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Ecosystem dynamics altered by pathogen-mediated changes following invasion of *Banksia* woodland and *Eucalyptus marginata* forest biomes of south-western Australia by *Phytophthora cinnamomi*

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Abstract. Changes in plant species richness and composition, vegetation structure, ecosystem functioning and soil nutrients following invasion of *Banksia* woodland and *Eucalyptus marginata* forest biomes by the introduced soilborne multihost plant pathogen *Phytophthora cinnamom* were determined using space-for-time substitution of diseased and adjoining healthy areas. In most study areas, canopy closure, basal area and number of plant species were significantly lower in old diseased compared with adjoining healthy areas, with diseased front intermediate between the two. In half of the study areas, percentage ground cover and total plant species cover were significantly lower in old diseased compared with adjoining healthy areas, with diseased front intermediate between the two. Evenness, Shannon-Weiner H and Simpson's D did not significantly change between disease status for the majority of study areas. For ordination of percentage canopy closure and ground cover there was separation of study areas along a disease status gradient and a weak soil fertility gradient. There was significantly less percentage organic carbon, extractable phosphorus and extractable and total potassium in old diseased areas compared with adjoining healthy areas for one-quarter to a third of the study areas. Total phosphorus changed significantly between disease status, but this was due to higher levels in diseased front compared with the old diseased or adjoining healthy areas. For all study areas there was no significant effect of disease status on percentage total nitrogen and pH. The cover of a majority of plant species did not change significantly between disease status with 16% of the total number of perennial species in healthy areas significantly decreasing and 10% significantly increasing in cover in old diseased compared with adjoining healthy areas. As with significant differences in cover between disease status, change in cover of a majority of plant species was not significantly correlated with canopy closure. Cover of 20% of the total number of perennial species in healthy areas was significantly linearly positively correlated with canopy closure and the cover of 10% of plant species was significantly negatively correlated with canopy closure. These species were herbs and shrubs from a range of families with a mixture of functional properties such as *Phytophthoria cinnamomi* susceptibility, response to fire, rooting type and mycorrhizal association. The paper concludes with a conceptual analysis of core issues and those that cascade out of core issues involved in pathogen and patch plant community interactions.

Additional keywords: adaptive management, climate change, functional traits, nutrient cycling, patch dynamics, triage, secondary succession, structure, surrounding matrix, unplanned removal experiments.

Introduction

Invasions following human spread of non-native species are considered to be the most prominent force for depletion of biodiversity worldwide (McKinney and Lockwood 1999; Olden and Poff 2003). In addition to development of sound conservation practices, the study of species invasion has utility for using exotic species as model organisms to improve understanding of functioning of native systems (Callaway and Maron 2006; Sax *et al*. 2007). Although changes in biodiversity influence ecosystem processes (Chapin *et al*. 2000), little is known of the level of functional diversity needed to sustain ecosystem processes in response to patterns of loss of biodiversity (Loreau 2000; Hooper *et al*. 2005). Identification of appropriate functional groups (Cornelissen *et al*. 2003) within tropic levels is needed to predict diversity effects on ecosystem functioning (Loreau 2000; Hooper *et al*. 2005).

Invasion of the introduced soilborne multi-host plant pathogen *Phytophthora cinnamomi* is a major threatening process for the diverse flora of the South-West Botanical Province of Western Australia (Shearer *et al*. 2007), an internationally recognised hotspot of biodiversity (Myers 2001). Of the 5710 described plant species in the South-West

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Botanical Province, Shearer *et al*. (2004*a*) estimate that 2284 species are susceptible to *P. cinnamomi* and 800 of these 2284 species are highly susceptible to the pathogen. Within the province, *Banksia* woodland biome remnants in the Swan Coastal Plain bioregion (Shearer and Dillon 1996*a*) and *Eucalyptus marginata* biomes on watergaining soils in the Jarrah Forest bioregion (Shearer and Tippett 1989) are vulnerable to infestation.

Banksia woodland biomes of the Swan Coastal Plain bioregion contain at least one dominant *Banksia* species with other trees of low diversity and an understorey of predominantly woody shrubs (Beard 1989; Shearer and Dillon 1996*a*; Pate and Bell 1999). *Eucalyptus marginata* forest biomes of the Jarrah Forest bioregion are characterised by a dry sclerophyll forest dominated by *E. marginata*, with an understorey of small trees and a groundcover of woody shrubs (Dell and Havel 1989).

The bioregions experience a dry Mediterranean climate with hot and dry summers of 5–6 months (Beard 1984). The soils of both bioregions are nutrient-poor, being derived from a quartz sand terrain for *Banksia* woodland biomes (Semeniuk and Glassford 1989) and an ancient highly weathered lateritic profile for *E. marginata* forest (Churchward and Dimmock 1989). Fire is an integral component of the environment and the sclerophyll communities within *Banksia* woodland and *E. marginata* forest biomes have numerous adaptations enabling survival after fire (Bell *et al*. 1984, 1989).

Environmental characteristics of low fertile soils subject to drought and fire have resulted in a variety of functional responses by the vegetation to cope with these stresses. Such responses have evolved a diversity of strategies for regeneration after fire (Bell *et al*. 1984, 1989), rooting patterns to cope with drought (Dodd *et al*. 1984) and modifications related to symbiotic and non-symbiotic uptake, storage and cycling of nutrients (Lamont 1984; Brundrett and Abbott 1991).

Phytophthora cinnamomi is a relatively recent invader into the complex, species-rich Mediterranean ecosystems of the South-West Botanical Province of Western Australia (Shearer *et al*. 2007). Studies of the effects of *P. cinnamomi* invasion need to be from a synecological or community dynamics context rather than an autecological perspective (Shearer 1992). There is a need to focus on the invaded ecosystem rather than the invader (Hobbs and Humphries 1995).

Consequences of invasion of ecosystems of the South-West Botanical Province of Western Australian have primarily been determined from a botanical viewpoint using taxonomic compilations of changes in plant species richness and composition following infestation (Shearer and Hill 1989; Wills 1993; McDougall 1996; Shearer and Dillon 1996*a*; McDougall *et al*. 2002, 2005; Crane and Shearer 2007). However, change in plant species richness has been a poor predictor of the effects of invasion of several life forms of invaders (Yurkonis *et al*. 2005). Largely ignored are the ecological effects of *P. cinnamomi* invasion on structural and functional components of plant communities of the province. Using canopy closure as a measure of structural change, Crane and Shearer (2007) found significantly less canopy closure in *P. cinnamomi* invaded areas than in the adjoining healthy vegetation in three biomes. The effect of *P. cinnamomi* invasion on ecosystem functioning of plant communities of the Stirling Range National Park was determined by the frequency of occurrence of susceptible plant taxa in functional groupings (Wills 1993; Hobbs 1997). Similar to assessment of impact of *P. cinnamomi* in Western Australia, taxonomic compilations of plant species compositional change were mainly used to assess the impact of *P. cinnamomi* in Eastern Australian ecosystems (Weste *et al*. 1973; Weste 1986, 2003; Weste and Kennedy 1997; Laidlaw and Wilson 2003). In studies that examined vegetation structural change, infestation reduced canopy cover by a third over 20 years (Dawson *et al*. 1985) or no difference was found in canopy cover (Newell 1998) or height (Laidlaw and Wilson 2003) between infested and adjoining healthy areas. Inter-variable relationships and the effects on ecosystem dynamics have not been determined for *P. cinnamomi* invaded areas.

The changes in floristic composition that influence the structure and functioning of ecosystems affect trophic interactions and nutrient dynamics (Chapin *et al*. 1997). By exerting top-down control of populations from lower trophic levels, parasites may substantially alter host species diversity and in turn ecosystem processes including nutrient cycling (Loreau *et al*. 2005). Even though invasive exotics have the potential to change many components of the cycling of materials in an ecosystem, little attention has been paid to the potential effects of these invasions on nutrient cycling processes in the soil (Ehrenfeld 2003). Similarly, although mortality following *P. cinnamomi* invasion induces changes in flora structure and composition, little is known of subsequent consequences to nutrient cycling in affected communities (Shearer *et al*. 2007).

Detailed measurements have been made of *P. cinnamomi* soil inoculum dynamics, rates of disease extension and the conduciveness of soils in disease centres of several *Banksia* woodland and *E. marginata* forest biomes (Shearer *et al*. 1989; Shearer in preparation). Analysis of the data from the associated study areas gave the opportunity to undertake an examination of the processes underlying changes in flora richness, composition and structure, ecosystem functioning and soil nutrients in relation to invasion of *Banksia* woodland and *E. marginata* forest biomes by *P. cinnamomi*. Understanding these processes is fundamental to relevant quantification of the impact of pathogen invasion, determining communities at risk and restoration options.

Methods

Study areas

Six active disease centre infestations of *P. cinnamomi* with deaths in many susceptible plant species were located in *Banksia* woodland biomes of the Swan Coastal Plain bioregion and two were located in *E. marginata* forest biomes of the Jarrah Forest bioregion (Table 1). Areas were chosen because they were used in studies on pathogen and disease dynamics (Shearer *et al*. 1989; Shearer in preparation). A disease centre of *P. cinnamomi* is defined as ‘an area of disease expression around the point of initial inoculum introduction, with the outer perimeter usually delimited by a disease front of dead

Table 1. Characteristics of *Phytophthora cinnamomi* disease centres in *Banksia* woodland and *Eucalyptus marginata* forest biomes of the Swan Coastal Plain and Jarrah Forest bioregions, respectively, of the South-West Botanical Province of Western Australia, within which pathogen-mediated changes were determined

Study area[A]	Latitude, longitude	Disease centre area (ha)	Pathogen isolated from:	Vegetation		Soil		Soil system or Havel site type[B]
				Overstorey	Understorey	Colour	Type	
BW1	32.8778°S, 115.8228°E	0.5	*Banksia attenuata*, *Hibbertia hypericoides*	*B. attenuata*	*Acacia pulchella*, *H. hypericoides*, *Stirlingia latifolia*	Grey	Sand	Bassendean
BW2	32.8750°S, 115.8244°E	1	*B. attenuata*	*B. attenuata*	*A. pulchella*, *H. hypericoides*, *M. thymoides*	Grey	Sand	Bassendean
BW3	32.8933°S, 115.8275°E	4.5	*B. attenuata*, *H. hypericoides*	*B. attenuata*, *Eucalyptus marginata*	*A. pulchella*, *Calytrix flavescens*, *H. hypericoides*	Grey	Sand	Bassendean
BW4	33.6500°S, 115.0469°E	0.1	*B. attenuata*, *Hypocalymma robustum*	*Agonis flexuosa*, *Allocasuarina fraseriana*, *B. attenuata*	*D. hookeri*, *H. hypericoides*, *S. latifolia*	Orange-brown	Sand	Yoongarillup
BW5	33.8383°S, 115.0356°E	30	*B. ilicifolia*, *Dasypogon bromeliifolius*	*A. flexuosa*, *A. fraseriana*, *B. attenuata*	*D. bromeliifolius*, *C. flavescens*, *Lindsaea linearis*, *Xanthorrhoea preissii*	Grey	Sand	Bassendean
BW6	33.8556°S, 114.9958°E	1	*B. attenuata*, *Melaleuca thymoides*	*A. flexuosa*, *B. attenuata*	*C. flavescens*, *H. hypericoides*, *M. thymoides*	Grey	Sand	Bassendean
EmF1	32.7250°S, 116.0250°E	2	*B. grandis*	*Corymbia calophylla*, *E. marginata*	*B. grandis*, *Bossiaea ornata*	Brown	Laterite	Havel S
EmF2	32.7595°S, 115.9913°E	3	*B. grandis*	*A. fraseriana*, *E. marginata*	*B. grandis*, *B. ornata*, *X. preissii*	Brown	Laterite	Havel P

[A]BW = *Banksia* woodland biome in the Swan Coastal Plain bioregion, EmF = *Eucalyptus marginata* forest biome in the Jarrah Forest bioregion.
[B]Soil systems for *Banksia* woodland according to McArthur (1991). Havel site – vegetation types according to Havel (1975).

and dying infected vegetation' (Shearer *et al*. 2004*a*). Disease centres produced patches or expanding centres of mortality in the environment defined as an opening in the canopy of >200 m^2 that exhibits sufficient structural and behavioural differences from the surrounding matrix (McCarthy 2001). Symptoms of infection in susceptible flora (Shearer and Dillon 1995, 1996*a*, 1996*b*; Shearer *et al*. 2007) were used to distinguish between different disease status areas. An 'old' infection area surrounds the locality of initial introduction where most of the susceptible taxa have been killed, followed by the 'front' evident by a zone of recently killed vegetation that ingresses into adjoining 'healthy' vegetation beyond the front (see fig. 2 in Shearer *et al*. 2007).

Collar and root samples were taken from recently dead plant species on the active disease front in each disease centre. Presence of *P. cinnamomi* was determined by direct plating of the plant material to P10VPH agar as described in Shearer and Dillon (1995). Available aerial photographs of study areas BW1–3, 5 and 6 (Table 1) were examined to determine first occurrence of disease.

Experimental design

Biomes (*Banksia* woodland and *E. marginata* forest), *P. cinnamomi* disease status (old and front diseased areas and adjoining healthy area) were the independent variables. Canopy closure, basal area, estimates of ground cover, plant species number, total plant species cover and soil nutrients and properties were measured variables.

