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Impact of *Phytophthora*-dieback on birds in *Banksia* woodlands in south west Western Australia

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Abstract

Invasive plant pathogens have impacted forest and woodland systems globally and can negatively impact biodiversity. The soil-borne plant pathogen *Phytophthora cinnamomi* is listed as one of the world's worst invasive species and alters plant community composition and habitat structure. Few studies have examined how these *Phytophthora*-induced habitat changes affect faunal communities.

We examined bird communities in *Banksia* woodland with, and without, *Phytophthora* dieback in a biodiversity hotspot, southwestern Australia. Seven sites along dieback fronts, with paired 1-ha plots in diseased and healthy vegetation, were surveyed monthly for birds over seven months. Vegetation assessments showed that diseased sites had reduced plant species richness, litter, shrub, tree and canopy cover, high bare ground and significantly lower flowering scores, than healthy sites. Bird community composition differed significantly between diseased and healthy sites, although total bird abundance, total species richness and foraging guilds, did not. Average species richness of birds per survey and the abundance of brown honeyeaters, western spinebills and silvereyes was lower in diseased than healthy sites. The tawny-crowned honeyeater had higher abundances in diseased sites. Similarity matrices of habitat structure, flowering scores and bird assemblages were congruent, indicating that habitat structural differences were influencing bird community composition. Our results suggest that this pathogen is potentially a serious threat to avian biodiversity and especially for nectarivores, and populations in fragmented landscapes. Since elimination of the pathogen is not currently possible, management should focus on methods of preventing its spread until techniques to eliminate the pathogen are developed.

Keywords: Phytophthora cinnamomi; Bird; Disturbance; Vegetation; Structure; Floristics

1. Introduction

Invasive species have the ability to rapidly transform community composition and ecosystem-level processes (Vitousek et al., 1997). Invasive plant pathogens have impacted many forest and woodland communities at regional scales, resulting in major alterations to ecosystem structure, plant community diversity, plant productivity and vegetation structure and floristics (Castello et al., 1995; Mack et al., 2000). Some of the structural and floristic changes wrought by invasive plant pathogens include the loss of keystone or nectar-producing species, loss of canopy or overstorey cover and decreases in litter cover (Hansen, 2008; Smith et al., 2009; Tomback and Achuff, 2010). These structural and floristic changes are likely to influence faunal communities (Barringer et al., 2012; McKinney et al., 2009),

but the indirect effects of invasive plant pathogens on faunal communities remains poorly studied and poorly understood. Given the large scale over which invasive plant pathogens can infest areas (e.g. Lovett et al., 2006; Meentemeyer et al., 2004), such pathogens present a potential threat to many faunal communities, and hence global biodiversity, and there is an urgent need to evaluate, and better understand the indirect effects of invasive plant pathogens on faunal communities (Lovett et al., 2006; Monahan and Koenig, 2006).

Ecosystem structure and function can be permanently changed when keystone species are damaged, or removed by pathogens (Barringer et al., 2012; Lovett et al., 2006). The catastrophic ecological impacts on forests in North America, of the introduced chestnut blight fungus, *Cryphonectria parasitica*, are a well-known example (Rizzo et al., 2002). American chestnut trees, *Castanea dentata*, in eastern forests were all but eliminated following the swift extension of the pathogen in the early 1900s (Grunwald, 2012). More recently, the plant pathogen *Phytophthora ramorum* is responsible for causing the sudden oak death epidemic and decimating oak forests in the western United States (Grunwald, 2012; Rizzo et al., 2005). There is evidence that this pathogen has strong indirect impacts on vertebrate communities with models predicting negative impacts to the populations of several oak-dependent bird species (Monahan and Koenig, 2006).

A forest pathogen that is of great conservation threat to native and agricultural systems worldwide is *Phytophthora cinnamomi*, a soilborne water mould (Class Oomycetes) that is listed as one of the world's 100 worst invasive alien species (Lowe et al., 2000; Hansen, 2008). The epidemic of *P. cinnamomi* 'dieback' (the process of an area becoming infested with *P. cinnamomi*) is a major concern in southern Europe (Brasier, 1996; Vettraino et al., 2002), USA (Mircetich et al., 1977), Mexico (Tainter et al., 2000), New Zealand (Podger and Newhook, 1971), South Africa (van Broembsen and Kruger, 1985) and Australia, where it is listed as a key threatening process (Cahill et al., 2008). The presence of *P. cinnamomi* dieback in a community is often highly visible with old diseased areas typically displaying reduced biomass and reduced structural complexity as a result of the death and subsequent disappearance of susceptible plant taxa (Shearer et al., 2007). Although many studies have examined the effects of *P. cinnamomi*on vegetation, relatively few have examined its effects on fauna populations and communities (Cahill et al., 2008). The significant alterations to habitat and floristics associated with *P. cinnamomi* dieback have been predicted to substantially affect fauna through changes to important resources, such as food and nesting sites (Garkaklis et al., 2004; Wilson et al., 1994). Studies in southern Australia have tended to support these predictions, with declines in species richness and abundance of faunal communities recorded in areas with *P. cinnamomi* dieback (Armstrong and Nichols, 2000; Laidlaw and Wilson, 2006; Nichols and Barnford, 1985; Nichols and Burrows, 1985; Wilson et al., 1994), primarily due to changes in habitat structure. The negative effects of *P. cinnamomi*-induced floristic changes on faunal communities are likely to be significant given the wide range of plant species that are susceptible to *P. cinnamomi*-induced changes to habitat affect faunal communities (but see Laidlaw and Wilson, 2006).

