site (McDougall et al. 2002). However, these results contrast the majority of studies that report a reduction in species richness following *P. cinnamomi* introduction (e.g. Shearer & Dillon 1996a, Shearer & Dillon 1995, Weste 2003). This suggests a variable response to *P. cinnamomi* presence likely dependent on time since initial infestation, soil type, vegetation type and disturbance history (Bishop et al. 2010).

Despite substantial changes through reductions in species abundances, canopy cover and leaf litter, weeds did not colonise diseased sites. This is likely due to the absence of vacant niches following disturbance in combination with no close or large source of weed propagules. The concept of vacant niches suggests that following disturbance, removal or reduction of resident species results in areas of trait space able to be utilised by opportunistic weed species suited to local conditions (Moles et al. 2008). In the case of *Banksia* woodlands infestation, it is likely that the high levels of species richness and endemism reduce the potential for weed invasion as the trait space is super-saturated by highly adapted resident species. These species fill the trait space through possession of physiological adaptations that maximise nutrient acquisition from the highly oligotrophic soils (Dodd et al. 1984, Pate & Bell 1999). Following pathogen infestation, species richness and identity remained unchanged which suggests the trait space may remain somewhat saturated despite reductions in species abundance.

Distance from a source of weed propagules may also contribute to the lack of weed colonisation in diseased vegetation. The sites examined were contained within a matrix of relatively undisturbed vegetation types comparative to high intensity and frequently disturbed areas such as farmland and road verges (Wardell-Johnson et al. 2004). As a result, the study sites were isolated from a suitable source of weed propagules. The combination of continued saturation of trait space and

distance from a weed source combine to explain the lack of weed colonisation following pathogen infestation.

Change in plant functional trait composition

Altered ecosystem function from forest pathogen presence is frequently assumed in the literature, though documentation of pathogen impact is limited to composition and structural change (e.g. Burdon et al. 2006, Hansen 1999, Lovett et al. 2006, Shearer et al. 2009a). Deduced links have been made between selected plant traits and ecosystem functions which were used as indicators of potential pathogen-driven change in ecosystem function. Clear shifts in species abundances are linked to the substantial changes found in functional trait composition. Bishop et al. (2011) have previously found substantial shifts in the majority of plant traits measured, which suggests a reduction in productivity, reduced capacity as a carbon sink and altered site water balance. However, as the links between plant traits and ecosystem function are deduced, verification of these potential changes in function is required using traditional quantitative techniques.

Banksia attenuata may be considered a key species through its dominance and substantial contribution to *Banksia* woodland identity and function. Grime's Mass Ratio Hypothesis (Grime 1998) and similarly Walker's "drivers and passengers" hypothesis (Walker 1992, Walker 1995), both summarize that dominant species have the greatest contribution to ecosystem function, while the subordinate species occupy niches created by the dominants (Grime 1998). Structurally dominant tree species *B. attenuata* is a key contributor to site canopy closure, leaf litter and basal area with substantial reductions in these characteristics following pathogen infestation (Bishop et al. 2010). The 63% decline in *B. attenuata* (Bishop et al. 2010) and subsequent reduction in plant trait values indicates the importance of *B. attenuata* in the stability of ecosystem function.

An irreversible regime shift

Measurement of pathogen-induced changes in *Banksia* woodland structure, function and composition has documented an irreversible regime shift consistent with resilience theory (Folke et al. 2004, Holling 1973). This regime shift has resulted in a system that, although substantially altered, has retained some-pre-disturbance characteristics and identify as a hybrid ecosystem.

Pre and post pathogen infested *Banksia* woodlands present two alternate regimes. Prior to infestation *Banksia* woodlands have higher abundances of susceptible species (most notably *B. attenuata*) and greater structural diversity with higher basal area and canopy closure. In contrast, post-pathogen vegetation is structurally simplified through considerable reductions in canopy closure and basal area coupled with a substantial decrease in trait abundances. The substantial shifts in trait abundances suggest altered ecosystem function linked to a reduction in total vegetation cover through direct and indirect pathogen impact (Bishop et al. 2011).

In some cases, hybrid ecosystems are able to return to the original pre-disturbance state through restoration efforts (Hobbs et al. 2009). However, *Banksia* woodlands infested with *P. cinnamomi* are an example of a hybrid ecosystem that is unlikely to return to a pre-infestation state. This is due primarily to persistence of the pathogen in the landscape; anticipated interactions between disease, climate change and altered fire regimes; and altered site conditions. There is currently no long-term, landscape level treatment for *P. cinnamomi*, with management limited to slowing rates of disease spread through hygiene and small-scale application of the systemic fungicide phosphite (Hardy et al. 2001). Phosphite temporarily reduces the mortality of susceptible species through reduced rates of spread (Hardy et al. 2001, Shearer et al. 2004b). The expense and unknown impact of continued application of phosphite on other ecosystem components (i.e. invertebrates, mycorrhizal fungi, soil chemistry) currently deems this method unsuitable for long-term, landscape-level management.

Further support for an irreversible regime shift are the anticipated interactions between disease, climate change and fire that are hypothesized to further impact diseased ecosystems (Burdon et al. 2006). Chronosequence transects used in this study have been permanently marked for future re-sampling and study of potential interactions. The study area is currently tracking above the worst case scenario for predicted climate change with significant declines in autumn and early winter rainfall (10 – 20%) since the 1970's (Bates et al. 2008, Ryan & Hope 2006). These changes have been partly attributed to global climate change. A slight increase in summer rainfall coupled with increased temperatures will provide enhanced conditions for *P. cinnamomi* sporulation and spread by providing moist conditions in a typically drier period (Shearer et al. 2009a).

Substantial changes in site conditions may inhibit the potential for re-colonization (Bishop et al. 2010). Reductions in canopy cover, litter cover and seed availability coupled with altered site hydrology may alter the conditions necessary for seedling germination and survival. As the majority of species require fire for germination, the impact on recruitment is likely to be greatest following fire. The interaction between *Phytophthora* and fire requires investigation in the fire-prone ecosystems of the SWAFR. Additional research could also explore the persistence of susceptible species following disease. Questions regarding genetic resistance may be investigated by monitoring recruitment and seedlings from surviving individuals of susceptible species following fire.

Conclusion

This study has demonstrated the use of resilience theory as criteria to describe a pathogen-induced hybrid ecosystem. As the resultant system identifies as a hybrid ecosystem and not novel, a degree of resilience to the pathogen is evident. Through practical application of resilience theory and quasi-manipulation of field conditions, I have applied the theoretical concepts of resilience theory using empirical measurement.

The *Banksia* woodland hybrid ecosystem is characterised by substantial shifts in species dominance, structure and function but maintenance of species richness and functional diversity. Although the changes are substantial, I anticipate the intensity of pathogen impact is localised to the highly susceptible *Banksia* woodlands. It is expected that other vegetation types may not exhibit *P. cinnamomi* impacts to the same extent due to lower complements of susceptible species (e.g. karri, tingle, marri/jarraah dominated forests) and soil types being less conducive to sporulation and spread due to higher microbial loads. In a landscape context, *P. cinnamomi* will result in localised regime shifts and hybrid ecosystems. However, they are likely to be contained by other more resilient vegetation types and not form a dominant part of the landscape. This study has shown that diseased *Banksia* woodlands in the SWAFR show some resilience to *P. cinnamomi* as they are not novel, but have undergone substantial shifts to identify as hybrid ecosystems.

Acknowledgements

This paper is a component of a PhD project of the senior author and was supported by a University of Queensland APAI scholarship and Australian Research Council Linkage Project Grant LP0560809 “Towards a landscape conservation culture – broadening the spatio-temporal scope of ecological studies to anticipate change in Australian forested ecosystems”. Field work was supported by the Western Australian Department of Environment and Conservation (Science Division). All experiments and analyses in this manuscript comply with Australian federal and Western Australian state laws and codes of practice.

CHAPTER EIGHT: CONCLUSION

Overview

Through integration and application of ecological theories, I have comprehensively described pathogen-induced impact at both the species and community-level. Resilience theory has been used as criteria to identify and describe the type of ecosystem that results following disturbance. This has been integrated with novel/hybrid ecosystem theory to provide a method that comprehensively describes the impacts of disturbance by measuring change across a range of ecosystem components. The resilience theory framework was used to guide experimental design and derive both the research questions and subsequent thesis structure (Figure 23). This chapter provides a summary of how each research question was addressed within the relevant chapters and outlines opportunities for further research.