Trends in pathogen-mediated changes were determined using space-for-time substitution (Pickett 1989) of diseased and adjoining healthy areas (Crane and Shearer 2007; Shearer *et al*. 2007). The adjoining healthy area was used as the standard for comparison and evaluation (Aronson *et al*. 1995). Vegetation measurements were made in 2003 at three random positions in the old disease area along a line parallel to, and 20 m from, the active disease front delineated by dying plants. Measurements were also made at three random positions along the active front and at three random positions in the adjoining healthy area along a line parallel to, and 20 m ahead, of the active disease front. Three replicates were chosen because mean values of canopy closure and ground cover from measurements of three replicates in a *Banksia* woodland and an *E. marginata* forest biome were not significantly different from mean values for transects of 17–28 point measurements (Crane and Shearer 2007). The front in study area BW4 was very small and no vegetation measurements were made for the front in this study area. Three soil samples were taken within diseased and adjoining healthy areas in spring 2002 and on further advice (R. Harper, pers. comm.), a further 10 replicates per disease status in each study area were sampled in spring 2003. Study areas had not been burnt for at least 15 years before sampling.

Assessment

Canopy and basal area measurements

Canopy closure is defined as 'the proportion of the sky hemisphere obscured by vegetation when viewed from a single point' (Jennings *et al*. 1999). Canopy closure was obtained from hemispherical field-of-view digital images analysed with Gap Light Analyzer software (Frazer *et al*. 1999), as detailed in Crane and Shearer (2007). Basal area was determined using a basal area wedge (West 2004). Basal area in the old diseased area and the adjoining healthy area was determined at the three locations along the front.

Plant species number, total plant species and ground cover

The number of perennial live plant species present within a 25 m^2 quadrat at each measuring point was determined. Plant species number in *Banksia* woodland biomes had started to level off after 25 m^2 (Shearer and Dillon 1996*a*). The percentage of ground covered by each plant species within the quadrat was determined (Kennedy and Weste 1986; Crane and Shearer 2007) and added together to give total plant species cover. Percentage of ground not covered by live plant species was visually estimated within the 25 m^2 quadrats (Crane and Shearer 2007). Percentage ground cover was then determined by subtracting estimates of ground not covered by live vegetation from 100. Plant species cover and ground cover was the average from two observers per quadrat. No measure of plant species number and total plant species cover were made in study areas BW2 and EmF1 (Table 1) because the areas were burnt after soil sampling and measurement of canopy closure and ground cover.

Soil properties

Samples were taken from the top 3 cm of soil and the soil sieved through a 2-mm sieve, dried at 40°C for 48 h and analysed using the following methods. Phosphorus (P) content was determined colourimetrically using the method of Murphy and Riley (1962). Using the same solution, potassium (K) content was determined with a flame photometer. The organic carbon (C) content was determined by the Walkley-Black method (Piper 1942). Soil nitrogen (N) was determined by extracting the soil with 1 M potassium chloride solution and using the Kjeldahl method of McKenzie and Wallace (1954). The pH was determined from a 1 : 5 solution of soil and water. Percentage by weight of coarse (200–2000 μm) sand, fine (20–200 μm) sand, silt (2–20 μm) and clay (<2 μm) of the fine fraction were determined by the pipette method (Day 1965).

Analysis

The Shannon-Weiner index (H) and Simpson's index (D) of plant species diversity and plant species evenness (E) (McCune and Grace 2002) was calculated using the software PC-ORD Version 5.11 (McCune and Mefford 2006).

For ANOVA, assumptions of normality were checked by plotting residuals (Kirby 1993) and dependent variables were either log-transformed or percentage data arcsin $\sqrt{X/100}$-transformed to homogenise the variance. For ANOVA on the effect of disease status on either species occurrence or soil nutrients, disease status was the fixed variable and species cover or soil nutrient was the random factor. Where relevant, the mean and standard error of the mean were calculated. Regression and Pearson correlation coefficients were calculated as a measure of association between variables. The Bonferroni correction was not applied to correlation coefficients as recommended by Moran (2003). Significance was determined at $P \leq 0.055$ as a number of biological meaningful relationships had significant values of $0.050 < P \leq 0.055$.

Study areas were ordinated in multi-dimensional space by non-metric multi-dimensional scaling using the software PC-ORD Version 5.11. Non-metric multi-dimensional scaling was ordination of choice because the technique is one of the most defensible for graphical representation of community relationships (McCune and Grace 2002) and has a flexibility and generality bestowed by a dependence only on a biological meaningful view of the data (Clarke 1993). Either plant species cover or canopy closure and ground cover were ordinated in two dimensions because the greatest reduction in stress (McCune and Grace 2002) occurred in the first two dimensions. The Sørensen (Bray–Curtis) distance measure was used with soil properties as the second matrix.

Results

Study areas

There was high visual impact of disease observed in each study area. That disease expressed was due to *P. cinnamomi* was based on the pattern of deaths of many susceptible plant species, interpreted from extensive experience of the disease syndrome over many years (Shearer and Tippett 1989; Shearer and Hill 1989; Shearer 1994; Shearer and Dillon 1995, 1996*a*, 1996*b*; Crane and Shearer 2007; Shearer *et al*. 2007). Presence of *P. cinnamomi* was confirmed by isolation from recently dead plants of susceptible plant species from the disease front of each disease centre (Table 1). *Phytophthora cinnamomi* disease centres ranged in size from less than a hectare in study area BW4, to 30 ha in study area BW5 (Table 1). Study areas were infested with the pathogen for ~40 years before assessment. Disease was not evident in aerial photographs of BW1–3 taken in 1957, but was evident in the next photographs taken in 1965. For study areas BW5 and 6, disease was not evident in aerial photographs taken in 1955, but was evident in the next photographs taken in 1963.

Plant community varied among study areas of the *Banksia* woodland biomes and between *Banksia* woodland and *E. marginata* forest biomes (Table 1). As no system of site-vegetation typing has been developed for the Swan Coastal Plain bioregion, soil systems were used instead. Most of the *Banksia* woodland biomes occurred on leached grey sand of the Bassandean Dune System (Table 1). Study area BW4 was an exception, with orange-brown soil over limestone of the Yoongarillup System (McArthur 1991).

Eucalyptus marginata forest biomes occurred on laterite compared with the sandy soils of the *Banksia* woodland biomes (Table 1). The two study areas in the northern Jarrah Forest bioregion occurred on S and P Havel site-vegetation type (Havel 1975) for study areas EmF1 and EmF2, respectively

(Table 1). Type P occurs as gravelly sands in mid-slope positions. Type S is the broadest and most common type, flanking type P upslope on laterite mantled uplands (Havel 1975).

Variation in soil properties for the healthy study areas is given in Table 2. Sorting healthy study areas according to percentage coarse sand fraction showed a trend from the least fertile study area BW6 to the less sandy *E. marginata* forest biome study areas (Table 2). This overall trend was similar for other soil properties, although there was some variation from the trend for a few biomes.

Because space-for-time substitution was used to determine expression of disease over time, it is important to show that changes in disease expression were not due to site changes across the study areas. Figure 1*a* plots two physical soil properties that would change with site. Percentage coarse sand fraction was linearly related to percentage clay fraction, but within the relationship all areas were intermixed and there was no separation between disease status. In comparison, a plot of the vegetation variables of percentage ground cover and canopy closure that would respond to disease status, shows a separation of old diseased from adjoining healthy areas (Fig. 1*b*). Front areas tend to be intermediate between old disease and adjoining healthy areas.

Interrelationships among vegetation variables and disease status

Vegetation variables were plotted against each other and the effects of disease status determined (Table 3; Fig. 2). Forty three percent of the pair-wise correlation coefficients between canopy closure and other vegetation variables were significant (Table 3). In comparison only a few of the pair-wise correlation coefficients between other vegetation variables were significant.

Old diseased areas had lower canopy closure and basal area than adjoining healthy areas (Fig. 2*a*). No measurements of basal area were made in the front diseased area. Old diseased areas also tended to have lower plant species number (Fig. 2*b*) and total percentage plant species cover (Fig. 2*c*) than adjoining healthy areas. Vegetation variables for front diseased areas

Table 2. Variation in mean (±s.e.) of soil properties for healthy areas adjoining to *Phytophthora cinnamomi* disease centres in *Banksia* woodland and *Eucalyptus marginata* forest biomes of the Swan Coastal Plain and Jarrah Forest bioregions, respectively, of the South-West Botanical Province of Western Australia

Study area[A]	Soil properties								
	Coarse sand (%)	Clay (%)	Organic carbon (%)	Nitrogen (%)	Total phosphorus (µg/g)	Extractable phosphorus (µg/g)	Total potassium (µg/g)	Extractable potassium (µg/g)	pH
BW6	96.7 ± 0.3	0.7 ± 0.2	2.0 ± 0.2	0.07 ± 0.01	5.0 ± 0.7	0.6 ± 0.1	14.1 ± 2.2	10.8 ± 2.0	4.9 ± 0.1
BW1	93.9 ± 0.6	0.9 ± 0.2	1.6 ± 0.3	0.05 ± 0.004	11.7 ± 3.6	0.4 ± 0.002	37.1 ± 2.6	10.5 ± 1.1	5.0 ± 0.1
BW2	93.3 ± 1.2	2.1 ± 0.6	2.6 ± 0.8	0.06 ± 0.02	51.6 ± 6.4	0.4 ± 0.001	32.4 ± 1.7	13.2 ± 0.3	4.6 ± 0.1
BW3	91.6 ± 1.4	2.7 ± 0.7	3.9 ± 0.5	0.11 ± 0.02	19.2 ± 2.7	2.1 ± 0.4	60.8 ± 12.2	45.1 ± 9.5	4.7 ± 0.1
BW5	84.4 ± 1.5	4.8 ± 0.6	4.9 ± 0.3	0.18 ± 0.02	13.1 ± 1.5	2.0 ± 0.3	145.7 ± 42.0	113.4 ± 37.1	4.6 ± 0.1
BW4	81.0 ± 1.1	3.6 ± 0.6	4.3 ± 0.6	0.16 ± 0.03	17.1 ± 3.6	1.4 ± 0.3	47.1 ± 6.6	27.0 ± 4.6	5.2 ± 0.1
EmF2	50.8 ± 2.5	5.4 ± 0.7	6.5 ± 0.8	0.22 ± 0.04	56.7 ± 7.7	2.3 ± 0.8	121.4 ± 18.4	91.7 ± 18.8	5.2 ± 0.2
EmF1	49.5 ± 2.0	6.8 ± 0.7	2.6 ± 0.2	0.09 ± 0.01	30.5 ± 6.7	1.6 ± 0.4	55.9 ± 3.8	27.2 ± 4.2	4.9 ± 0.2

[A]BW = *Banksia* woodland biome in the Swan Coastal Plain bioregion, EmF = *Eucalyptus marginata* forest biome in the Jarrah Forest bioregion. See Table 1 for study area details.

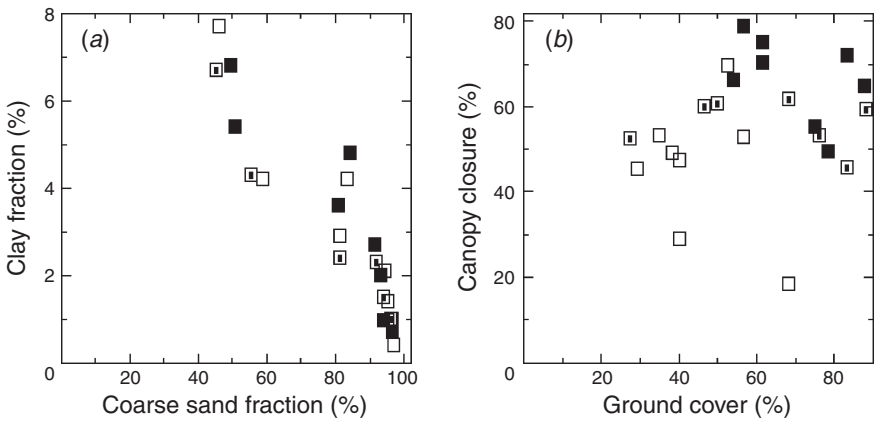


Fig. 1. Distribution of study areas of old (□), front (▣) and adjoining healthy (■) disease status in relationships between (*a*) soil property variables and (*b*) vegetation variables for *Phytophthora cinnamomi* disease centres in *Banksia* woodland and *Eucalyptus marginata* forest biomes of the Swan Coastal Plain and Jarrah Forest bioregions, respectively, of the South-West Botanical Province of Western Australia.

Table 3. Correlation coefficients for linear relationships between community structure and plant species composition components of *Phytophthora cinnamomi* disease centres of *Banksia* woodland and *Eucalyptus marginata* forest biomes of the South-West Botanical Province of Western Australia

Significant correlation coefficients in bold ($P \leq 0.055$)

Vegetation variable	% canopy closure	% ground cover	Basal area	Number of species	% species cover	Evenness (E)	Shannon-Weiner H
% ground cover	0.19 (23)[A]	1					
Basal area	**0.74** (23)	0.19 (14)	1				
Number of species	**0.51** (14)	0.05 (17)	0.12 (10)	1			
% species cover	**0.57** (17)	**0.67** (17)	0.51 (10)	0.31 (17)	1		
Evenness (E)	–0.36 (17)	–0.20 (17)	–0.55 (10)	–0.04 (17)	–0.33 (17)	1	
Shannon-Weiner H	0.38 (17)	0.03 (17)	–0.11 (10)	**0.90** (17)	0.24 (17)	0.36 (17)	1
Simpson's D	0.26 (17)	0.05 (17)	–0.18 (10)	**0.72** (17)	0.21 (17)	0.59 (17)	**0.94** (17)

[A]Number of values in parentheses: $n = 23$ for seven study areas with old, front and healthy disease status, one study area with old and healthy disease status; $n = 17$ for five study areas with old, front and healthy disease status, one study area with old and healthy disease status; $n = 14$ for seven study areas with old and healthy disease status; $n = 10$ for five study areas with old and healthy disease status.