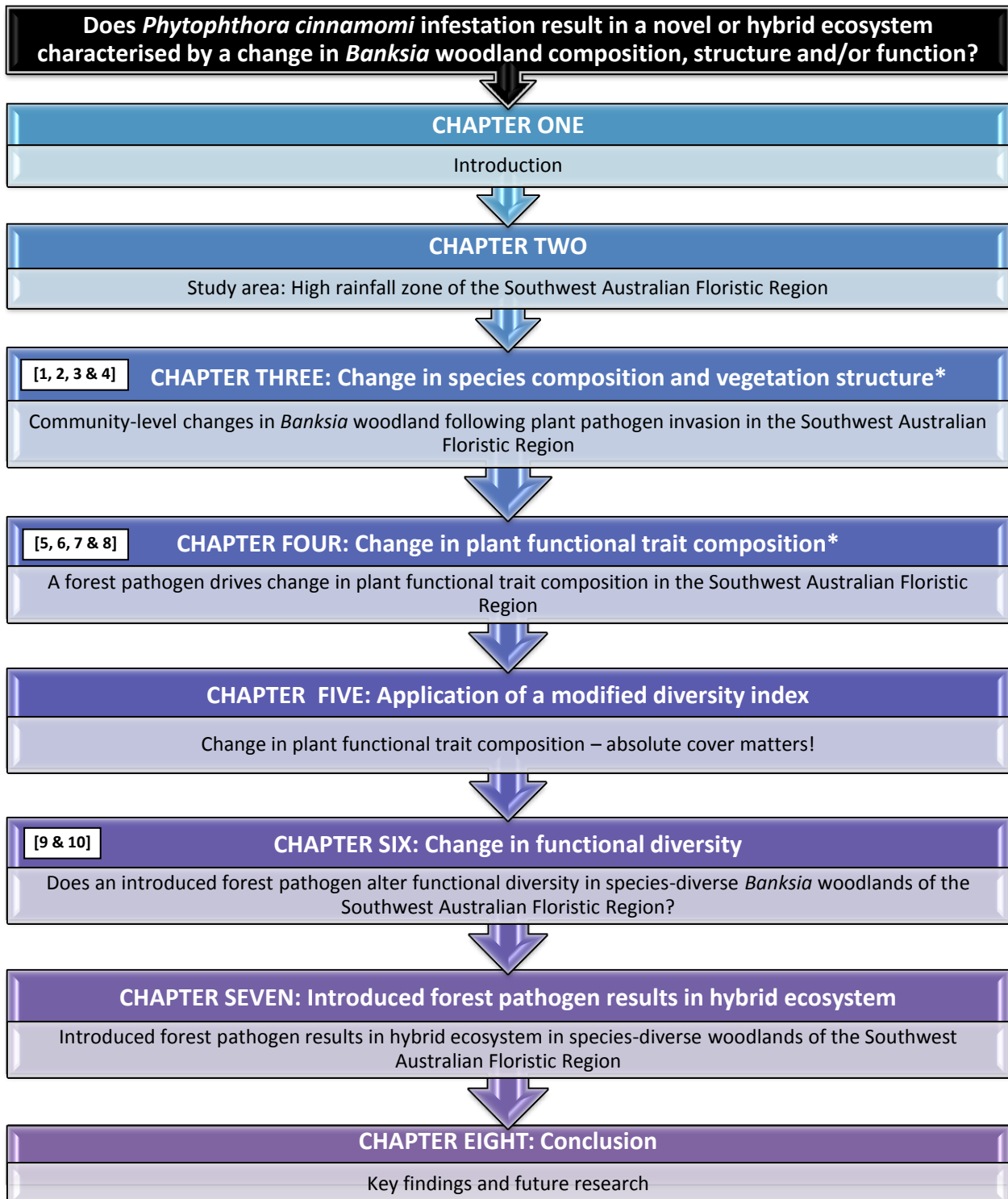


Figure 23: Thesis structure and chapter titles. Bracketed numbers refer to research questions addressed in data chapters. * signifies chapter published or in press.

Research outcomes

The key research question was:

Does *Phytophthora cinnamomi* infestation result in a novel or hybrid ecosystem characterised by a change in *Banksia* woodland composition, structure and/or function?

The introduction of forest pathogen *P. cinnamomi* has resulted in a hybrid ecosystem in *Banksia attenuata* woodlands of the SWAFR. The 10 sub-questions outlined below were constructed to answer the key research question regarding pathogen infestation and the identity of the resultant ecosystem. Three key components of ecosystem change were used as criteria to determine whether a novel or hybrid ecosystem resulted after disturbance. This includes floristic composition, vegetation structure and plant functional trait composition (Figure 24).

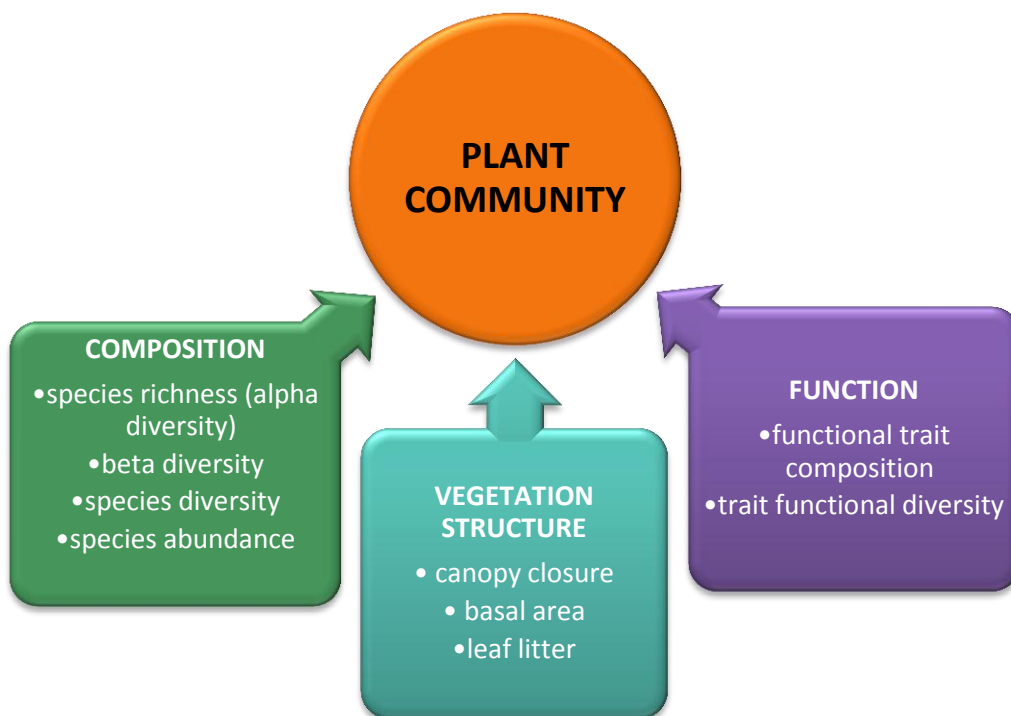


Figure 24: Resilience theory components (composition, structure & function) used as criteria in *Banksia* woodland to detect potential regime shift and determine and describe subsequent novel, hybrid or resilient ecosystem.

CHANGE IN FLORISTIC COMPOSITION & STRUCTURE: CHAPTER THREE

Chapter three explores questions 1 through 4.

1. How do species abundances change along a disease chronosequence and over time?
2. Does alpha or beta species diversity change along a disease chronosequence and over time?
3. How does plant community structure change?
4. How do the stand variables; basal area, leaf litter, canopy closure and percentage bare ground change?

Chapter Three: Community-level changes in *Banksia* woodland following plant pathogen invasion in the Southwest Australian Floristic Region. This chapter addresses the first four questions by exploring the species and community-level changes in floristic composition and vegetation structure along the disease chronosequence. A range of community-level variables and factors were measured to identify floristic change and associated stand variables relevant to *Banksia* woodlands. Species richness was unchanged across the chronosequence which is unexpected but has been documented elsewhere (Laidlaw & Wilson 2003, McDougall et al. 2002). This result was unexpected as the majority of similar studies in Western Australia reported a decrease in species richness (e.g. Shearer & Dillon 1996a, Shearer & Dillon 1995, Weste 2003). Beta diversity was found to vary following disease, linked to changes in species abundance. Substantial shifts in species abundances altered species dominance in association with species susceptibility to the pathogen. The dominant canopy species by cover and biomass (*Banksia attenuata*, *Banksia ilicifolia* & *Allocasuarina fraseriana*), were substantially reduced which had implications for associated stand variables. The reduction in canopy cover, basal area and leaf litter was evident in post-pathogen sites. In regards to species abundance/dominance and alpha & beta diversity, comparative results were found in the temporal data from the historic quadrats. This indicates validity of the space-for-time approach that was used.

CHANGE IN PLANT FUNCTIONAL TRAIT COMPOSITION: CHAPTER FOUR

Chapter four addresses questions 5 through 8 regarding plant functional traits.

5. Are there changes in site productivity traits specific leaf area (SLA) and leaf dry matter content (LDMC)?
6. Does the pathogen alter nutrient cycling rates?
7. Does pathogen introduction alter *Banksia* woodlands capacity for carbon immobilisation?
8. a) Does the dominance of particular root patterns change following disease infestation?
b) What are the potential implications regarding hydraulic lift and site water balance?

Chapter Four: A forest pathogen drives change in plant functional trait composition in the Southwest Australian Floristic Region. This chapter addresses questions 5 to 8 to collectively describe pathogen-driven shifts in plant functional trait composition. Changes in functional trait composition were used to identify potential shifts in *Banksia* woodland function in lieu of direct experimental measurement which was beyond the scope of this project. Through measurement of species abundance across the disease chronosequence, *P. cinnamomi* reduced total (absolute) vegetation cover by 40%. I compared traditional community-weighted means (CWM) which use relative cover data with a modified index using absolute cover (community-weighted totals - CWT). The CWM index doesn't incorporate changes in total vegetation cover which is key to Grime's (1998) Mass Ratio Hypothesis suggesting that abundant species dominate ecosystem function. The modified CWT index incorporates the absolute cover changes found following disease, which can be linked to potential shifts in ecosystem function. The CWT index is complementary to traditional CWMs and can be used when a change in absolute vegetation cover has been identified.

Shifts in trait composition found using CWT indicate a potential reduction in site productivity, reduced capacity as a carbon sink and altered site water balance. It is anticipated that nutrient cycling rates will remain constant due to unchanged litter quality. This chapter demonstrates the considerable indirect impacts of disease beyond the substantial floristic change. Additionally, the importance of absolute cover changes has been shown in regards to shifts in ecosystem function.

Chapter Five: Change in plant functional trait composition – absolute cover matters!

This chapter supplements the previous chapter by applying the modified community-weighted total (CWT) index regarding plant trait composition. The traditional index used for this analysis (community-weighted means) doesn't take into account shifts in total vegetation cover, which has implications for ecosystem function. In this chapter I compared the indices to demonstrate how shifts in total species cover are relevant to changes in ecosystem function despite no change in CWMs. CWMs conceal absolute changes (through use of relative abundance data) which are intrinsically linked to ecosystem function through Grime's (1998) Mass Ratio Hypothesis.

CHANGE IN PLANT FUNCTIONAL TRAIT DIVERSITY: CHAPTER SIX

Chapter six covers questions 9 and 10 regarding functional diversity and functional redundancy.

9. Does *Phytophthora cinnamomi* alter the functional diversity of species-diverse *Banksia* woodlands?
10. Do *Banksia attenuata* woodlands exhibit functional redundancy as characterised by the presence of functionally similar species?

Chapter Six: Does an introduced forest pathogen alter functional diversity?

This chapter explores questions 9 and 10 regarding functional diversity (trait variance) and redundancy. The previous chapters have identified potential shifts in ecosystem function through cover changes. However, this gives no indication as to whether disease is homogenising plant functional traits or selecting for particular traits. Using Rao's index of functional diversity (Lepš et al. 2006, Rao 1982, Ricotta 2005) to identify shifts in trait variance, I found no changes indicating that *P. cinnamomi* does not cause functional homogenization of *Banksia* woodlands. Rao's index was found to correlate with Simpson's reciprocal index but not species richness. As functional diversity did not increase with species richness, this demonstrates that *Banksia* woodlands exhibit low levels of functional redundancy. Low functional redundancy is characterised by the presence of taxonomically distinct species in a system that have little overlap in functional traits.

STUDY SYNTHESIS

Chapter Seven: Introduced forest pathogen results in hybrid ecosystem

This chapter combines the key findings of previous data chapters to provide a synthesis of disturbance-induced change through combination of resilience and novel ecosystem theory. This chapter answers the primary research question: “Does *Phytophthora cinnamomi* infestation result in a novel or hybrid ecosystem characterised by a change in *Banksia* woodland composition, structure and/or function?” The chapter uses the resilience theory framework as criteria to determine if a novel, hybrid or resilient ecosystem results following pathogen infestation. Resilience and novel/hybrid ecosystem theory are not new but their combination and application provides a comprehensive approach to quantifying and describing disturbance. I identified an irreversible regime shift with shifts in species abundance, vegetation structure and functional trait composition. As species richness, species diversity and functional diversity were maintained, the post-pathogen ecosystem identifies as hybrid. As the resultant ecosystem identifies as hybrid, partial resilience to *P. cinnamomi* has been demonstrated despite the substantial structural and functional changes. The highly susceptible *Banksia* woodland communities of the study area have retained conservation value despite the considerable changes following pathogen infestation.

Further research

I have provided a comprehensive and novel investigation of the species and community-level impacts of *P. cinnamomi* on *Banksia attenuata* woodlands in the SWAFR. A combination of long-term and space-for-time studies are required to accurately document changes over time and test hypotheses put forward by this study. The study has been designed to allow future re-sampling of quadrats and for development of additional projects exploring potential interactions between *P. cinnamomi*, fire and climate change.

The plant functional trait work could be further enhanced through quantitative testing of the deduced changes in ecosystem function. This would determine the accuracy of plant trait methods for assessing ecosystem function in this woodland type. Beyond the analysis of changes in ecosystem function, the potential interactions between disease, fire and climate change require investigation.

REFERENCES

- Aarssen, L.W. 1997. High productivity in grassland ecosystems: effected by species diversity or productive species? *Oikos* 80: 183-184.
- Abbott, I. 2003. Aboriginal fire regimes in south-west Australia: evidence from historical documents. In: Abbott, I. & Burrows, N.C. (eds.) *Fire in ecosystems of the south-west of Western Australia: impacts and management*, 119-146. Backhuys, Leiden, NL.
- Abbott, I. & Burrows, N. 1999. Biodiversity conservation in the forests and associated vegetation types of Southwest Western Australia. *Australian Forestry* 62: 27.
- Abbott, I. & Burrows, N. 2003. *Fire in ecosystems of South-west Western Australia: impacts and management*. Backhuys, Leiden, NL.
- Addinsoft 2006. XL Stat-Pro version 2006. In: Anon (ed.) Addinsoft US, New York, US.
- Aerts, R. 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos* 79: 439-449.
- Allen, C.R., Gunderson, L. & Johnson, A.R. 2005. The use of discontinuities and functional groups to assess relative resilience in complex systems. *Ecosystems* 8: 958-966.
- Allen, C.R. & Holling, C.S. 2008. *Discontinuities in ecosystems and other complex systems*. Columbia University Press, New York, US.
- Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26: 32-46.
- Anderson, M.J., Gorley, R.N. & Clarke, K.R. 2008. PERMANOVA+ for PRIMER: Guide to software and statistical methods. In: PRIMER-E Ltd, Plymouth, UK.
- Anderson, M.J. & Willis, T.J. 2003. Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology* 84: 511-525.
- Barkai, A. & McQuaid, C. 1988. Predator-prey role reversal in a marine benthic ecosystem. *Science* 242: 62-64.

- Bates, B., Hope, P., Ryan, B., Smith, I. & Charles, S.P. 2008. Key findings from the Indian Ocean Climate Initiative and their impact on policy development in Australia. *Climatic Change* 89: 339-354.
- Bishop, C.L., Wardell-Johnson, G.W. & Williams, M.R. 2010. Community-level changes in *Banksia* woodland following plant pathogen invasion in the Southwest Australian Floristic Region. *Journal of Vegetation Science* 21: 888-898.
- Bishop, C.L., Williams, M.R. & Wardell-Johnson, G.W. 2011. A forest pathogen drives change in plant functional trait composition in the Southwest Australian Floristic Region. *Agriculture, Ecosystems and Environment* 145: 59-66.
- Bormann, F.H. & Likens, G.E. 1979. *Pattern and process in a forested ecosystem*. Springer, New York, US.
- Bowman, D. 2003. Australian landscape burning: a continental and evolutionary perspective. In: Abbott, I. & Burrows, N. (eds.) *Fire in South-western Australian ecosystems: impacts and management*, 107-118. Backhuys, Leiden, NL.
- Bradstock, R.A., Williams, J.E. & Gill, A.M. 2002. *Flammable Australia: the fire regimes and biodiversity of a continent*. Cambridge University Press, Cambridge, UK.
- Braun-Blanquet, J. 1932. *Plant sociology: the study of plant communities*. McGraw Hill, New York, US.
- Broadbent, P. & Baker, K.F. 1974. Association of bacteria with sporangium formation and breakdown of sporangia in *Phytophthora* spp. *Australian Journal of Agricultural Research* 25: 139-145.
- Brown, L.B. & Allen-Diaz, B. 2009. Forest stand dynamics and sudden oak death: mortality in mixed-evergreen forests dominated by coast live oak. *Forest Ecology and Management* 257: 1271-1280.
- Burdon, J.J., Thrall, P.H. & Ericson, L. 2006. The current and future dynamics of disease in plant communities. *Annual Review of Phytopathology* 44: 19-39.