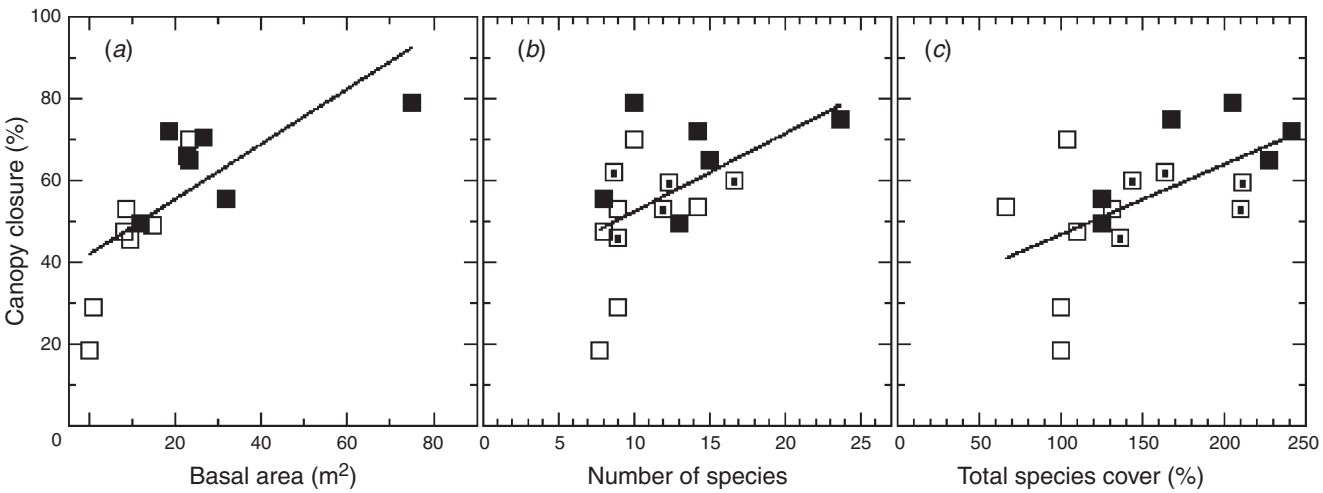


Fig. 2. Relationships between canopy closure and either (*a*) basal area, (*b*) number of plant species or (*c*) total percentage plant species cover for old (□), front (▣) and adjoining healthy (■) disease status for *Phytophthora cinnamomi* disease centres in *Banksia* woodland and *Eucalyptus marginata* forest biomes of the Swan Coastal Plain and Jarrah Forest bioregions, respectively, of the South-West Botanical Province of Western Australia. Lines indicate significant linear relationships between variables: (*a*): Canopy closure = 41.604 + 0.675. Basal area ($r = 0.74$); (*b*): Canopy closure = 33.269 + 1.890. Number of plant species ($r = 0.51$); (*c*): Canopy closure = 29.578 + 0.172. Total percentage species cover ($r = 0.57$).

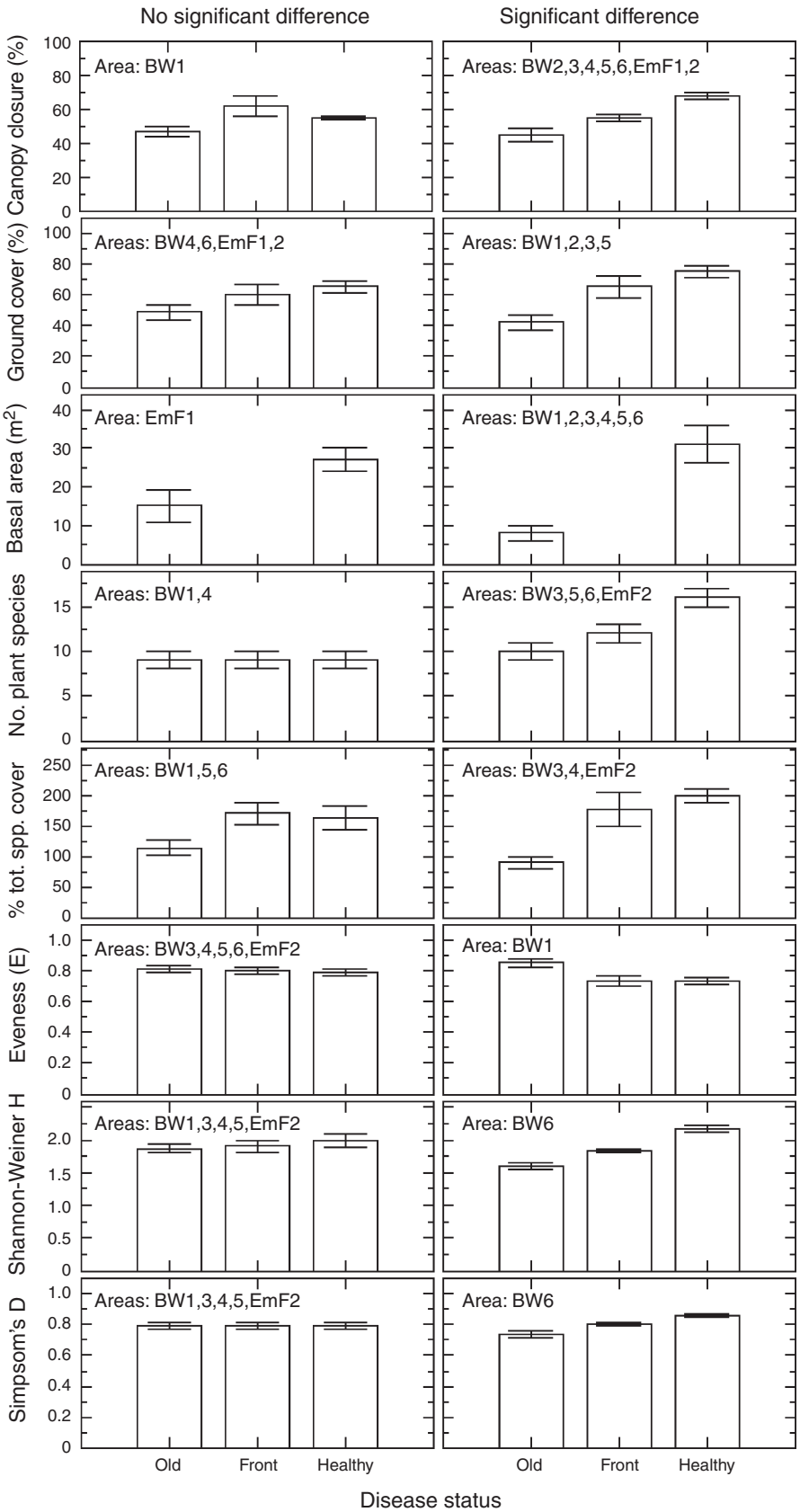
tended to be intermediate between old diseased areas and adjoining healthy vegetation (Fig. 2).

Although trends in vegetation variables between disease status were apparent, there was some overlap between old diseased and adjoining healthy areas for a few study areas (Fig. 2). Therefore, differences in vegetation variables between disease status are shown in greater detail in Fig. 3. In all but one or two study areas, canopy closure, basal area and number of plant species were significantly lower in old diseased compared with adjoining healthy areas, with diseased front intermediate between the two. In half of the study areas percentage ground cover and total plant species cover were significantly lower in old diseased areas compared with adjoining healthy areas, with diseased front intermediate between the two. Evenness, Shannon-Weiner H and Simpson's D did not significantly change between disease status for the majority of study areas (Fig. 3).

Vegetation and study area gradients

For ordination of percentage plant species cover (Fig. 4*a*), axes 1 and 2 explained 32 and 44% of the variation, respectively. The ordination of percentage plant species cover showed strongest separation of study areas along a soil fertility gradient. Study areas of lowest fertility tended to occur in the lowest right hand corner of the graph, grading up to areas of

Fig. 3. Mean (±s.e.) of vegetation variables for study areas having no significant or significant ($P \leq 0.055$) differences between disease status of *Phytophthora cinnamomi* disease centres in *Banksia* woodland and *Eucalyptus marginata* forest biomes of the Swan Coastal Plain and Jarrah Forest bioregions, respectively, of the South-West Botanical Province of Western Australia. The study areas having no significant or significant differences are indicated for each vegetation variable: BW = *Banksia* woodland, EmF = *E. marginata* forest.


No significant difference
Significant difference
Canopy closure (%)
Area: BW1
Areas: BW2,3,4,5,6,EmF1,2
Ground cover (%)
Areas: BW4,6,EmF1,2
Areas: BW1,2,3,5
Basal area (m2)
Area: EmF1
Areas: BW1,2,3,4,5,6
No. plant species
Areas: BW1,4
Areas: BW3,5,6,EmF2
% tot. spp. cover
Areas: BW1,5,6
Areas: BW3,4,EmF2
Eveness (E)
Areas: BW3,4,5,6,EmF2
Area: BW1
Shannon-Weiner H
Areas: BW1,3,4,5,EmF2
Area: BW6
Simpsom's D
Areas: BW1,3,4,5,EmF2
Area: BW6
Old
Front
Healthy
Disease status

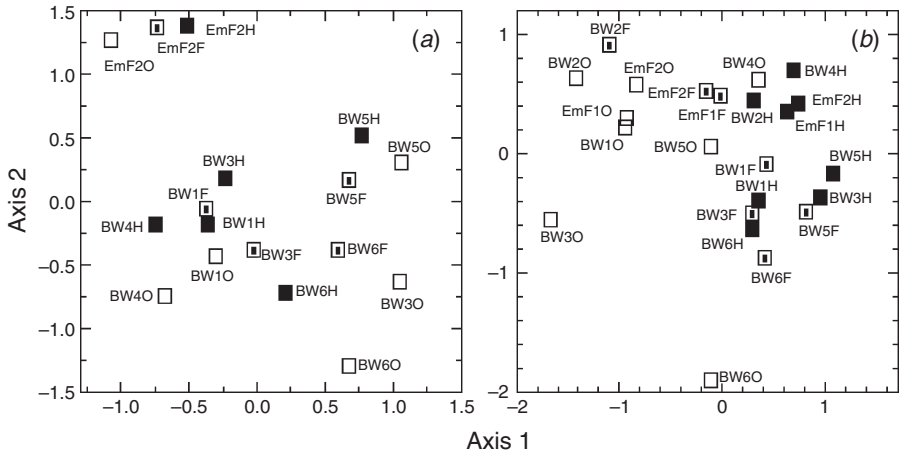


Fig. 4. Non-metric multi-dimensional scaling of (*a*) percentage plant species cover and (*b*) percentage canopy closure and ground cover for study areas of old (□), front (▣) and adjoining healthy (■) disease status of *Phytophthora cinnamomi* disease centres in *Banksia* woodland and *Eucalyptus marginata* forest biomes of the Swan Coastal Plain and Jarrah Forest bioregions, respectively, of the South-West Botanical Province of Western Australia. Study area names: BW = *Banksia* woodland, EmF = *E. marginata* forest, O = old diseased, F = diseased front and H = adjoining healthy. Study area details given in Table 1.

highest fertility in the top left hand corner of the graph (Fig. 4*a*). Areas of different disease status were intermixed (Fig. 4*a*).

For ordination of percentage canopy closure and ground cover (Fig. 4*b*) axes 1 and 2 explained 54 and 44% of the variation, respectively. There was separation of study areas along a disease status gradient. Old disease areas occurred on the left hand side of the graph, adjoining healthy areas on the right hand side of the graph and front areas intermediate between the two (Fig. 4*b*). An exception was the old diseased area of BW4 (Fig. 4*b*), which had orange-brown soil with low percentage of coarse sand compared with grey sands of the other *Banksia* woodland biome areas (Tables 1 and 2). There was a weak soil fertility gradient, with study areas of lowest fertility tending to occur at the bottom of the graph, grading up to areas of highest fertility at the top of the graph (Fig. 4*b*).