- Burgess, S.S.O., Adams, M.A., Turner, N.C. & Ong, C.K. 1998. The redistribution of soil water by tree root systems. *Oecologia* 115: 306-311.
- Burrows, N. 2008. Linking fire ecology and fire management in south-west Australian forest landscapes. *Forest Ecology and Management* 255: 2394-2406.
- Burrows, N. & Abbott, I. 2003. Fire in south-west Western Australia: synthesis of current knowledge. In: Abbott, I. & Burrows, N. (eds.) *Fire in ecosystems of south-west Western Australia: impacts and management*, 437-452. Backhuys, Leiden, NL.
- Burrows, N. & Wardell-Johnson, G. 2003. Fire and plant interactions in forested ecosystems of south-west Western Australia. In: Abbott, I. & Burrows, N. (eds.) *Fire in South-western Australian ecosystems: impacts and management*, 225-268. Backhuys, Leiden, NL.
- Cahill, D.M., Rookes, J.E., Wilson, B.A., Gibson, L. & McDougall, K.L. 2008. *Phytophthora cinnamomi* and Australia's biodiversity: impacts, predictions and progress towards control. *Australian Journal of Botany Supplementary Series* 56: 279-310.
- Caldwell, M.M., Dawson, T.E. & Richards, J.H. 1998. Hydraulic lift: consequences of water efflux from the roots of plants. *Oecologia* 113: 151-161.
- Carpenter, S., Jansson, B.O., Ludwig, D., Pastor, J., Peterson, G. & Walker, B. 1996. A comparative analysis of total system resilience. In: *Beijer Institute Resilience Network Planning Workshop April 10-16*.
- Carpenter, S. & Lathrop, R. 2008. Probabilistic estimate of a threshold for eutrophication. *Ecosystems* 11: 601-613.
- Carpenter, S., Ludwig, D. & Brock, W.A. 1999. Management of eutrophication for lakes subject to potentially irreversible change. *Ecological Applications* 9: 751-771.
- Carpenter, S., Walker, B., Anderies, J.M. & Abel, N. 2001. From metaphor to measurement: resilience of what to what? *Ecosystems* 4: 765-781.
- Castello, J.D., Leopold, D.J. & Smallidge, P.J. 1995. Pathogens, patterns, and processes in forest ecosystems. *Bioscience* 45: 16-24.

- Chakraborty, S., Murray, G.M., Magarey, P.A., Yonow, T., Sivasithamparam, K., O'Brien, R.G., Croft, B.J., Barbetti, M.J., Old, K.M., Dudzinski, M.J., Sutherst, R.W., Penrose, L.J., Archer, C. & Emmett, R.W. 1998. Potential impact of climate change on plant diseases of economic significance to Australia. *Australasian Plant Pathology* 27: 15-35.
- Chapin, F.S. 2003. Effects of plant traits on ecosystem and regional processes: a conceptual framework for predicting the consequences of global change. *Annals of Botany* 91: 455-463.
- Chapin, F.S. & Starfield, A.M. 1997. Time lags and novel ecosystems in response to transient climatic change in arctic Alaska. *Climatic Change* 35: 449-461.
- Churchward, H.M., McArthur, W.M., Sewell, P.L. & Bartle, G.A. 1988. Landforms and soils of the south coast and hinterland, Western Australia. Northcliffe to Manypeaks. Report 88/1. In: CSIRO Division of Water Resources, Canberra, AU.
- Clarke, K.R. & Gorley, R.N. 2008. PRIMER 6 v 6.1.11 & PERMANOVA+ v 1.0.1. In: PRIMER-E Ltd, Plymouth, UK.
- Clarke, K.R. & Warwick, R.M. 2001. Change in marine communities: an approach to statistical analysis and interpretation. In: PRIMER-E Ltd, Plymouth, UK.
- Commonwealth and Western Australian Regional Forest Agreement Steering Committee 1998. Comprehensive regional assessment : a Regional Forest Agreement for Western Australia. Volume 1. Canberra, AU.
- Conway, G. 1997. *The double green revolution: food for all in the twenty-first century*. Comstock Publishing Associates, New York, US.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heijden, M.G.A., Pausas, J.G. & Poorter, H. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51: 335-380.
- Crane, C.E. & Shearer, B.L. 2007. Hemispherical digital photographs offer advantages over conventional methods for quantifying pathogen-mediated changes caused by infestation of *Phytophthora cinnamomi*. *Australasian Plant Pathology* 36: 466-474.

- Davison, E.M. & Shearer, B.L. 1989. *Phytophthora spp.* in indigenous forests in Australia. *New Zealand Journal of Forestry Science* 19: 277-289.
- Dawson, N. 2005. Review of progress on invasive species - final report to Department of Environment and Heritage. In: Department of Environment and Heritage, Toowong, AU.
- Dawson, T.E. 1993. Hydraulic lift and water use by plants: implications for water balance, performance and plant-plant interactions. *Oecologia* 95: 565-574.
- de Bello, F., Leps, J. & Sebastià, M.T. 2006. Variations in species and functional plant diversity along climatic and grazing gradients. *Ecography* 29: 801-810.
- de Bello, F., Thuiller, W., Leps, J., Choler, P., Clément, J., Macek, P., Sebastià, M. & Lavorel, S. 2009. Partitioning of functional diversity reveals the scale and extent of trait convergence and divergence. *Journal of Vegetation Science* 20: 475-486.
- Department of Environment and Conservation 2008. *Walpole Wilderness Area and adjacent parks and reserves management plan*. DEC, Perth, AU.
- Diaz, S. & Cabido, M. 1997. Plant functional types and ecosystem function in relation to global change. *Journal of Vegetation Science* 8: 463-474.
- Diaz, S. & Cabido, M. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution* 16: 646-655.
- Díaz, S., Cabido, M., Zak, M., Carretero, E.M. & Aranibar, J. 1999. Plant functional traits, ecosystem structure and land-use history along a climatic gradient in Central-western Argentina. *Journal of Vegetation Science* 10: 651-660.
- Diaz, S., Lavorel, S., Chapin III, F.S., Tecco, P.A., Gurvich, D.E. & Grigulis, K. 2007. Functional diversity - at the crossroads between ecosystem functioning and environmental filters. In: Canadell, J.G., Pataki, D.E. & Pitelka, L.F. (eds.) *Terrestrial ecosystems in a changing world*, 81-90. Springer-Verlag, Berlin, DE.
- Dixon, K. & Barrett, R. 2003. Defining the role of fire in south-west Western Australian plants. In: Abbott, I. & Burrows, N.C. (eds.) *Fire in ecosystems of the south-west of Western Australia: impacts and management*, Backhuys, Leiden, NL.

- Dodd, J. & Bell, D.T. 1993. Water relations of the canopy species in a *Banksia* woodland, Swan Coastal Plain, Western Australia. *Austral Ecology* 18: 281-293.
- Dodd, J., Heddle, E.M., Pate, J.S. & Dixon, K.W. 1984. Rooting patterns of sandplain plants and their significance. In: Pate, J.S. & Beard, J.S. (eds.) *Kwongan: plant life of the sandplain*, University of Western Australia Press, Perth, AU.
- Dodson, J.R. & Lu, J.J. 2000. A late Holocene vegetation and environmental record from Byenup Lagoon, south-western Australia. *Australian Geographer* 31: 41-54.
- Dodson, J.R. & Ramrath, A. 2001. An upper Pliocene lacustrine environmental record from southwestern Australia. *Palaeogeography, Palaeoclimatology and Palaeoecology* 167: 309-320.
- Dupuy, J.M. & Chazdon, R.L. 2008. Interacting effects of canopy gap, understorey vegetation and leaf litter on tree seedling recruitment and composition in tropical secondary forests. *Forest Ecology and Management* 255: 3716-3725.
- Enright, N.J., Marsula, R., Lamont, B.B. & Wissel, C. 1998. The ecological significance of canopy seed storage in fire-prone environments: a model for resprouting shrubs. *Journal of Ecology* 86: 960-973.
- Environment Australia 2001. Threat abatement plan for dieback caused by the root-rot fungus *Phytophthora cinnamomi*. In: Environment Australia, Canberra, AU.
- Evans, R.A. & Young, J.A. 1970. Plant litter and establishment of alien annual weed species in rangeland communities. *Weed Science* 18: 697-703.
- Eviner, V.T. & Chapin III, F.S. 2003. Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. *Annual Review of Ecology, Evolution and Systematics* 34: 455-485.
- Fischer, J., Peterson, G.D., Gardner, T.A., Gordon, L.J., Fazey, I., Elmqvist, T., Felton, A., Folke, C. & Dovers, S. 2009. Integrating resilience thinking and optimisation for conservation. *Trends in Ecology and Evolution* 24: 549-554.