Disease and soil nutrient cycling variables

Table 4 shows significant linear correlation between soil nutrient cycling and vegetation variables. Ninety-one percent of soil nutrient cycling variables were significantly linearly correlated with number of plant species or Shannon-Weiner H (Table 4). Fifty-four percent of soil nutrient cycling variables were significantly linearly correlated with percentage canopy

Table 4. Correlation coefficients for linear relationships between vegetation variables and soil properties of *Phytophthora cinnamomi* disease centres of *Banksia* woodland and *Eucalyptus marginata* forest biomes of the South-West Botanical Province of Western Australia

Significant correlation coefficients in bold ($P \leq 0.055$)

Soil property	Vegetation variable							
	% canopy closure	% ground cover	Basal area	Number of species	% total species cover	Evenness (E)	Shannon-Weiner H	Simpson's D
% organic carbon	**0.58** (23)[A]	0.10 (23)	0.41 (14)	**0.80** (17)	**0.48** (17)	–0.13 (17)	**0.71** (17)	**0.55** (17)
% nitrogen	**0.54** (23)	0.12 (23)	0.42 (14)	**0.74** (17)	0.38 (17)	–0.10 (17)	**0.67** (17)	**0.53** (17)
Total phosphorus (µg/g)	0.28 (23)	–0.40 (23)	0.11 (14)	**0.66** (17)	–0.11 (17)	–0.28 (17)	**0.47** (17)	0.24 (17)
Extractable phosphorus (µg/g)	**0.41** (23)	0.05 (23)	0.20 (14)	**0.77** (17)	0.43 (17)	–0.19 (17)	**0.64** (17)	**0.49** (17)
Total potassium (µg/g)	**0.54** (23)	–0.03 (23)	0.24 (14)	**0.75** (17)	0.30 (17)	–0.16 (17)	**0.64** (17)	0.46 (17)
Extractable potassium (µg/g)	**0.49** (23)	0.07 (23)	0.12 (14)	**0.78** (17)	0.42 (17)	–0.11 (17)	**0.69** (17)	**0.53** (17)
pH	0.30 (23)	–0.14 (23)	**0.53** (14)	0.24 (17)	–0.42 (17)	0.01 (17)	0.19 (17)	0.12 (17)
% coarse sand	–0.39 (23)	0.28 (23)	–0.22 (14)	**–0.77** (17)	0.05 (17)	0.12 (17)	**–0.64** (17)	–0.43 (17)
% fine sand	0.36 (23)	–0.30 (23)	0.22 (14)	**0.74** (17)	–0.11 (17)	–0.12 (17)	**0.61** (17)	0.40 (17)
% silt	0.34 (23)	–0.26 (23)	0.10 (14)	**0.84** (17)	–0.07 (17)	–0.08 (17)	**0.71** (17)	**0.49** (17)
% clay	**0.49** (23)	–0.16 (23)	0.23 (14)	**0.67** (17)	0.36 (17)	–0.09 (17)	**0.61** (17)	**0.48** (17)

[A]Number of values in parentheses: $n = 23$ for seven study areas with old, front and healthy disease status, one study area with old and healthy disease status; $n = 17$ for five study areas with old, front and healthy disease status, one study area with old and healthy disease status; $n = 14$ for seven study areas with old and healthy disease status.

closure or Simpson's D. Very few or none of the pair-wise correlation coefficients between soil properties and other vegetation variables were significant.

There were significant linear relationships between percentage canopy closure and percentage organic C, total N and extractable P and K (Table 4; Fig. 5). Relative infertile areas had lower canopy closure than more fertile areas. However within the relationships, study areas were intermixed and there was no separation between disease status (Fig. 5). Therefore, study areas where there were significant differences in soil nutrient cycling variables between disease status were determined (Fig. 6).

There was significantly less percentage organic C, extractable P and extractable and total K in old diseased areas compared with adjoining healthy areas for one-quarter to a third of the study areas (Fig. 6). While differences were not significant for the other study areas, there were consistent lower values of the soil nutrient cycling properties in the old diseased areas compared with adjoining healthy areas. Total P changed significantly between disease status, but this was due to higher levels in diseased front compared with the old diseased or adjoining healthy areas. For all study areas there was no significant effect of disease status on percentage total N and pH (Fig. 6).

In two study areas (BW4 and EmF1) there was no significant effect of disease status on the soil nutrient cycling variables (Fig. 6). In four study areas (BW1, 2, 6, EmF2) disease status significantly affected only one soil nutrient cycling variable. In study area BW3 disease status significantly affected four of the seven soil nutrient cycling variables and in study area BW5 disease status significantly affected five of the seven soil nutrient cycling variables (Fig. 6).

Plant species that change with disease status and their functional grouping

The cover of a majority of plant species did not change significantly between disease status (Table 5). The cover of 16% of the total number of perennial species in healthy areas significantly decreased and the cover of 10% increased in old diseased compared with adjoining healthy areas. Plant species for which there was significantly less cover in the old diseased compared with the adjoining healthy area were mainly Dilleniaceae, susceptible to *P. cinnamomi* and shrubs that resprouted after fire with 50 percent of the species of deep rooting habit with a mycorrhizal association (Table 5). In comparison, plant species that significantly increased in cover in the old diseased areas compared with the adjoining

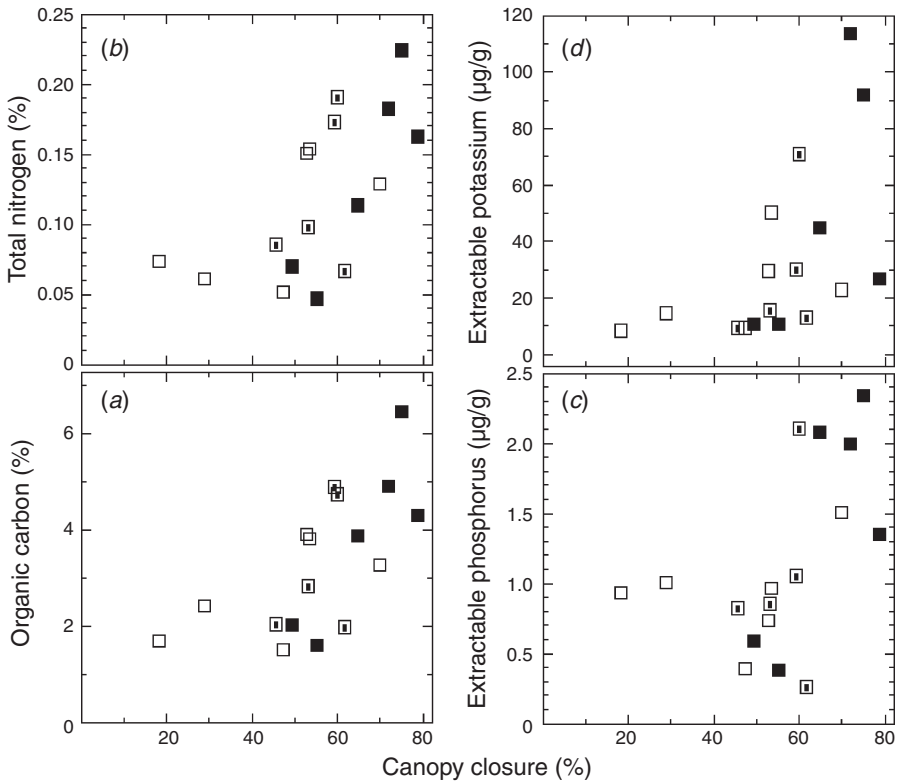


Fig. 5. Relationships between canopy closure and the soil nutrient cycling variables: (*a*) percentage organic carbon; (*b*) percentage total nitrogen; (*c*) extractable phosphorus; and (*d*) extractable potassium for old (□), front (▣) and adjoining healthy (■) disease status of *Phytophthora cinnamomi* disease centres in *Banksia* woodland and *Eucalyptus marginata* forest biomes of the Swan Coastal Plain and Jarrah Forest bioregions, respectively, of the South-West Botanical Province of Western Australia.

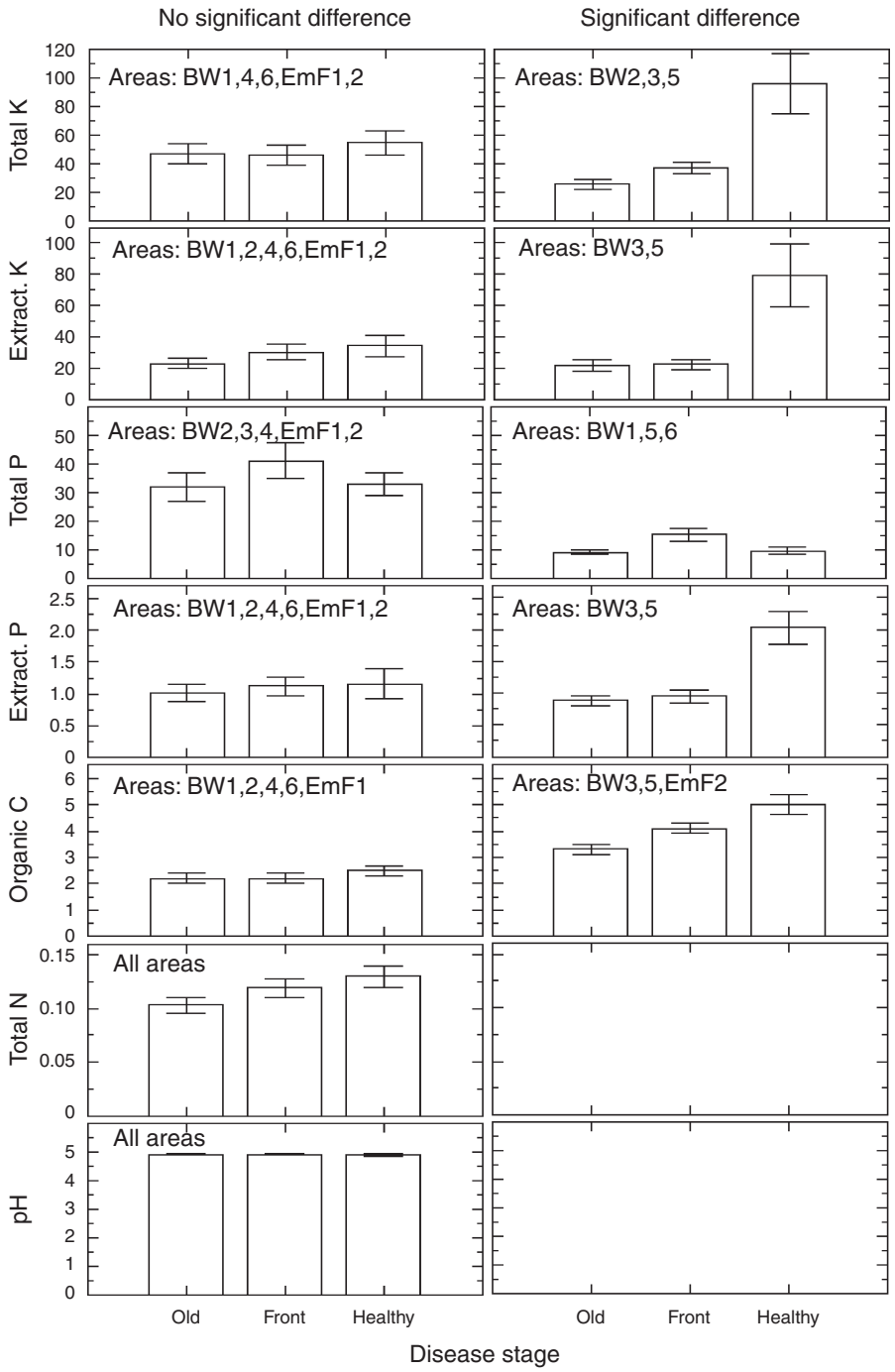


Fig. 6. Mean (±s.e.) of soil nutrient cycling variables for study areas having no significant or significant ($P \leq 0.055$) differences between disease status of *Phytophthora cinnamomi* disease centres in *Banksia* woodland and *Eucalyptus marginata* forest biomes of the Swan Coastal Plain and Jarrah Forest bioregions, respectively, of the South-West Botanical Province of Western Australia. Soil nutrients: K = potassium (µg/g), P = phosphorus (µg/g), C = carbon (%), N = nitrogen (%). The study areas having no significant or significant differences are indicated for each soil nutrient cycling variable: BW = *Banksia* woodland, EmF = *E. marginata* forest.

healthy area were herbs and shrubs from a range of families, mainly resistant to *P. cinnamomi* with a mixture of responses to fire, rooting type and mycorrhizal association (Table 5).

Correlation between canopy closure and plant species cover can also be used to differentiate plant species responses to *P. cinnamomi* invasion (Table 6). As with significant

Table 5. Family and functional responses of plant species that either significantly ($P \leq 0.055$) decreased or increased in cover in diseased old compared with adjoining healthy areas of *Phytophthora cinnamomi* disease centres of *Banksia* woodland and *Eucalyptus marginata* forest biomes of the South-West Botanical Province of Western Australia

Blank for functional response indicates no data for the plant species

Significant change in old compared with healthy	Plant species	# areas change/ # areas occurred	Family	Functional responses				
				Susceptibility[A]	Growth form[B]	Fire response[C]	Rooting type[D]	Mycorrhizal association type[E]
Decrease	*Allocasuarina fraseriana*	1/2	Casuarinaceae	Va	Tr	R	D	ECM/VAM
	Banksia attenuata	1/6	Proteaceae	Su	Tr	R/OS	D	
	B. grandis	1/1	Proteaceae	Su	Tr	R/OS	D	NM
	Dasypogon hookeri	1/1	Dasypogonaceae		He			
	Eucalyptus marginata	1/5	Myrtaceae	Su	Tr	R	D	ECM/VAM
	Hibbertia acerosa	1/1	Dilleniaceae		Sh	R		VAM
	H. amplexicaulis	1/1	Dilleniaceae	Su	Sh			VAM
	H. furfuracea	1/2	Dilleniaceae		Sh			
	H. hypericoides	3/5	Dilleniaceae	Su	Sh	R	S	VAM
	H. quadricolor	1/1	Dilleniaceae	Su	Sh			
	Hypocalymma robustum	3/5	Myrtaceae	Su	Sh	R	S	ECM/VAM
	Leucopogon parviflorus	2/2	Epacridaceae		Sh			
	Xanthorrhoea preissii	2/6	Xanthorrhoeaceae	Su	TLM	R	S	VAM
Increase	*Acacia pulchella*	1/4	Mimosaceae	Re	Sh	OS	D	VAM
	Anarthria prolifera	1/2	Restionaceae		He			
	Boronia spathulata	1/1	Rutaceae	Re	Sh			VAM
	Calytrix flavescens	1/4	Myrtaceae	Re	Sh		D	
	Lomandra nigricans	1/2	Dasypogonaceae	Re	He		S	
	Desmocladus flexuosus	1/1	Restionaceae	Re	He	R	S	NM
	Melaleuca thymoides	2/4	Myrtaceae	Su	Sh	R		
	Stirlingia latifolia	1/3	Proteaceae	Va	Sh	R	D	NM