- Folke, C., Carpenter, S., Walker, M., Scheffer, M., Elmqvist, T., Gunderson, L. & Holling, C.S. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology and Systematics* 35: 557-581.
- Fox, D. 2007. Ecology: Back to the No-Analog Future? *Science* 316: 823-825.
- Frazer, G.W., Canham, C.D. & Letzman, K.P. 1999. Gap Light Analyzer (GLA): imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs. Version 2.0. In: Users manual and program documentation. Simon Fraser University, Burnaby, BC.
- Garkaklis, M.J., Calver, M.C., Wilson, B.A. & Hardy, G.E.S.J. 2004. Habitat alteration caused by an introduced plant disease, *Phytophthora cinnamomi*: a potential threat to the conservation of Australian forest fauna. In: Lunney, D. (ed.) *Conservation of Australia's forest fauna (second edition)*, Royal Zoological Society of New South Wales, Mosman, AU.
- Garnier, E., Cortez, J., Billes, G., Navas, M., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C. & Toussaint, J. 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85: 2630-2637.
- Gilbert, G.S. 2002. Evolutionary ecology of plant disease in natural ecosystems. *Annual Review of Phytopathology* 40: 13-43.
- Gole, C. 2006. The Southwest Australia ecoregion: jewel of the Australian continent. In: Southwest Australia Ecoregion Initiative, Perth, AU.
- Grant, M. & Barrett, S. 2003. The distribution and impact of *Phytophthora cinnamomi* Rands in the south coast region of Western Australia. In: McComb, J.A., Hardy, G.E.S. & Tommerup, I.C. (eds.) *Phytophthora in forests and natural ecosystems: 2nd international IUFRO working party*, 34-40. Murdoch University Print, Albany, AU.
- Greenhalgh, F.C. 1978. Evaluation of techniques for quantitative detection of *Phytophthora cinnamomi*. *Soil Biology and Biochemistry* 10: 257-259.
- Grehan, J. 2005. SCRIPT *Phytophthora cinnamomi* susceptible species database.
- Grime, J.P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* 86: 902-910.

- Groom, P.K. 2004. Rooting depth and plant water relations explain species distribution patterns within a sandplain landscape. *Functional Plant Biology* 31: 423-428.
- Gunderson, L.H. 2001. Managing surprising ecosystems in southern Florida. *Ecological Economics* 37: 371-378.
- Gunderson, L.H., Holling, C.S. & Light, S.S. 1995. *Barriers and bridges to the renewal of ecosystems and institutions*. Columbia University Press, New York, US.
- Hansen, E.M. 1999. Disease and diversity in forest ecosystems. *Australasian Plant Pathology* 28: 313-319.
- Hardy, G., Barrett, S. & Shearer, B.L. 2001. The future of phosphite as a fungicide to control the soilborne plant pathogen *Phytophthora cinnamomi* in natural ecosystems. *Australasian Plant Pathology* 30: 133-139.
- Harris, J.A., Kassaby, F.Y. & Smith, I.W. 1985. Variations in mortality in families of *Eucalyptus regnans* caused by *Phytophthora cinnamomi* up to 5 years after planting. *Australian Forest Research* 15: 57-65.
- Hassell, C.W. & Dodson, J.R. 2003. The fire history of south-west Western Australia prior to European settlement in 1826-1829. In: Abbott, I. & Burrows, N.C. (eds.) *Fire in ecosystems of the south-west of Western Australia: impacts and management*, Backhuys, Leiden, NL.
- Havel, J.J. 1979. Identification of vulnerable communities and prediction of disease spread. In: Old, K.M. (ed.) *Phytophthora and forest management in Australia*, 64-72. CSIRO, Melbourne, AU.
- Havel, J.J. & Matisse, E.M. 2002. Delineation of landscape conservation units in the Southwest region of Western Australia. In: Matisse Consulting Pty Ltd & Havel Land Consultants, Perth, AU.
- Havel, J.J. & Matisse, E.M. 2000. Vegetation mapping of South West Forest Regions of Western Australia. In: Matisse Consulting Pty Ltd, Perth, AU.
- He, T., Krauss, S.L., Lamont, B.B., Miller, B.P. & Enright, N.J. 2004. Long-distance seed dispersal in a metapopulation of *Banksia hookeriana* inferred from a population allocation analysis of amplified fragment length polymorphism data. *Molecular Ecology* 13: 1099-1109.

- Higgins, S.I., Nathan, R. & Cain, M.L. 2003. Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? *Ecology* 84: 1945-1956.
- Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A., Epstein, P.R., Ewel, J.J., Klink, C.A., Lugo, A.E., Norton, D., Ojima, D., Richardson, D.M., Sanderson, E.W., Valladares, F., Vila, M., Zamora, R. & Zobel, M. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography* 15: 1-7.
- Hobbs, R.J., Higgs, E. & Harris, J.A. 2009. Novel ecosystems: implications for conservation and restoration. *Trends in Ecology and Evolution* 24: 599-605.
- Holdenrieder, O., Pautasso, M., Weisberg, P.J. & Lonsdale, L. 2004. Tree diseases and landscape processes: the challenge of landscape pathology. *Trends in Ecology and Evolution* 19: 446-452.
- Holling, C.S. 1996. Engineering resilience versus ecological resilience. In: Schulze, P. (ed.) *Engineering within ecological restraints*, 31-44. National Academy, Washington DC, US.
- Holling, C.S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4: 1-23.
- Holling, C.S. 1978. The spruce-budworm/forest-management problem. In: Holling, C.S. (ed.) *Adaptive environmental assessment and management*, 143-182. John Wiley & Sons, New York, US.
- Holling, C.S. & Gunderson, L.H. 2002. Resilience and adaptive cycles. In: Gunderson, L.H. & Holling, C.S. (eds.) *Panarchy: understanding transformations in human and natural systems*, 25-62. Island Press, Washington DC, US.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75: 3-35.
- Hooper, D.U., Solan, M., Symstad, A., Diaz, S., Gessner, M.O., Buchmann, N., Degrange, V., P., G., Hulot, F., Mermillod-Blondin, F., Roy, J., Spehn, E. & van Peer, L. 2004. Species diversity, functional diversity, and ecosystem functioning. In: Loreau, M., Naeem, S. & Inchausti, P. (eds.) *Biodiversity*

and ecosystem functioning: synthesis and perspectives, 195-281. Oxford University Press, Oxford, UK.

Hopper, S.D. 1979. Biogeographical aspects of speciation in the south-west Australian flora. *Annual Review of Ecology and Systematics* 10: 399-422.

Hopper, S.D. 2009. OCBIL Theory: towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically-buffered, infertile landscapes. *Plant and Soil* 322: 49-86.

Hopper, S.D. 1992. Patterns of diversity at the population and species levels in south-west Australian mediterranean ecosystems. In: Hobbs, R.J. (ed.) *Biodiversity of mediterranean ecosystems in Australia*, 27-46. Surrey Beatty and Sons, Chipping Norton, UK.

Hopper, S.D. & Gioia, P. 2004. The Southwest Australian Floristic Region: evolution and conservation of a global hot spot of biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 35: 623-650.

Hughes, T.P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265: 1547-1551.

Huston, M. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* 110: 449-460.

Huston, M. 2003. Understanding the effects of fire and other mortality-causing disturbances on species diversity. In: Abbott, I. & Burrows, N. (eds.) *Fire in South-western Australian forests: impacts and management*, 37-70. Backhuys, Leiden, NL.

Irwin, J.A.G., Cahill, D.M. & Drenth, A. 1995. *Phytophthora* in Australia. *Australian Journal of Agricultural Research* 46: 1311-1337.

James, S. 1984. Lignotubers and burls - their structure, function and ecological significance in Mediterranean ecosystems. *The Botanical Review* 50: 225-266.

Jost, L. 2006. Entropy and diversity. *Oikos* 113: 363-375.

Kareiva, P. 1996. Diversity and sustainability on the prairie. *Nature* 379: 673-674.

- Kareiva, P. 1994. Diversity begets productivity. *Nature* 368: 686-687.
- Kassi N' Dja, J.K. & Decocq, G. 2008. Successional patterns of plant species and community diversity in a semi-deciduous tropical forest under shifting cultivation. *Journal of Vegetation Science* 19: 809-820.
- Keighery, G.J., Coates, D.J. & Gibson, N. 1994. Future ecosystems - ecological balance (ecological impact of disease causing fungi in south-western Australia). *Journal of the Royal Society of Western Australia* 77: 181-184.
- Kinal, J. 1993. Soil temperature in the northern jarrah forest in relation to plant and litter cover and implications for the periods and depths at which temperature permit *Phytophthora cinnamomi* activity. Master of Philosophy - Murdoch University, Perth, AU.
- Kitron, U. 1998. Landscape ecology and epidemiology of vector-borne diseases: tools for spatial analysis. *Journal of Medical Entomology* 35: 435-445.
- Laidlaw, W.S. & Wilson, B.A. 2003. Floristic and structural characteristics of a coastal heathland exhibiting symptoms of *Phytophthora cinnamomi* infestation in the eastern Otway Ranges, Victoria. *Australian Journal of Botany* 51: 283-293.
- Lamont, B.B. 1995. Testing the effect of ecosystem composition/structure on its functioning. *Oikos* 74: 283-295.
- Lavelle, P., Blanchart, E., Martin, A., Martin, S., Spain, A., Toutain, F., Barois, I. & Schaefer, R. 1993. A hierarchical model for decomposition in terrestrial ecosystems: application to soils of the humid tropics. *Biotropica* 25: 130-150.
- Lavorel, S., Díaz, S., Cornelissen, J.H.C., Garnier, E., Harrison, S.P., McIntyre, S., Pausas, J.G., Pérez-Harguindeguy, N., Roumet, C. & Urcelay, C. 2007. Plant functional types: are we getting any closer to the holy grail? In: Canadell, J.G., Pataki, D.E. & Pitelka, L.F. (eds.) *Terrestrial Ecosystems in a Changing world*, 149-159. Springer-Verlag, Berlin, DE.
- Lavorel, S. & Garnier, E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the holy grail. *Functional Ecology* 16: 545-556.

- Lawton, J.H. & Brown, V.K. 1993. Redundancy in ecosystems. In: Schulze, E.D. & Mooney, H.A. (eds.) *Biodiversity and Ecosystem Function*, 255-270. Springer-Verlag, Berlin, DE.
- Lepš, J., de Bello, F., Lavorel, S. & Berman, S. 2006. Quantifying and interpreting functional diversity of natural communities: practical considerations matter. *Preslia* 78: 481-501.
- Levia, D.F. & Frost, E.E. 2006. Variability of throughfall volume and solute inputs in wooded ecosystems. *Progress in Physical Geography* 30: 605-632.
- Levin, S.A. 1998. Ecosystems and biospheres as complex adaptive systems. *Ecosystems* 1: 431-436.
- Lindenmayer, D.B., Fischer, J., Felton, A., Crane, M., Michael, D., Macgregor, C., Montague-Drake, R., Manning, A. & Hobbs, R.J. 2008. Novel ecosystems resulting from landscape transformation create dilemmas for modern conservation practice. *Conservation Letters* 1: 129-135.
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D. & Wardle, D.A. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294: 804-808.
- Lovett, G.M., Canham, C.D., Arthur, M.A., Weathers, K.C. & Fitzhugh, R.D. 2006. Forest ecosystem responses to exotic pests and pathogens in eastern North America. *Bioscience* 56: 395-405.
- Ludwig, D., Walker, B. & Holling, C.S. 1997. Sustainability, stability, and resilience. *Conservation Ecology Series* 1: <URL:<http://www.consecol.org/vol1/iss1/art7>>.
- Magurran, A.E. 2004. *Measuring biological diversity*. Blackell Publishing, Victoria, AU.
- Malajczuk, N. 1988. Interaction between *Phytophthora cinnamomi* zoospores and microorganisms on non-mycorrhizal and ectomycorrhizal roots of *Eucalyptus marginata*. *Transactions of the British Mycological Society* 90: 375-382.
- Malajczuk, N. 1983. Microbial antagonism to *Phytophthora*. In: Erwin, D.C., Bartnicki-Garcia, S. & Tsao, P.H. (eds.) *Phytophthora: its biology, taxonomy, ecology and pathology*, 197-218. The American Phytopathological Society, St Paul, US.
- Marks, G.C. & Kassaby, F.Y. 1974. Detection of *Phytophthora cinnamomi* in soils. *Australian Forestry* 36: 198-203.

Matson, P.A. & Boone, R.D. 1984. Natural disturbance and nitrogen mineralization: wave-form dieback of mountain hemlock in the Oregon Cascades. *Ecology* 65: 1511-1516.

Mattiske, E.M. & Havel, J.J. 1998. Vegetation mapping in the south west of Western Australia. In: Department of Conservation and Land Management, Perth, AU.

McCaw, L. & Hanstrum, B. 2003. Fire environment of mediterranean south-west Western Australia. In: Abbott, I. & Burrows, N.C. (eds.) *Fire in ecosystems of the south-west of Western Australia: impacts and management*, 171-187. Backhuys, Leiden, NL.

McDougall, K.L. 1997. Vegetation patterns in the Northern Jarrah Forest of Western Australia in relation to dieback history and the current distribution of *Phytophthora cinnamomi*. Doctor of Philosophy - Murdoch University, Perth, AU.

McDougall, K.L., Hobbs, R.J. & Hardy, G.E.S. 2005. Distribution of understorey species in forest affected by *Phytophthora cinnamomi* in south-western Western Australia. *Australian Journal of Botany* 53: 813-819.

McDougall, K.L., Hobbs, R.J. & Hardy, G.E.S. 2002. Vegetation of *Phytophthora cinnamomi* infested and adjoining uninfested sites in the northern jarrah (*Eucalyptus marginata*) forest of Western Australia. *Australian Journal of Botany* 50: 277-288.

Meers, T.L., Bell, T.L., Enright, N.J. & Kasel, S. 2008. Role of plant functional traits in determining vegetation composition of abandoned grazing land in north-eastern Victoria, Australia. *Journal of Vegetation Science* 19: 515-524.

Micheli, F. & Halpern, B.S. 2005. Low functional redundancy in coastal marine assemblages. *Ecology Letters* 8: 391-400.

Moles, A.T., Gruber, M.A.M. & Bonser, S.P. 2008. A new framework for predicting invasive plant species. *Journal of Ecology* 96: 13-17.

Moore, N., Barrett, S., Bowen, B., Shearer, B.L. & Hardy, G.E.S. 2007. The role of fire on *Phytophthora* dieback caused by the root pathogen *Phytophthora cinnamomi* in the Stirling Ranges National Park, Western Australia. In: Rokich, D., Wardell-Johnson, G.W., Yates, C., Stevens, J.,

- Dixon, K., McLellan, R. & Moss, G. (eds.) *MEDECOS XI: The International Mediterranean Ecosystem Conference*, Kings Park and Botanic Gardens, Perth, AU.
- Mucina, L. & Wardell-Johnson, G.W. 2011. Landscape age and soil fertility, climatic stability, and fire regime predictability: beyond the OCBIL framework. *Plant Soil* 341: 1-23.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853-858.
- Naeem, S. 1998. Species redundancy and ecosystem reliability. *Conservation Biology* 12: 39-45.
- Naeem, S., Colwell, R., Diaz, S., Hughes, J., Jouseau, C., Lavorel, S., Morin, P., Petchey, O. & Wright, J. 2007. Predicting the ecosystem consequences of biodiversity loss: the biome framework. In: Canadell, J.G., Pataki, D.E. & Pitelka, L.F. (eds.) *Terrestrial ecosystems in a changing world*, 113-126. Springer-Verlag, Berlin, DE.
- Naeem, S. & Li, S. 1997. Biodiversity enhances ecosystem reliability. *Nature* 390.
- Naeem, S., Loreau, M. & Inchausti, P. 2004. Biodiversity and ecosystem functioning: the emergence of a synthetic ecological framework. In: Loreau, M., Naeem, S. & Inchausti, P. (eds.) *Biodiversity and ecosystem functioning: synthesis and perspectives*, 3-10. Oxford University Press, Oxford, UK.
- Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. & Woodfin, R.M. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* 368: 734-737.
- Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. & Woodfin, R.M. 1995. Empirical evidence that declining species diversity may alter the performance of terrestrial ecosystems. *Proceedings of the Royal Society Biological Sciences Series B* 347: 249-262.
- National biological information infrastructure & IUCN/SSC invasive species specialist group 2005. *Phytophthora cinnamomi* ecology. In: *Global invasive species database*.
- Nesbitt, H.J., Malajczuk, N. & Glenn, A.R. 1979a. Effect of organic matter on the survival of *Phytophthora cinnamomi* in soil. *Soil Biology and Biochemistry* 11: 133-136.

- Nesbitt, H.J., Malajczuk, N. & Glenn, A.R. 1979b. Effect of soil moisture and temperature on the survival of *Phytophthora cinnamomi* in soil. *Soil Biology and Biochemistry* 11: 137-140.
- Newman, S.J., Schuette, J., Grace, J.B., Rutchey, K., Fontaine, T., Reddy, K.R. & Pietrucha, M. 1998. Factors influencing cattail abundance in the northern everglades. *Aquatic Botany* 60: 265-280.
- Noss, R.F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* 4: 355-364.
- Nystrom, M., Folke, C. & Moberg, F. 2000. Coral reef disturbance and resilience in a human-dominated environment. *Trends in Ecology and Evolution* 15: 413-417.
- Paczkowska, G. & Chapman, A.R. 2000. *The Western Australia flora: a descriptive catalogue*. Wildflower Society of Western Australia, Western Australian Herbarium and Botanic Gardens and Parks Authority, Perth, AU.
- Pakeman, R.J., Lep, J., Kleyer, M., Lavorel, S. & Garnier, E. 2009. Relative climatic, edaphic and management controls of plant functional trait signatures. *Journal of Vegetation Science* 20: 148-159.
- Pate, J.S. & Beard, J.S. 1984. *Kwongan: plant life of the sandplain*. University of Western Australia Press, Nedlands, AU.
- Pate, J.S. & Bell, T.L. 1999. Application of the ecosystem mimic concept to the species-rich *Banksia* woodlands of Western Australia. *Agroforestry Systems* 45: 303-341.
- Pavoine, S. & Doledec, S. 2005. The apportionment of quadratic entropy: a useful alternative for partitioning diversity in ecological data. *Environment and Ecological Statistics* 12: 125-138.
- Pech, R.P., Sinclair, A.R.E., Newsome, A.E. & Catling, P.C. 1992. Limits to predator regulation of rabbits in Australia - evidence from predator-removal experiments. *Oecologia* 89: 102-112.
- Petchey, O.L. & Gaston, K.J. 2002. Functional diversity (FD), species richness and community composition. *Ecology Letters* 5: 402-411.
- Petchey, O.L. & Gaston, K.J. 2006. Functional diversity: back to basics and looking forward. *Ecology Letters* 9: 741-758.