[A]From Shearer and Dillon (1995), Shearer *et al.* 1996*b*). Su = susceptible, Re = resistant, Va = variable response.
[B]From Western Australian Herbarium (1998). He = herb, Sh = shrub, Tr = tree, TLM = tree-like monocot.
[C]From Van der Moezel *et al*. (1987), Stewart *et al*. (1993), Pate and Bell (1999), Moore (2005). R = resprouter, OS = obligate seeder.
[D]From Dodd *et al*. (1984), Stewart *et al*. (1993), Pate and Bell (1999). D = deep (>2 m), S = shallow (<2 m).
[E]From Lamont (1984), Brundrett and Abbott (1991), Stewart *et al*. (1993). VAM = vesicular-arbuscular mycorrhizal, ECM = ectomycorrhizal, NM = non-mycorrhizal.

differences in cover between disease status, change in cover of a majority of plant species was not significantly correlated with canopy closure. The cover of 20% of the total number of perennial species in healthy areas was significantly positively, and 10% of species was significantly negatively linearly correlated with canopy closure. The β_1 regression coefficients were positive for plant species whose cover was correlated with canopy closure and had less cover in the old diseased area compared with the adjoining healthy area. These species were mainly Dilleniaceae and Proteaceae that were susceptible to *P. cinnamomi* and were shrubs that resprouted after fire with 50 percent of the species of deep rooting habit with a mycorrhizal association (Table 6). The cover of two species resistant to *P. cinnamomi*, *Agonis flexuosa* and the fern *Linsaea linearis*, decreased in the old diseased area compared with the adjoining healthy area.

The β_1 regression coefficients were negative for plant species that increased in cover in the old diseased area compared with the adjoining healthy area (Table 6). These species were herbs and shrubs from a range of families with a mixture of responses to *P. cinnamomi*, fire, rooting type and mycorrhizal association (Table 6).

Discussion

Studies of the effects of *P. cinnamomi* invasion have been more often from an autecological rather than a synecological or community dynamics perspective (Shearer 1992). The biology, life cycles and host preferences of plant pathogens of native ecosystems have been relatively well studied, but the consequences of disturbance caused by pathogen invasion on ecosystem dynamics have received less attention and are poorly understood (Lewis and Lindgren 2000; McCarthy 2001; Lovett *et al*. 2006). As in the case for exotic plant invasions (Levine *et al*. 2003), there has been little testing of the processes or pathways through which impact of plant pathogens develop. Plant pathogens need to be viewed as disturbance vectors as much as fire, wind, insects (McCarthy 2001), long-term climate change and human activity. As plant pathogens may induce more permanent long-term changes in species composition than other agents of disturbance (Lovett *et al*. 2006), the role of plant pathogens in the evolution and continuation of modified communities needs to be determined. Plant pathogens target specific host species and once established, become permanent components that continually influence ecosystem processes.

Table 6. Regression and correlation coefficients, family and functional responses of plant species that had a significant ($P \leq 0.055$) linear correlation between cover and canopy closure for *Phytophthora cinnamomi* disease centres of *Banksia* woodland and *Eucalyptus marginata* forest biomes of the South-West Botanical Province of Western Australia

Plant species cover either decreased (positive β_1) or increased (negative β_1) in the old diseased compared with adjoining healthy areas. Blank for functional response indicates no data for the plant species

Change in old compared with healthy	Dependent variable percentage cover of:	Study area[A]	Regression coefficient β_0	Regression coefficient β_1	Correlation coefficient *R*	Family	Functional responses: Susceptibility[B]	Growth form[C]	Fire response[D]	Rooting type[E]	Mycorrhizal association type[F]
Decrease	*Agonis flexuosa*	BW5	–127.9	2.46	0.76	Myrtaceae	Re	Tr			VAM/ECM
	Allocasuarina fraseriana	EmF2	–52.8	0.99	0.72	Casuarinaceae	Va	Tr	R	D	ECM/VAM
	Adenanthos barbiger	EmF2	–10.8	0.24	0.65	Proteaceae	Su	Sh	R		NM
	Banksia attenuata	BW6	–17.0	0.98	0.85	Proteaceae	Su	Tr	R/OS	D	
	B. grandis	EmF2	–73.8	1.43	0.74	Proteaceae	Su	Tr	R/OS	D	NM
	Dasypogon hookeri	BW4	–121.2	1.79	0.82	Dasypogonaceae		He			
	Eucalyptus marginata	BW6	–2.6	0.10	0.67	Myrtaceae	Su	Tr	R	D	ECM/VAM
	Hibbertia acerosa	EmF2	–8.8	0.17	0.94	Dilleniaceae		Sh	R		VAM
	H. amplexicaulis	EmF2	–3.34	0.06	0.85	Dilleniaceae	Su	Sh			VAM
	H. hypericoides	BW3	–60.0	2.09	0.98	Dilleniaceae	Su	Sh	R	S	VAM
	H. quadricolor	EmF2	–13.1	0.24	0.77	Dilleniaceae	Su	Sh			
	Hypocalymma robustum	BW3	–15.70	0.55	0.96	Myrtaceae	Su	Sh	R	S	ECM/VAM
	Leucopogon parviflorus	BW3	–0.8	0.23	0.73	Epacridaceae		Sh			
	L. propinquus	BW1	–6.4	0.21	0.80	Epacridaceae	Va	Sh		S	
	Lindsaea linearis	BW5	–104.8	2.4	0.78	Lindsaeaceae	Re	He			
	Xanthorrhoea preissii	BW1	–46.5	0.92	0.79	Xanthorrhoeaceae	Su	TLM	R	S	VAM
		EmF2	–27.6	0.63	0.69						
	Xylomelum occidentale	BW1	–15.9	0.31	0.80	Proteaceae	Su	Tr			
Increase	*Acacia pulchella*	BW4	9.0	–0.12	0.84	Mimosaceae	Re	Sh	OS	D	VAM
	Anarthria prolifera	BW3	19.60	–0.31	0.75	Restionaceae		He			
	Calytrix flavescens	BW1	13.9	–0.21	0.74	Myrtaceae	Re	Sh		D	
		BW3	46.2	–0.61	0.78						
	Conostylis aculeata	BW4	32.1	–0.41	0.84	Haemodoraceae		He	R	S	NM
	Dasypogon bromeliifolius	BW5	107.0	–1.23	0.74	Dasypogonaceae	Su	He	R	S	
	Lyginia imberbis	BW6	1.0	–0.02	0.75	Restionaceae		He		S	
	Melaleuca thymoides	BW4	97.6	–1.26	0.95	Myrtaceae	Su	Sh	R		
		BW6	47.5	–0.66	0.65						
	Stirlingia latifolia	BW4	154.0	–1.94	0.83	Proteaceae	Va	Sh	R	D	NM

[A]BW = *Banksia* woodland, EmF = *E. marginata* forest.
[B]From Shearer and Dillon (1995, 1996*b*), Shearer *et al*. (2007). Su = susceptible, Re = resistant, Va = variable response.
[C]From Western Australian Herbarium (1998). He = herb, Sh = shrub, Tr = tree, TLM = tree-like monocot.
[D]From Van der Moezel *et al*. (1987), Stewart *et al*. (1993), Pate and Bell (1999), Moore (2005). R = resprouter, OS = obligate seeder.
[E]From Dodd *et al*. (1984), Crombie *et al*. (1988), Stewart *et al*. (1993), Pate and Bell (1999). D = deep (>2 m), S = shallow (<2 m).
[F]From Lamont (1984), Brundrett and Abbott (1991), Stewart *et al*. (1993). VAM = vesicular-arbuscular mycorrhizal, ECM = ectomycorrhizal, NM = non-mycorrhizal.

There has been no long-term monitoring of *P. cinnamomi* invasion of plant communities of the South-West Botanical Province of Western Australia (Shearer *et al*. 2007). Therefore, ecosystem changes mediated by pathogen invasion were measured across disease centres into the adjoining healthy areas in a space-for-time substitution discussed by Pickett (1989). Underpinning use of space-for-time substitution is the assumption that disease centres and adjoining healthy

areas are of the same site type and therefore differences between diseased and adjoining healthy areas are due to pathogen-mediated changes. The proportion of soil clay and sand would be physical soil properties not expected to be affected by disease, but show site type differences. The intermixing of diseased and adjoining healthy areas on the clay-sand continuum give confidence that these areas were on the same site type. In contrast, when vegetation variables affected by disease were plotted, areas separated out along diseased-healthy gradients according to disease status.

Space-for-time substitution is not a replacement for long-term monitoring of species invasion. The substitution studies are often not placed in an explicit temporal context because the duration of invasions is not known. In addition, space-for-time substitution studies are generally of short duration. Processes that can alter in time include changes in the invading species and invaded community, the abiotic environment and various interactions between invading species and ecosystem dynamics, but little is known of the temporal variable effects for individual invaders (Strayer *et al*. 2006). Short-term plant composition monitoring is also a poor predictor of the success of restoration of invaded communities (Herrick *et al*. 2006). Long-term monitoring of disease and pathogen dynamics and species composition in plant communities in Victoria invaded by *P. cinnamomi* showed initial decline of species richness followed by a decline in the pathogen and increased regeneration of susceptible plant species (Weste 2003). Further long-term monitoring is required to determine whether understorey regeneration is stable or whether successive cycles of disease and recovery will occur (Weste 2003). In addition to these temporal patterns in disease and pathogen dynamics and species composition, little is known of the interaction of ecosystem dynamics with disease and pathogen dynamics over time. As suggested for the study of invasive species by ecologists (Strayer *et al*. 2006), plant pathologists should adopt much more long-term perspectives of the effects of *P. cinnamomi* on ecosystem dynamics, than currently being undertaken (Shearer *et al*. 2007).

Changes in the number of plant species or richness have often been used as a conservation indicator and a measure of the impact of invading species (Yurkonis *et al*. 2005; Fleishman *et al*. 2006). The consequences of *P. cinnamomi* invasion have primarily been determined from a botanical viewpoint using taxonomic compilations of changes in plant species number and composition following infestation (Weste *et al*. 1973; Weste 1986, 2003; Shearer and Hill 1989; Wills 1993; Shearer and Dillon 1996*a*; Weste and Kennedy 1997; Laidlaw and Wilson 2003; McDougall *et al*. 2002, 2005; Crane and Shearer 2007). Plant species richness was significantly less in diseased *Banksia* woodland and *E. marginata* forest biomes invaded by *P. cinnamomi* compared with adjoining healthy areas. In contrast, McDougall *et al*. (2002) found no differences in species richness between infested and healthy *E. marginata* forest. In agreement with our study, Shearer and Hill (1989), Keighery *et al*. (1994), Shearer and Dillon (1996*a*) and Shearer *et al*. (2004*b*) also report a decrease in species numbers following invasion of *Banksia* woodland biomes by *P. cinnamomi*.

Pathogen-mediated changes in species richness will be due to direct and indirect effects of *P. cinnamomi* infestation on plant species occurrence. Direct effects were identified as significant decrease in plant species cover or positive correlation with canopy closure between disease status. That the cover of 16% of the total number of perennial species in healthy areas significantly decreased with disease status and canopy closure decreased by 25%, suggests that death of a relatively few species have a considerable contribution to disease expression following infestation. This is supported by the estimate of Shearer *et al*. (2004*a*) that 14% of the flora of the South-West Botanical Province of Western Australia is highly susceptible to *P. cinnamomi* and their death would be expected to cause a conspicuous decline in biomass. Similarity of estimates from different independent assessment methods gives confidence that a realistic evaluation of the susceptibility of flora to *P. cinnamomi* infection has been obtained.

While direct impacts of *P. cinnamomi* have been poorly documented in the South-West Botanical Province, even less attention has been given to indirect impact of the pathogen. This is despite the fact that indirect impact following infestation by plant pathogens can be greater than the direct impact of killed plants (Hansen 1999). Indirect impact of *P. cinnamomi* can lead to resistant species increasing in infested areas as occurred for 10% of the total number of perennial species in healthy areas. Presumably factors such as reduced competition allowed better exploitation of old infested areas by resistant hosts following removal of susceptible hosts killed by infection. Alternatively, taxa not directly affected by infection may decline due to habitat destruction by the pathogen. Habitat destruction probably accounted for the observed decline of the resistant species *A. flexuosa* and *L. linearis* in study area BW5. In the few reports of indirect impact of *P. cinnamomi* in the literature, Wills (1993) suggested that reduced occurrence of apparently resistant *Stylidium scandens* in disease centres in the Stirling Range National Park was due to reduced canopy resulting from *P. cinnamomi* killing susceptible hosts, rather than the direct effects of infection on *S. scandens*. McDougall *et al*. (2005) observed in *E. marginata* forest that several apparently resistant understorey species persisted only where canopy survived the infestation. The present poor understanding and quantification of indirect impacts of *P. cinnamomi* through habitat destruction results in an underestimation of the true impact of the pathogen on the flora.

Changes in species richness alone does not adequately predict or describe the effects of invasion (Yurkonis *et al*. 2005) because the measure provides no information on species identity or the functional roles of individual species as contributors to ecosystem processes (Fleishman *et al*. 2006). Ecosystems need to be viewed from functional integrity rather than specific components at any time (Main 1981). Changes in plant species number will differently affect ecosystem processes depending on the dominance and functional traits of the species lost or gained, their interactions with other species, the order in which species are lost and the

relative amount of biotic and abiotic control over process rates (Hooper *et al*. 2005). Determination of how an invader impacts on a community must link impacts with underlying community dynamics that result in altered community structure (Parker *et al*. 1999; Yurkonis *et al*. 2005), ecosystem processes (Levine *et al*. 2003) and functional diversity (Hooper *et al*. 2005).

Canopy closure is an important variable for measuring *P. cinnamomi*-mediated changes because of the linked changes in canopy closure to plant community structure, processes and functioning. Changes in overstorey canopy structure directly affects the quality and quantity of light, microclimate, litter production and decomposition, nutrient and hydrological cycling, energy budgets and thus the composition and functioning of plant communities (Specht and Specht 1989; Shaw and Bible 1996; Chen *et al*. 1999; Jennings *et al*. 1999; Prescott 2002; Levia and Frost 2006; Crane and Shearer 2007). In addition, canopy gaps will produce root gaps (McCarthy 2001) with associated changes in soil community structure and nutrient cycling processes. Despite the importance of canopy change to community functioning, this variable has been rarely used to quantify pathogen-mediated changes associated with *P. cinnamomi* infestation, or for that matter any plant disease (Crane and Shearer 2007; Shearer *et al*. 2007).

In this study, canopy closure was significantly reduced by infestation in all but one study area and was significantly correlated with most of the vegetation and soil property variables. Crane and Shearer (2007) and Shearer *et al*. (2007) also found that *P. cinnamomi* was important in gap creation through significant reduction in canopy closure following infestation of three biomes in the South-West Botanical Province of Western Australia. The pathogen in Eastern Australian plant communities either reduced canopy cover by a third over 20 years (Dawson *et al*. 1985) or had no significant effect on either canopy cover (Newell 1998) or height (Laidlaw and Wilson 2003) following infestation. Different compensation or complementary effects following invasion (Tilman 1999; Shearer and Smith 2000) may explain differences between geographic areas. Needing further study are the effects of gap creation through reduction in canopy closure on plant community structure, processes and functioning following *P. cinnamomi* invasion.

As disease-mediated canopy gap creation was one of the criteria for study area selection, there may be the possibility of a circular argument between selection criteria and effect. This appears not to be the case in this study because, as shown in Fig. 3, components of structural change did not significantly differ between disease status for all study areas. The study was able to identify communities such as BW4 that were invaded less by *P. cinnamomi* than others, possibly due to differences in soil type. In addition, plant species that declined or increased with disease were identified. Further research is required to identify factors that buffer some communities against invasion more than others.

Little is known of the effects of plant pathogen induced mortality on nutrient cycling (Edmonds and Sollins 1974; Yorks *et al*. 2000). Plant species of *Banksia* woodland and *E. marginata* forest biomes conserve nutrients by the efficient retrieval of key limiting elements from senescing organs and the continuous redeployment into new generations of photosynthetic structures (Pate and Dell 1984). Disease induced mortality would lead to increased organic matter inputs through more of the nutrient capital in dead as opposed to living biomass and increased release of nutrients by decomposition for uptake or loss from the soil. Vegetation cover influences nutrient cycling by effecting biomass storage of nutrient sinks, the microclimate at the soil surface, the chemical and physical nature of the litter and the hydrological cycle (Prescott 2002). Increased solar radiation at the soil surface after canopy removal following plant mortality increases soil temperature and moisture (Shearer and Tippett 1989), favouring accelerated litter decomposition rates (Postle *et al*. 1986). Thus reduction in canopy closure caused by *P. cinnamomi*-induced plant mortality would be expected to influence nutrient cycling in infested sites. However, total soil N did not differ significantly between disease status in all sites and soil K, P and organic C was significantly lower in old disease status compared with adjoining healthy areas in 25–38% of study areas. In one of the few studies following nutrient cycling after pathogen invasion Matson and Boone (1984) found elevated N mineralisation and N availability in a mountain hemlock stand infested with *Phellinus weirii*.

Reasons for the minimal effect of *P. cinnamomi* invasion on nutrient cycling could either be because one measurement of soil nutrients would not indicate temporal changes in nutrient levels with season and time after infestation, or due to soil characteristics of the region. The need to determine temporal changes in soil nutrients is supported by the findings of Grierson and Adams (2000) that soil P availability in *E. marginata* forest followed seasonal patterns of soil moisture availability and associated changes in fungal and root activity. In addition the ecosystems of South-West Botanical Province of Western Australia are buffered to cope with nutritional disturbance mainly through the dominant role of the soil as store of the small pools of nutrients (O'Connell and Grove 1991). Because of this, changes in the total pool of nutrients in the medial term would be difficult to measure against the variation occurring in natural systems (O'Connell and Grove 1991; Pate *et al*. 1993). Rather than measurement of total elemental concentrations, future studies need to determine nutrient fluxes, especially rates of mineralisation and the capacity of soil to supply nutrients for plant uptake (O'Connell and Grove 1991; Attiwill and Adams 1993).

Impact following *P. cinnamomi* invasion has largely been determined from taxonomic compilations of changes in floristic composition rather than ecosystem functioning. Averaging the frequency of occurrence of *P. cinnamomi*-susceptible plant taxa of the Stirling Range National Park into broad functional groupings found that susceptible taxa were mainly proteaceaous woody perennial vertebrate pollinated seeder shrubs (Wills 1993; Hobbs 1997). Interpretations of the likely impact of the pathogen on various aspects of ecosystem function is limited from this type of analysis as it assumes that all susceptible species are removed from infested areas, averages over ecosystems and ignores significant species interactions. Only a minority of susceptible species in *Banksia* woodland and *E. marginata* forest

bioregions significantly decreased in cover in diseased compared with adjoining healthy areas. Plant species that changed significantly with disease status were herbs and shrubs from a range of families with a mixture of functional properties such as *P. cinnamomi* susceptibility, response to fire, rooting type and mycorrhizal association. However, the gaps in Tables 5 and 6 indicate the importance of acquiring more information on the functional traits of the plant species occurring in the bioregions. In relation to invasion, the key questions would be whether loss of endemic species results in a collapse of function or whether functional analogues compensate for such changes resulting in continued critical ecosystem function with reduced species diversity (Main 1992). Suggested important functions that need to be maintained would be the ability to: fix C and N; provide an architectural structure or habitat; sharing of resources; and recycling of resources to minimise net loss from the system (Main 1992).

Establishment of the robustness of components of disturbed pathways may be determined from the characteristic sequences in secondary succession after invasion (Main 1981). For example in a study of a Mediterranean postcultural succession, Garnier *et al*. (2004) demonstrated that simple, quantitative, easily measurable plant traits of the dominant contributors to plant biomass yielded relevant information on key aspects of ecosystem functioning. *Phytophthora cinnamomi* invasion of *Banksia* woodland and *E. marginata* forest biomes resulted in selective changes in plant composition depending on susceptibility to the pathogen and the creation of environments favouring alternative replacement sequences. Thus the characteristics of successional sequences after infestation may indicate dominant pathways by which the system could be restored (Main 1981).

Animal and microbial communities experience sequential changes that coexist with vegetation seral changes (Yearsley and Parminter 1998) and preservation of plant genetic diversity is a means of conserving dependent animal species (Wimp *et al*. 2004). Vegetation is the main determinant of the physical structure of the environment and provides many essential habitats of animal species (Southwood 1977; Williams *et al*. 2002; Tews *et al*. 2004). Ameliorating disease-mediated changes to the flora will thus sustain dependent fauna habitat. Determining successional disease-mediated changes to the vegetation is therefore a major embracing research priority.

Recording secondary succession requires long-term monitoring. Weste (2003) found that monitoring secondary succession for 30 years after *P. cinnamomi* infestation was insufficient time to determine whether understorey regeneration was stable or whether successive cycles of disease and recovery would occur. A possible alternative to long-term monitoring would be a cronosequence of disease centres with different ages of infestation. Ideally, knowing time since infestation would give the potential of comparing secondary succession in a cronosequence of disease centres in plant communities having similar characteristics. Such a space-for-time substitution study would need to be setup and interpreted carefully. Accurate estimation of the age of the infestation could be difficult because there is little historical data of disease occurrence and aerial photographs taken at infrequent intervals would only provide an imprecise time for onset of infestation. In addition, as found in fire cronosequence studies (Hobbs and Atkins 1990), the effects of age on secondary succession may be masked by other factors. Secondary succession in disease centres would be affected by factors other than community characteristics regulating pathogen dynamics, such as environmental differences at the time of infestation. However, secondary succession in *Armillaria luteobubalina* disease centres in *Eucalyptus wandoo* woodland could be determined from the variation in stand components between non-infested woodland and disease centres with intermediate and high impact, without knowledge of age of infestation and environmental differences at the time of infestation (Shearer *et al*. 1997).

Future biotic reorganisation following *P. cinnamomi* invasion will be influenced by predicted climate change. Rainfall for the South-West Botanical Province of Western Australia has shifted from the most reliable rainfall in Australia before the 1960s to a step change to a drier state of 10–20% decrease in winter rainfall over the last 30 years (IOCI 2002). The reasons for the step change to a drier state is not known, but enhanced greenhouse effect (IOCI 2002), reduced land cover change (Pitman *et al*. 2004) and Indian Ocean sea-surface temperature (Baines 2005) have been implicated. Temperature within the province has increased by 0.7°C in the last 50 years, warming being greater in winter than summer and greater in daily minima than daily maxima (IOCI 2002). A future drying trend in winter is predicted for the next 50 years in association with reduced rainfall in spring and a reduction of heavy rainfall days and long wet spells (Timbal 2004).

The predicted drying trend for the South-West Botanical Province of Western Australia will probably have a negative effect on *P. cinnamomi* through impact on susceptible hosts and pathogen dynamics. Future climate changes may result in a decline in population vigour and restricted distribution of host species adapted to contemporary environments, especially non-sprouting taxa (Cowling *et al*. 2004) and overstorey taxa dependent on relatively shallow groundwater resources (Groom *et al*. 2001). Drying soil water conditions affect not only development of *P. cinnamomi* in the soil, but also plant water status and the growth rate of the pathogen in the secondary phloem of susceptible hosts. Plants suffering water stress were less susceptible to invasion by *P. cinnamomi* than well watered plants (Tippett *et al*. 1987). The pathogen is dependent on moisture to complete its life cycle and limiting soil moisture inhibits survival, reproduction, dispersal and the infection process in the environments of the South-West Botanical Province of Western Australia (Shearer and Tippett 1989). Past extensive deaths of susceptible hosts from *P. cinnamomi* infestation have been associated with extreme rainfall events (Shearer and Tippett 1989; McDougall 1996). A predicted reduction of heavy rainfall days and long wet spells may reduce the occurrence of future extensive deaths of susceptible hosts from *P. cinnamomi* infestation.

Appropriate long-term management of *P. cinnamomi*-infested communities is a major conservation dilemma (Shearer *et al*. 2007). Remediation is needed to control pathogen behaviour without undue consequences for long-term

community welfare. The concept of adaptive management (Holling 1978) has the potential for dealing with inevitable surprises with incomplete knowledge. Management need to incorporate ecosystems as having multiple potential futures that are uncertain and unpredictable by being flexible, adaptive and experimental at scales compatible with the scales of critical ecosystem functions (Holling and Meffe 1996). Evolving complex adaptive systems are interlinked in ongoing adaptive cycles of growth, accumulation, restructuring and renewal occurring over scales from a plant part to the biosphere and over periods from days to geologic epochs (Gunderson and Holling 2001). Conceptually, an understanding of these cycles and scales enables evaluation of their contribution to sustainability and identification of leverage points at which a system is either capable of accepting positive change or is vulnerable (Gunderson and Holling 2001). Adaptive management aims to increase the buffering capacity of a system, manage processes at multiple scales and nurture the sources of renewal (Kramer *et al*. 2005), appropriate strategies needing investigation for long-term management of *P. cinnamomi*-infested communities. In many instances nature will respond dynamically by re-sorting and selecting genotypes that are advantageous in changing physical and biotic environments (Main 1999), renewing infested areas that will be different to the original communities. For communities such as BW4 that are invaded by *P. cinnamomi* less than others, clarification of the factors that interact in ways that buffer some communities against invasion more than others would assist adaptive management.

Immediate remediation is required to protect rare taxa and communities of high conservation value threatened by nearby *P. cinnamomi* infestations. Current strategies for conserving flora and communities of the South-West Botanical Province of Western Australia threatened by the pathogen integrate hygiene and quarantine measures, long-term *ex situ* seed conservation, translocations and aerial application of the systemic fungicide phosphite (Shearer *et al*. 2007). Chemical barriers, surface water management and drying of sites by increasing the density of tolerant native species are being tested within a 185-ha infestation that threatens conservation values of the Fitzgerald River National Park, a World Biosphere Reserve (Schoch 2008). A system of triage similar to that developed by Barrett *et al*. (2008) for flora of the Stirling Range National Park is needed to prioritise taxa and communities in relation to the consequences of *P. cinnamomi* infestation and the need for remedial action.