- Peterson, G., Allen, C.R. & Holling, C.S. 1998. Ecological resilience biodiversity, and scale. *Ecosystems* 1: 6-18.
- Pillar, V.D. & Orloci, L. 1996. On randomization testing in vegetation science: multifactor comparisons of releve groups. *Journal of Vegetation Science* 7: 585-592.
- Podger, F.D. 1972. *Phytophthora cinnamomi*, a cause of lethal disease in Indigenous plant communities in Western Australia. *Phytopathology* 62: 972-981.
- Podger, F.D. & Brown, M.J. 1989. Vegetation damage caused by *Phytophthora cinnamomi* on disturbed sites in temperate rain-forest in Western Tasmania. *Australian Journal of Botany Supplementary Series* 37: 443-480.
- Podger, F.D., Mummery, D.C., Palzer, C.R. & Brown, M.J. 1990. Bioclimatic analysis of the distribution of damage to native plants in Tasmania by *Phytophthora cinnamomi*. *Austral Ecology* 15: 281-289.
- Poorter, H. & Garnier, E. 1999. Ecological significance of inherent variation in relative growth rate and its components. In: Pugnaire, F.I. & Valladares, F. (eds.) *Handbook of functional plant ecology*, 81-120. Marcel Dekker, New York, USA.
- Prescott, C.E. 2002. The influence of the forest canopy on nutrient cycling. *Tree Physiology* 22: 1193-1200.
- Pressland, A.J. 1976. Soil moisture redistribution as affected by throughfall and stemflow in an arid zone shrub community. *Australian Journal of Botany* 24: 641-649.
- Price, O., Edwards, A., Connors, G., Woinarski, J., Ryan, G., Turner, A. & Russell-Smith, J. 2005. Fire heterogeneity in Kakadu National Park, 1980-2000. *Wildlife Research* 32: 425-433.
- Quested, H., Eriksson, O., Fortunel, C. & Garnier, E. 2007. Plant traits relate to whole-community litter quality and decomposition following land use change. *Functional Ecology* 21: 1016-1026.
- Quetier, F., Thebault, A. & Lavorel, S. 2007. Plant traits in a state and transition framework as markers of ecosystem response to land-use change. *Ecological Monographs* 77: 33-52.

- Rao, C.R. 1982. Diversity and dissimilarity coefficients - a unified approach. *Theoretical Population Biology* 21: 24-43.
- Reich, P.B., Walters, M.B. & Ellsworth, D.S. 1997. From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the USA* 94: 13730-13734.
- Reich, P.B., Walters, M.B. & Ellsworth, D.S. 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs* 62: 365-392.
- Reiss, J., Bridle, J.R., Montoya, J.M. & Woodward, G. 2009. Emerging horizons in biodiversity and ecosystem functioning research. *Trends in Ecology and Evolution* 24: 505-514.
- Resilience Alliance 2007a. Assessing resilience in social-ecological systems: a workbook for practitioners. <http://www.resalliance.org>.
- Resilience Alliance 2007b. Assessing resilience in social-ecological systems: a workbook for scientists. <http://www.resalliance.org>.
- Resilience Alliance 2005. Resilience key concepts: adaptive cycles. *Santa Fe Institute* <http://www.resalliance.org>.
- Resilience Alliance 2004. Thresholds and alternate states in ecological and social-ecological systems. *Santa Fe Institute* <http://www.resalliance.org>.
- Resilience Alliance 2011. Thresholds database. *Santa Fe Institute* <http://www.resalliance.org>.
- Richards, J.H. & Caldwell, M.M. 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia* 73: 486-489.
- Ricotta, C. 2005. A note on functional diversity measures. *Basic and Applied Ecology* 6: 479-486.
- Ricotta, C. 2003. Parametric scaling from species relative abundances to absolute abundances in the computation of biological diversity: a first proposal using Shannon's entropy. *Acta Biotheoretica* 51: 181-188.
- Rizzo, D.M. & Garbelotto, M. 2003. Sudden oak death: endangering California and Oregon forest ecosystems. *Frontiers in Ecology and the Environment* 1: 197-204.

- Rockel, B.A., McGann, L.R. & Murray, D.I.L. 1982. *Phytophthora cinnamomi* causing death of *Dryandra sessilis* on old dieback sites in the Jarrah forest. *Australasian Plant Pathology* 11: 49-50.
- Russell-Smith, J., Ryan, P.G. & Cheal, D.C. 2002. Fire regimes and the conservation of sandstone heath in monsoonal northern Australia: frequency, interval, patchiness. *Biological Conservation* 104: 91-106.
- Ryan, B. & Hope, P. 2006. Indian Ocean climate initiative stage 2: report of phase 2 activity: January 2005 - June 2006. In: *Indian Ocean Climate Initiative*, Indian Ocean Climate Initiative, Perth, AU.
- Scheffer, M., Carpenter, S., Foley, J.A., Folkes, C. & Walker, B. 2001. Catastrophic shifts in ecosystems. *Nature* 413: 591-596.
- Schroder, A., Persson, L. & De Roos, A.M. 2005. Direct experimental evidence for alternative stable states: A Review. *Oikos* 110: 3-9.
- Schumpeter, P. 1950. *Capitalism, socialism and democracy*. Harper and Row, New York, US.
- Seastedt, T.R., Hobbs, R.J. & Suding, K.N. 2008. Management of novel ecosystems: are novel approaches required? *Frontiers in Ecology and the Environment* 6: 547-553.
- Shea, S.R., Shearer, B.L., Tippett, J. & Deegan, P.M. 1983. Distribution, reproduction, and movement of *Phytophthora cinnamomi* on sites highly conducive to Jarrah dieback in South Western Australia. *Plant Disease* 67: 970-973.
- Shearer, B.L. 1990. Dieback of native plant communities caused by *Phytophthora* species: a major factor affecting land use in south-western Australia. In: *Land and Water Research News*, 15-26. Western Australian Steering Committee for Research on Land Use and Water Supply, Perth, AU
- Shearer, B.L., Crane, C.E., Barrett, S. & Cochrane, A. 2007. *Phytophthora cinnamomi* invasion, a major threatening process to conservation of flora diversity in the South-west Botanical Province of Western Australia. *Australian Journal of Botany* 55: 225-238.

- Shearer, B.L., Crane, C.E. & Cochrane, A. 2004a. Quantification of the susceptibility of the native flora of the South-west botanical province, Western Australia to *Phytophthora cinnamomi*. *Australian Journal of Botany* 52: 435-443.
- Shearer, B.L., Crane, C.E. & Fairman, R.G. 2004b. Phosphite reduces disease extension of a *Phytophthora cinnamomi* front in *Banksia* woodland, even after fire. *Australasian Plant Pathology* 33: 249-254.
- Shearer, B.L., Crane, C.E., Fairman, R.G. & Dunne, C.P. 2009a. Ecosystem dynamics altered by pathogen-mediated changes following invasion of *Banksia* woodland and *Eucalyptus marginata* forest biomes of south-western Australia by *Phytophthora cinnamomi*. *Australasian Plant Pathology* 38: 1-20.
- Shearer, B.L. & Dillon, M. 1996a. Impact and disease centre characteristics of *Phytophthora cinnamomi* infestations of *Banksia* woodlands on the Swan Coastal Plain, Western Australia. *Australian Journal of Botany* 44: 79-90.
- Shearer, B.L. & Dillon, M. 1996b. Susceptibility of plant species in *Banksia* woodlands on the Swan Coastal Plain, Western Australia, to infection by *Phytophthora cinnamomi*. *Australian Journal of Botany* 44: 713-713.
- Shearer, B.L. & Dillon, M. 1995. Susceptibility of plant species in *Eucalyptus marginata* forest to infection by *Phytophthora cinnamomi*. *Australian Journal of Botany* 43: 113-134.
- Shearer, B.L., Dillon, M.J., Kinal, J. & Buehrig, R.M. 2009b. Temporal and spatial soil inoculum dynamics following *Phytophthora cinnamomi* invasion of *Banksia* woodland and *Eucalyptus marginata* forest biomes of south-western Australia. *Australasian Plant Pathology* 2010: 293-311.
- Shearer, B.L. & Hill, T.C. 1989. Diseases of *Banksia* woodlands on the Bassendean and Spearwood Dune systems. *Journal of the Royal Society of Western Australia* 71: 113-114.
- Shearer, B.L. & Shea, S.R. 1987. Variation in seasonal population fluctuations of *Phytophthora cinnamomi* within and between infected *Eucalyptus marginata* sites of Southwestern Australia. *Forest Ecology and Management* 21: 209-230.