In conclusion, the introduced multi-host plant pathogen *P. cinnamomi* causes changes within susceptible plant communities that affect ecosystem processes. For *P. cinnamomi* there is a need to capitalise on the view that invasions are unplanned removal experiments (Díaz *et al*. 2003; Sax *et al*. 2007) that can aid better understanding of the interactions of pathogen dynamics with ecosystem functioning and evolutionary biology. Invasion of plant communities by *P. cinnamomi* will depend on attributes of the pathogen, the characteristics of the invaded habitat and their interactions, conceptualised in Table 7. As illustrated in Table 7, development of successful adaptive management procedures cascade out of core issues involved in the pathogen and patch plant community interactions. Patches within the surrounding matrix (Lewis and Lindgren 2000) develop with discrete temporal and spatial patterns as the result of *P. cinnamomi* infestation. This study has shown that the diseased patch exhibits sufficient changes in structure and processes to differentiate the patch or disease centre from the surrounding matrix. Process functioning in the patch are a combination of pathogen population dynamics and consequent community secondary succession, stand development and cycling systems (Table 7) that effect gradual change over time, potentially modified by predicted climate change. Whether or not changes over time result in similar or different functioning of the disease patch to the surrounding matrix influences conservation options. Combination of this study with other detailed studies of *P. cinnamomi* soil inoculum dynamics, rates of disease extension and the conduciveness of soils in disease centres of several *Banksia* woodland and *E. marginata* forest biomes (Shearer *et al*. 1989; Shearer in

Table 7. Conceptual analysis of core issues and those that cascade from core issues for *Phytophthora cinnamomi* disease centres of *Banksia* woodland and *Eucalyptus marginata* forest biomes of the South-West Botanical Province of Western Australia

Components investigated in this study are shown in italics

Core issues	Cascading issues
Diseased patch in the surrounding matrix	Nested hierarchies of transitory patch dynamics structural constraints operating on organisms functional constraints operating on processes
Plant community matrix	*Structural, compositional and functional components*
Pathogen invasion	Receptivity/pathogen invasion success arrival establishment self-sustaining population growth persistence spread phenotypic/genetic plasticity
Pathogen impact measured at multiple scales and levels of organisation	*Plant community changes* *canopy* *composition* habitat *direct/indirect impact* *nutrient cycling* fauna interactions Changes in ecosystem function
Secondary succession	Recruitment *Persistence* Compensation/complementarity *Function* Pathogen dynamics Genetic and evolutionary processes
Climate change	Community dynamics Pathogen dynamics
Conservation options	Adaptive management Inevitable surprises with incomplete knowledge *Priorities*

preparation) will link autecological dynamics of the pathogen with synecological dynamics of the ecosystem.

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References

Aronson J, Dhillion S, Le Floc'h E (1995) On the need to select an ecosystem of reference, however imperfect: a reply to Pickett and Parker. *Restoration Ecology* **3**, 1–3. doi: 10.1111/j.1526-100X.1995.tb00069.x

Attiwill PM, Adams MA (1993) Tansley Review No. 50. Nutrient cycling in forests. *The New Phytologist* **124**, 561–582. doi: 10.1111/j.1469-8137.1993.tb03847.x

Baines PG (2005) Long-term variations in winter rainfall of southwestern Australia and the African monsoon. *Australian Meteorological Magazine* **54**, 91–102.

Barrett S, Shearer BL, Crane CE, Cochrane A (2008) An extinction-risk assessment tool for flora threatened by *Phytophthora cinnamomi*. *Australian Journal of Botany* **56**, 477–486. doi: 10.1071/BT07213

Beard JS (1984) Biogeography of the Kwongan. In 'Kwongan plant life of the sandplain'. (Eds JS Pate, JS Beard) pp. 1–26. (University of Western Australia Press: Nedlands)

Beard JS (1989) Definition and location of *Banksia* woodlands. *Journal of the Royal Society of Western Australia* **71**, 85–86.

Bell DT, Hopkins AJM, Pate JS (1984) Fire in the Kwongan. In 'Kwongan plant life of the sandplain'. (Eds JS Pate, JS Beard) pp. 178–204. (University of Western Australia Press: Nedlands)

Bell DT, McCaw WL, Burrows ND (1989) Influence of fire on jarrah forest vegetation. In 'The jarrah forest. A complex Mediterranean ecosystem'. (Eds B Dell, JJ Havel, N Malajczuk) pp. 203–215. (Kluwer Academic Publishers: Dordrecht)

Brundrett MC, Abbott LK (1991) Roots of jarrah forest plants. I. Mycorrhizal associations of shrubs and herbaceous plants. *Australian Journal of Botany* **39**, 445–457. doi: 10.1071/BT9910445

Callaway RM, Maron JL (2006) What have exotic plant invasions taught us over the past 20 years? *Trends in Ecology & Evolution* **21**, 369–374. doi: 10.1016/j.tree.2006.04.008

Chapin FS, Walker BH, Hobbs RJ, Hooper DU, Lawton JH, Sala OE, Tilman D (1997) Biotic control over the functioning of ecosystems. *Science* **277**, 500–504. doi: 10.1126/science.277.5325.500

Chapin FS, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL, Hooper DU, Lavorel S, Sala OE, Hobbie SE, Mack MC, Diaz S (2000) Consequences of changing biodiversity. *Nature* **405**, 234–242. doi: 10.1038/35012241

Chen J, Saunders SC, Crow TR, Naiman RJ, Brosofske KD, Mroz GD, Brookshire BL, Franklin JF (1999) Microclimate in forest ecosystem and landscape ecology. *Bioscience* **49**, 288–297. doi: 10.2307/1313612

Churchward HM, Dimmock GM (1989) The soils and landforms of the northern jarrah forest. In 'The jarrah forest. A complex Mediterranean ecosystem'. (Eds B Dell, JJ Havel, N Malajczuk) pp. 13–21. (Kluwer Academic Publishers: Dordrecht)

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**, 117–143. doi: 10.1111/j.1442-9993.1993.tb00438.x

Cornelissen JHC, Lavorel S, Garnier E, Diaz S, Buchmann N, Gurvich DE, Reich PB, Ter Seege H, Morgan HD, Van der Heijden MGA, Pausas JG, Poorter H (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* **51**, 335–380. doi: 10.1071/BT02124

Cowling RM, Ojeda F, Lamont BB, Rundel PW (2004) Climate stability in Mediterranean-type ecosystems: implications for the evolution and conservation of biodiversity. In 'Proceedings of the 10th MEDECOS conference, 25 April–1 May, Rhodes, Greece'. (Eds M Arianoutsou, VP Papanastasis) pp. 1–11. (Millpress: Rotterdam)

Crane CE, Shearer BL (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. doi: 10.1071/AP07052

Crombie DS, Tippett JT, Hill TC (1988) Dawn water potential and root depth of trees and understorey species in south-western Australia. *Australian Journal of Botany* **36**, 621–631. doi: 10.1071/BT9880621

Dawson P, Weste G, Ashton D (1985) Regeneration of vegetation in the Brisbane Ranges after fire and infestation by *Phytophthora cinnamomi*. *Australian Journal of Botany* **33**, 15–26. doi: 10.1071/BT9850015

Day PR (1965) Particle fraction and particle-size analysis. In 'Methods of soil analysis. Part 1'. Agronomy Monograph 9. (Ed. CA Black) pp. 545–567. (ASA and SSSA: Madison, WI)

Dell B, Havel JJ (1989) The jarrah forest, an introduction. In 'The jarrah forest. A complex Mediterranean ecosystem'. (Eds B Dell, JJ Havel, N Malajczuk) pp. 1–10. (Kluwer Academic Publishers: Dordrecht)

Díaz S, Symstad AJ, Chapin FS III, Wardle DA, Huenneke LF (2003) Functional diversity revealed by removal experiments. *Trends in Ecology & Evolution* **18**, 140–146. doi: 10.1016/S0169-5347(03)00007-7

Dodd J, Heddle EM, Pate JS, Dixon KW (1984) Rooting patterns of sandplain plants and their functional significance. In 'Kwongan plant life of the sandplain'. (Eds JS Pate, JS Beard) pp. 146–177. (University of Western Australia Press: Nedlands)

Edmonds RL, Sollins P (1974) The impact of forest diseases on energy and nutrient cycling and succession in coniferous forest ecosystems. *American Phytopathological Society Proceedings* **1**, 175–180.

Ehrenfeld JG (2003) Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems (New York, NY)* **6**, 503–523. doi: 10.1007/s10021-002-0151-3

Fleishman E, Noss RF, Noon BR (2006) Utility and limitations of species richness metrics for conservation planning. *Ecological Indicators* **6**, 543–553. doi: 10.1016/j.ecolind.2005.07.005

Frazer GW, Canham CD, Letzman KP (1999) 'Gap Light Analyzer (GLA): imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs. Users manual and program documentation, Version 2.0.' (Simon Frazer University: Burnaby, British Columbia and the Institute of Ecosystem Studies: Millbrook, New York)

Garnier E, Cortez J, Billès G, Navas ML, Roumet C, Debussche M, Laurent G, Blanchard A, Aubry D, Bellmann A, Neill C, Toussaint JP (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology* **85**, 2630–2637. doi: 10.1890/03-0799

Grierson PF, Adams MA (2000) Plant species affect acid phosphatase, ergosterol and microbial P in a jarrah (*Eucalyptus marginata* Donn ex Sm.) forest in south-western Australia. *Soil Biology & Biochemistry* **32**, 1817–1827. doi: 10.1016/S0038-0717(00)00155-3

Groom PK, Froend RH, Mattiske EM, Gurner RP (2001) Long-term changes in vigour and distribution of *Banksia* and *Melaleuca* overstorey species on the Swan Coastal Plain. *Journal of the Royal Society of Western Australia* **84**, 63–69.

Gunderson LH, Holling CS (2001) 'Panarchy: understanding transformations in human and natural systems.' (Island Press: Washington, DC)

Hansen EM (1999) Disease and diversity in forest ecosystems. *Australasian Plant Pathology* **28**, 313–319. doi: 10.1071/AP99050

Havel JJ (1975) Site-vegetation mapping in the northern jarrah forest (Darling Range). 1. Definition of site-vegetation types. Bulletin 86. (Forests Department, Perth)

Herrick JE, Schuman GE, Rango A (2006) Monitoring ecological processes for restoration projects. *Journal for Nature Conservation* **14**, 161–171. doi: 10.1016/j.jnc.2006.05.001

Hobbs RJ (1997) Can we use plant functional types to describe and predict responses to environmental change? In 'Plant functional types: their relevance to ecosystem properties and global change'. (Eds TM Smith, HH Shugart, FI Woodward) pp. 66–90. (Cambridge University Press: Cambridge)

Hobbs RJ, Atkins L (1990) Fire-related dynamics of *Banksia* woodland in south-western Western Australia. *Australian Journal of Botany* **38**, 97–110. doi: 10.1071/BT9900097

Hobbs RJ, Humphries SE (1995) An integrated approach to the ecology and management of plant invasions. *Conservation Biology* **9**, 761–770. doi: 10.1046/j.1523-1739.1995.09040761.x

Holling CS (1978) 'Adaptive environment assessment and management.' (John Wiley and Sons: Chichester)

Holling CS, Meffe GK (1996) Command and control and the pathology of natural resource management. *Conservation Biology* **10**, 328–337. doi: 10.1046/j.1523-1739.1996.10020328.x

Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* **75**, 3–35. doi: 10.1890/04-0922

IOCI (2002) 'Climate variability and change in the south-west. Indian Ocean climate initiative.' (Department of Environment Water and Catchment Protection: Perth)

Jennings SB, Brown ND, Sheil D (1999) Assessing forest canopies and understory illumination: canopy closure, canopy cover and other measures. *Forestry* **72**, 59–73. doi: 10.1093/forestry/72.1.59

Keighery GJ, Coates DJ, 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.

Kennedy J, Weste G (1986) Vegetation changes associated with invasion by *Phytophthora cinnamomi* on monitored sites in the Grampians, Western Victoria. *Australian Journal of Botany* **34**, 251–279. doi: 10.1071/BT9860251

Kirby KN (1993) 'Advanced data analysis with SYSTAT.' (Van Nostrad Reinhold: New York)

Kramer K, Brinkman B, Kuiters L, Verdonschot P (2005) 'Is ecological succession predictable? Theory and applications.' Alterra Report 1277. (Alterra: Wageningen)

Laidlaw WS, Wilson BA (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. doi: 10.1071/BT02100

Lamont BB (1984) Specialised modes of nutrition. In 'Kwongan plant life of the sandplain'. (Eds JS Pate, JS Beard) pp. 136–145. (University of Western Australia Press: Nedlands)

Levia DF, Frost E (2006) Variability of throughfall volume and solute inputs in wooded ecosystems. *Progress in Physical Geography* **30**, 605–632. doi: 10.1177/0309133306071145

Levine JM, Vila M, D' Antonio CM, Dukes JS, Grigulis K, Lavorel S (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London. Series B. Biological Sciences* **270**, 775–781. doi: 10.1098/rspb.2003.2327

Lewis KJ, Lindgren BS (2000) A conceptual model of biotic disturbance ecology in the central interior of B.C.: How forest management can turn Dr Jekyll into Mr Hyde. *Forestry Chronicle* **76**, 433–443.