- Shearer, B.L. & Smith, I.W. 2000. Diseases of eucalypts caused by soilborne species of *Phytophthora* and *Pythium*. In: Keane, P.J., Kile, G.A., Podger, F.D. & Brown, B.N. (eds.) *Diseases and pathogens of eucalypts*, 259-284. CSIRO publishing, Collingwood, AU.
- Shearer, B.L. & Tippett, J.T. 1989. Jarrah dieback: the dynamics and management of *Phytophthora cinnamomi* in the Jarrah (*Eucalyptus marginata*) forest of south-western Australia. In: Department of Conservation and Land Management, Western Australia, Perth, AU.
- Specht, R.L. 1957. Soil moisture patterns produced by rainfall interception and stemflow. *Australian Journal of Botany* 5: 137-150.
- Stack, G. & Brown, A. 2003. Small-flowered snottygobble (*Personia micranthera*) interim recovery plan 2003-2008. In: Department of Conservation and Land Management, Albany, AU.
- Stukely, M.J.C. & Crane, C.E. 1994. Genetically based resistance of *Eucalyptus marginata* to *Phytophthora cinnamomi*. *Phytopathology* 84: 650-656.
- Stukely, M.J.C., Crane, C.E., McComb, J.A. & Bennett, I.J. 2007. Field survival and growth of clonal, micropropagated *Eucalyptus marginata* selected for resistance to *Phytophthora cinnamomi*. *Forest Ecology and Management* 238: 330-334.
- Suding, K.N. & Hobbs, R.J. 2009. Threshold models in restoration and conservation: a developing framework. *Trends in Ecology and Evolution* 24: 271-279.
- Suding, K.N., Lavorel, S., Chapin III, F.S., Cornelissen, J.H.C., Diaz, S., Garnier, E., Goldberg, D., Hooper, D.U., Jackson, S.T. & Navas, M.L. 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology* 14: 1125-1140.
- Sweedman, L. & Merritt, D. 2006. *Australian Seeds: a guide to their collection, identification and biology*. CSIRO Publishing, Collingwood, AU.
- Swenson, N.G. & Weiser, M.D. 2010. Plant geography upon the basis of functional traits: an example from eastern North American trees. *Ecology* 91: 2234-2241.
- TIBCO Spotfire 2007. S-PLUS statistical package.

- Tilman, D. 1996. Biodiversity: population versus ecosystem stability. *Ecology* 77: 350-363.
- Tilman, D. 2001. Functional diversity. In: Levin, S.A. (ed.) *Encyclopedia of Biodiversity*, 109-120. Academic Press, San Diego, US.
- Tippett, J. & Malajczuk, N. 1979. Interaction of *Phytophthora cinnamomi* and a resistant host *Acacia pulchella*. *Phytopathology* 69: 764-772.
- Trenbath, B.R., Conway, G. & Craig, I.A. 1989. Threats to sustainability in intensified agricultural systems: analysis and implications for management. In: Gliessman, S.R. (ed.) *Agroecology: researching the ecological basis for sustainable agriculture*, 337-365. Springer-Verlag, New York, US.
- Turner, M.G. 2005. Landscape ecology: what is the state of the science? *Annual Review of Ecology, Evolution, and Systematics* 36: 319-344.
- Turney, C.S.M., Bird, M.I., Fifield, L.K., Roberts, R.G., Smith, M., Dortch, C.E., Grun, R., Lawson, E., Ayliffe, L.K., Miller, G.H., Dortch, J. & Cresswell, R.G. 2001. Early human occupation at Devil's Lair, Southwestern Australia 50,000 years ago. *Quaternary Research* 55: 3-13.
- Vandermaast, D.B. & Van Lear, D.H. 2002. Riparian vegetation in the southern Appalachian mountains (USA) following chestnut blight. *Forest Ecology and Management* 155: 97-106.
- Vandermeer, J., De La Cerda, I.G., Perfecto, I., Boucher, D., Ruiz, J. & Kaufmann, A. 2004. Multiple basins of attraction in a tropical forest: evidence for nonequilibrium community structure. *Ecology* 85: 575-579.
- Vitousek, P.M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. *Oikos* 57: 7-13.
- Vitousek, P.M., D'Antonio, C.M., Loope, L.L. & Westbrooks, R. 1996. Biological invasions as global environmental change. *American Scientist* 84: 468-478.
- Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. 1997. Human domination of earth's ecosystems. *Science* 277: 494-499.
- Walker, B. 1992. Biological diversity and ecological redundancy. *Conservation Biology* 6: 18-23.

- Walker, B., Holling, C.S., Carpenter, S.R. & Kinzig, A. 2004. Resilience, adaptability and transformability in social-ecological systems. *Ecology and Society* 9: 1-5.
- Walker, B., Kinzig, A. & Langridge, J.L. 1999. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems* 2: 95-113.
- Walker, B. & Salt, D. 2006. *Resilience Thinking*. Island Press, Washington DC, US.
- Walker, B.H. 1995. Conserving biological diversity through ecosystem resilience. *Conservation Biology* 9: 747-752.
- Walker, B.H. & Langridge, J.L. 2002. Measuring functional diversity in plant communities with mixed life forms: a problem of hard and soft attributes. *Ecosystems* 5: 529-538.
- Wardell-Johnson, G.W., Burrows, N. & Li, S. 2006. Emergent patterns in the mosaic of patch burning vary with the fire environment and landscape context in south-western Australia. In: *Bushfire conference: life in a fire-prone environment - translating science into practice*, Griffith University, Brisbane, AU.
- Wardell-Johnson, G.W. & Horwitz, P. 2000. The recognition of heterogeneity and restricted endemism in the management of forested ecosystems in south-western Australia. *Australian Forestry* 63: 218-225.
- Wardell-Johnson, G.W. & Nichols, O. 1991. Forest wildlife and habitat management in southwestern Australia: knowledge, research and direction. In: Lunney, D. (ed.) *Conservation of Australia's forest fauna*, 161-192. Royal Zoological Society of NSW, Sydney, AU.
- Wardell-Johnson, G.W. & Williams, M.R. 1996. A floristic survey of the Tingle Mosaic, south-western Australia: applications in land use planning and management. *Journal of the Royal Society of Western Australia* 79: 249-276.
- Wardell-Johnson, G.W., Williams, M.R., Mellican, A.E. & Annells, A. 2004. Floristic patterns and disturbance history in karri forest, south-western Australia 1. Environment and species richness. *Forest Ecology and Management* 199: 449-460.
- Warton, D.I. 2008. Raw data graphing: an informative but under-utilized tool for the analysis of multivariate abundances. *Austral Ecology* 33: 290-300.

Weatherzone 2011. North Walpole Climate <http://www.weatherzone.com.au/>.

Weste, G. 2003. The dieback cycle in Victorian forests: A 30-year study of changes caused by *Phytophthora cinnamomi* in Victorian open forests, woodlands and heathlands. *Australasian Plant Pathology* 32: 247-256.

Weste, G. 1980. Vegetation changes as a result of invasion of forest on krasnozem by *Phytophthora cinnamomi*. *Australian Journal of Botany* 28: 139-150.

Weste, G. 1986. Vegetation Changes Associated with Invasion by *Phytophthora cinnamoni* of Defined Plots in the Brisbane Ranges Victoria Australia 1975-1985. *Australian Journal of Botany* 34: 633-648.

Weste, G. & Vithanage, K. 1979. Survival of chlamydospores of *Phytophthora cinnamomi* in several non-sterile, host-free forest soils and gravels at different soil water potentials. *Australian Journal of Botany* 27 1-9.

Weste, G., Walchhuetter, T. & Walshe, T. 1999. Regeneration of *Xanthorrhoea australis* following epidemic disease due to *Phytophthora cinnamomi* in the Brisbane Ranges, Victoria. *Australasian Plant Pathology* 28: 162-169.

Western Australian Herbarium 2010. FloraBase: The Western Australian Flora. <http://florabase.dec.wa.gov.au/>.

Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* 199: 213-227.

Wheeler, J., Marchant, N. & Lewington, M. 2002. *Flora of the South West*. University of Western Australia Press, Perth, AU.

Whittaker, R.H. 1975. *Communities and ecosystems*. Macmillan, New York, US.

Wills, R.T. 1992. The Ecological Impact of *Phytophthora cinnamomi* in the Stirling Range National Park, Western Australia. *Australian Journal of Ecology* 17: 145-159.