Loreau M (2000) Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* **91**, 3–17. doi: 10.1034/j.1600-0706.2000.910101.x

Loreau M, Roy J, Tilman D (2005) Linking ecosystem and parasite ecology. In 'Parasitism and ecosystems'. (Eds F Thomas, JF Guégan, F Renaud) pp. 13–21. (Oxford University Press: Oxford)

Lovett GM, Canham CD, Arthur MA, Weathers KC, Fitzhugh RD (2006) Forest ecosystem responses to exotic pests and pathogens in eastern North America. *Bioscience* **56**, 395–405. doi: 10.1641/0006-3568(2006)056[0395:FERTEP]2.0.CO;2

Main AR (1981) Ecosystem theory and management. *Journal of the Royal Society of Western Australia* **64**, 1–4.

Main AR (1992) The role of diversity in ecosystem function: an overview. In 'Biodiversity of Mediterranean ecosystems in Australia'. (Ed. RJ Hobbs) pp. 77–93. (Surrey Beatty and Sons: Chipping Norton)

Main AR (1999) How much diversity is enough? *Agroforestry Systems* **45**, 23–41. doi: 10.1023/A:1006203318425

Matson PA, Boone RD (1984) Natural disturbance and nitrogen mineralization: wave-form dieback of mountain hemlock in the Oregon Cascades. *Ecology* **65**, 1511–1516. doi: 10.2307/1939130

McArthur WM (1991) 'Reference soils of south-western Australia.' (Department of Agriculture, Western Australia: Perth)

McCarthy J (2001) Gap dynamics of forest trees: a review with particular attention to boreal forests. *Environment Reviews* **9**, 1–59. doi: 10.1139/er-9-1-1

McCune B, Grace JB (2002) 'Analysis of ecological communities.' (MjM Software Design: Gleneden Beach, OR)

McCune B, Mefford MJ (2006) 'PC-ORD. Multivariate analysis of ecological data. Version 5.11.' (MjM Software Design: Gleneden Beach, OR)

McDougall KL (1996) Vegetation patterns in the northern jarrah forest of Western Australia in relation to dieback history and the current distribution of *Phytophthora cinnamomi*. PhD Thesis, Murdoch University, Western Australia.

McDougall KL, Hobbs RJ, Hardy GEStJ (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. doi: 10.1071/BT01096

McDougall KL, Hobbs RJ, Hardy GEStJ (2005) Distribution of understorey species in forest affected by *Phytophthora cinnamomi* in south-western Western Australia. *Australian Journal of Botany* **53**, 813–819. doi: 10.1071/BT04203

McKenzie HA, Wallace HS (1954) The Kjeldahl determination of nitrogen: a critical study of digestion conditions – temperature, catalyst and oxidising agent. *Australian Journal of Chemistry* **7**, 55–70.

McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution* **14**, 450–453. doi: 10.1016/S0169-5347(99)01679-1

Moore NA (2005) Role of fire on *Phytophthora cinnamomi* in the Stirling Range National Park, Western Australia. Honours Thesis, Murdoch University, Western Australia.

Moran MD (2003) Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos* **100**, 403–405. doi: 10.1034/j.1600-0706.2003.12010.x

Murphy J, Riley T (1962) A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta* **27**, 31–36. doi: 10.1016/S0003-2670(00)88444-5

Myers N (2001) Mediterranean-climate regions: glowing hotspots of diversity. *Journal of Mediterranean Ecology* **2**, 157–163.

Newell GR (1998) Characterization of vegetation in an Australian open forest community affected by cinnamon fungus (*Phytophthora cinnamomi*): implications for faunal habitat quality. *Plant Ecology* **137**, 55–70. doi: 10.1023/A:1008056432001

O'Connell AM, Grove TS (1991) Processes contributing to the nutritional resilience or vulnerability of jarrah and karri forests in Western Australia. In 'Productivity in perspective. Proceedings of the third Australian forest soils and nutrition conference, Melbourne, 7–11 October'. (Ed. PJ Ryan) pp. 180–197. (Forestry Commission of NSW: Sydney)

Olden JD, Poff NL (2003) Towards a mechanistic understanding and prediction of biotic homogenization. *American Naturalist* **162**, 442–460. doi: 10.1086/378212

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* **1**, 3–19. doi: 10.1023/A:1010034312781

Pate JS, Bell TL (1999) Application of the ecosystem mimic concept to the species-rich *Banksia* woodlands of Western Australia. *Agroforestry Systems* **45**, 303–341. doi: 10.1023/A:1006218310248

Pate JS, Dell B (1984) Economy of mineral nutrients in sandplain species. In 'Kwongan plant life of the sandplain'. (Eds JS Pate, JS Beard) pp. 227–252. (University of Western Australia Press: Nedlands)

Pate JS, Stewart GR, Unkovich M (1993) ^{15}N natural abundance of plant and soil components of a *Banksia* woodland ecosystem in relation to nitrate utilisation, life form, mycorrhizal status and N_2 fixing abilities of component species. *Plant, Cell & Environment* **16**, 365–373. doi: 10.1111/j.1365-3040.1993.tb00882.x

Piper CS (1942) 'Soil and plant analysis.' (University of Adelaide: Adelaide)

Pickett STA (1989) Space-for-time substitution as an alternative to long-term studies. In 'Long-term studies in ecology. Approaches and alternatives'. (Ed. GE Likens) pp. 110–135. (Springer-Verlag: New York)

Pitman AJ, Narisma GT, Pielke RA, Holbrook NJ (2004) Impact of land cover change on the climate of southwest Western Australia. *Journal of Geophysical Research* **109**(D18109), 1–12. doi: 10.1029/2003JD004347

Postle AC, Majer JD, Bell DT (1986) Soil and litter invertebrates and litter decomposition in jarrah (*Eucalyptus marginata*) forest affected by jarrah dieback fungus (*Phytophthora cinnamomi*). *Pedobiologia* **29**, 47–69.

Prescott CE (2002) The influence of forest canopy on nutrient cycling. *Tree Physiology* **22**, 1193–1200.

Sax DF, Stachowicz JJ, Brown JH, Bruno JF, Dawson MN, Gaines SD, Grosberg RK, Hastings A, Holt RD, Mayfield MM, O'Connor MI, Rice WR (2007) Ecological and evolutionary insights from species invasions. *Trends in Ecology & Evolution* **22**, 465–471. doi: 10.1016/j.tree.2007.06.009

Schoch K (2008) Last stand at Bell Track. *Landscope* **25**(4), 29–31.

Semeniuk V, Glassford DK (1989) Bassendean and Spearwood Dunes: their geomorphology, stratigraphy and soils as a basis for habitats of *Banksia* woodlands. *Journal of the Royal Society of Western Australia* **71**, 87–88.

Shaw DC, Bible K (1996) An overview of forest canopy ecosystem functions with reference to urban and riparian systems. *Northwest Science* **70**, 1–6.

Shearer BL (1992) The ecological implications of disease in the southern forest of south-western Australia. In 'Research on the impact of forest management in south-western Australia'. Occasional Paper 2/92. (Ed. M Lewis) pp. 99–113. (Department of Conservation and Land Management: Perth)

Shearer BL (1994) The major plant pathogens occurring in native ecosystems of south-western Australia. *Journal of the Royal Society of Western Australia* **77**, 113–122.

Shearer BL, Dillon M (1995) Susceptibility of plant species in *Eucalyptus marginata* forest to infection by *Phytophthora cinnamomi. Australian Journal of Botany* **43**, 113–134. doi: 10.1071/BT9950113

Shearer BL, Dillon M (1996*a*) 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. doi: 10.1071/BT9960079

Shearer BL, Dillon M (1996*b*) Susceptibility of plant species in *Banksia* woodlands on the Swan Coastal Plain, Western Australia, to infection by *Phytophthora cinnamomi. Australian Journal of Botany* **44**, 433–445. doi: 10.1071/BT9960433

Shearer BL, Hill TC (1989) Diseases of *Banksia* woodlands on the Bassendean and Spearwood Dune Systems. *Journal of the Royal Society of Western Australia* **71**, 113–114.

Shearer BL, Smith IW (2000) Diseases of eucalypts caused by soilborne species of *Phytophthora* and *Pythium*. In 'Diseases and pathogens of Eucalypts'. (Eds PJ Keane, GA Kile, FD Podger, BN Brown) pp. 259–291. (CSIRO Publishing: Melbourne)

Shearer BL, Tippett JT (1989) Jarrah dieback: the dynamics and management of *Phytophthora cinnamomi* in the jarrah (*Eucalyptus marginata*) forest of south-western Australia. Research Bulletin, 3 (Department of Conservation and Land Management: Perth)

Shearer BL, Dillon MJ, Buehrig RM (1989) Population dynamics of *Phytophthora cinnamomi* in *Banksia* woodlands and jarrah forest of south-western Australia. In 'Proceedings of the 7th biennial conference of the Australasian Plant Pathology Society'. p. 148. (Australasian Plant Pathology Society: Brisbane)

Shearer BL, Byrne A, Dillon M, Buehrig R (1997) Distribution of *Armillaria luteobubalina* and its impact on community diversity and structure in *Eucalyptus wandoo* woodland of southern Western Australia. *Australian Journal of Botany* **45**, 151–165. doi: 10.1071/BT95083

Shearer BL, Crane CE, Cochrane A (2004*a*) 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. doi: 10.1071/BT03131

Shearer BL, Crane CE, Fairman RG (2004*b*) Phosphite reduces disease extension of a *Phytophthora cinnamomi* front in *Banksia* woodland, even after fire. *Australasian Plant Pathology* **33**, 249–254. doi: 10.1071/AP04002

Shearer BL, Crane CE, 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. doi: 10.1071/BT06019

Southwood TRE (1977) Habitat, the templet for ecological strategies? *Journal of Animal Ecology* **46**, 337–365.

Specht RL, Specht A (1989) Species richness of sclerophyll (healthy) plant communities in Australia – the influence of overstorey cover. *Australian Journal of Botany* **37**, 337–350. doi: 10.1071/BT9890337

Stewart GR, Pate JS, Unkovich M (1993) Characteristics of inorganic nitrogen assimilation of plants in fire-prone Mediterranean-type vegetation. *Plant, Cell & Environment* **16**, 351–363. doi: 10.1111/j.1365-3040.1993.tb00881.x

Strayer DL, Eviner VT, Jeschke JM, Pace ML (2006) Understanding the long-term effects of species invasions. *Trends in Ecology & Evolution* **21**, 645–651. doi: 10.1016/j.tree.2006.07.007

Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* **31**, 79–92.

Tilman D (1999) The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* **80**, 1455–1474.

Timbal B (2004) Southwest Australia past and future rainfall trends. *Climate Research* **26**, 233–249. doi: 10.3354/cr026233

Tippett JT, Crombie DS, Hill TC (1987) Effect of phloem water relations on the growth of *Phytophthora cinnamomi* in *Eucalyptus marginata*. *Phytopathology* **77**, 246–250. doi: 10.1094/Phyto-77-246

Van der Moezel PG, Loneragan WA, Bell DT (1987) Northern sandplain kwongan: regeneration following fire, juvenile period and flowering phenology. *Journal of the Royal Society of Western Australia* **69**, 123–132.

West PW (2004) 'Tree and forest measurement.' (Springer: Berlin)

Weste G (1986) Vegetation changes associated with invasion by *Phytophthora cinnamomi* of defined plots in the Brisbane ranges, Victoria, 1975–1985. *Australian Journal of Botany* **34**, 633–648. doi: 10.1071/BT9860633

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. doi: 10.1071/AP03013

Weste G, Kennedy J (1997) Regeneration of susceptible native species following a decline of *Phytophthora cinnamomi* over a period of 20 years in defined plots in the Grampians, Western Victoria. *Australian Journal of Botany* **45**, 167–190. doi: 10.1071/BT96048

Weste G, Cooke D, Taylor P (1973) The invasion of native forest by *Phytophthora cinnamomi* II. Post-infection vegetation patterns, regeneration, decline in inoculum, and attempted control. *Australian Journal of Botany* **21**, 13–29. doi: 10.1071/BT9730013

Western Australian Herbarium (1998) FloraBase – The Western Australia flora. Available at http://florabase.dec.wa.gov.au/ [Verified 4 March 2009]

Williams SE, Marsh H, Winter J (2002) Spatial scale, species diversity, and habitat structure: small mammals in Australian tropical rain forest. *Ecology* **83**, 1317–1329.

Wills RT (1993) The ecological impact of *Phytophthora cinnamomi* in the Stirling Range National Park, Western Australia. *Australian Journal of Ecology* **18**, 145–159. doi: 10.1111/j.1442-9993.1993.tb00439.x

Wimp GM, Young WP, Woolbright SA, Martinsen GD, Keim P, Whitham TG (2004) Conserving plant genetic diversity for dependent animal communities. *Ecology Letters* **7**, 776–780. doi: 10.1111/j.1461-0248.2004.00635.x

Yearsley K, Parminter J (1998) Seral stages across forested landscapes: relationships to biodiversity. British Columbia Ministry of Forests Research Program. Extension Note 18. (British Columbia Ministry of Forests Research Branch: Victoria, BC)

Yorks TE, Jenkins JC, Leopold DJ, Raynal DJ, Orwig DA (2000) Influences of eastern hemlock mortality on nutrient cycling. In 'Proceedings: symposium on sustainable management of hemlock ecosystems in eastern North America'. General Technical Report NE-267. (Eds KA McManus, KS Shields, DR Souto) pp. 126–133. (Northeastern Research Station, US Department of Agriculture Forest Service: Radnor, PA)

Yurkonis KA, Meiners SJ, Wachholder BE (2005) Invasion impacts diversity through altered community dynamics. *Journal of Ecology* **93**, 1053–1061. doi: 10.1111/j.1365-2745.2005.01029.x

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