To address the questions of whether *P. cinnamomi*-induced changes to both habitat structure and floristics affect faunal communities, we examined the response of the bird community in *Banksia* woodlands to *P. cinnamomi* dieback. *Banksia* woodlands are low open woodlands with high species richness, confined to coastal and sub-coastal southern Australia, where the canopy is dominated by *Banksia* species and the understory contains many other proteaceous species (Bishop et al., 2010). These woodlands also support a diverse nectarivorous bird community (Newland and Wooller, 1985; Ramsey, 1989) that is predicted to be particularly susceptible to *P. cinnamomi* dieback (Cahill et al., 2008) because most major nectar-producing proteaceous plants are highly susceptible to *P. cinnamomi* (Shearer et al., 2007). We surveyed the bird community, and habitat structure, floristics and flowering to examine how *P. cinnamomi* dieback affected the bird community by asking the following questions: (1) Are there differences in bird community composition, the abundance of foraging guilds or individual species between *Banksia* woodlands with and without *P. cinnamomi* dieback? (2) Are any differences in the bird community related to alterations in

habitat structure from *P. cinnamomi* dieback? and (3) Are any differences in the bird community related to dieback-induced changes in floristics and flowering?

2. Methods

2.1. Study area and site selection

Our study area was located north of Perth in south-western Australia (Fig. 1), in one of the global biodiversity hotspots (Myers et al., 2000). Vegetation in the study area is predominantly *Banksia* woodland comprised of a *Banksia* overstorey, interspersed with scattered stands of *Corymbia calophylla*, *Eucalyptus* spp. and *Allocasuarina* spp. and a diverse understorey, primarily species of Proteaceae, Myrtaceae and Fabaceae (Mitchell et al., 2003). The study area experiences a Mediterranean climate, with hot, dry summers and cool, wet winters and annual rainfall averaging 656 mm (Bureau of Meteorology, weather station #009053). Our study area has been infested with *P. cinnamomi* since the 1940s (Hill et al., 1994; Wilson et al., 2012) and, currently >20,000 ha has been identified as infected by *P. cinnamomi* (Wilson et al., 2009).

We identified seven sites containing a mixture of diseased (*P. cinnamomi* detected) and healthy (*P. cinnamomi* not detected) *Banksia* woodlands, with clearly defined disease fronts (Fig. 2) using GISbased spatial mapping combined with ground-truthing. At each site, we established paired 1-ha plots $(100 \times 100 \text{ m})$, one each in diseased and healthy *Banksia* woodland (Fig. 1). All sites were located on the same soil and vegetation types (prior to *P. cinnamomi* invasion) with dominant canopy species of *B. attenuata* and *B. menziesii* with occasional scattered *C. calophylla*, *B. ilicifolia* and a dense understorey.

2.2. Plant taxa and habitat structure estimates

Fourteen floristic quadrats (10×10 m) were established at the seven paired sites, with one quadrat in each 1-ha plot. Within each quadrat, we recorded plant taxa richness by identifying all vascular plant taxa in spring 2008. Specimens were collected and dried in plant presses prior to identification by

botanists, with nomenclature verified using the Western Australian Herbarium's plant database MAX. The proportion of bare-ground, litter cover and small shrub <1 m, shrub (1–2 m) and tree cover (<2 m) in each quadrat was visually estimated to the nearest 5% by visually projecting the area of cover within the quadrat for each variable according to procedures outlined in Keighery (1994), a guide that was specifically designed to assess bushland plants in southwestern Australian habitats. Canopy cover was estimated using Lemnon spherical densiometers at the centre of each quadrat. Paired sites were matched for time since last fire (determined from Department of Environment and Conservation databases), which varied from 2 to 13 years since last fire, except for one pair (13 vs 19 years since last fire).

2.3. Flowering score estimates

During each survey month (described below), flowering activity of dominant plant species (*B. attenuata*, *B. menziesii* and *B. ilicifolia*) and the combined understory, was recorded on an ordinal scale: (1) No flowering; (2) <5% flowering; (3) 5–25% flowering; (4) 25–50% flowering; (5) 50–75% flowering; and (6) 75–100% flowering. Scores were based on the overall proportion of individual plants flowering in each 1-ha plot and averaged across all survey months for analysis.

2.4. Bird survey methods

We surveyed for birds in each of seven months (April to August, October and November 2008) using an area search, which involved actively searching each 1-ha for ten minutes and recording all birds seen or heard on that plot. We included flying birds utilising the habitat (e.g. swallows) but excluded birds that were only flying through the plot. As diseased and healthy plots were adjacent to one another, we were careful to record only birds seen or heard on the 1-ha plot being surveyed and exclude birds on the adjacent plot. All surveys were conducted within five hours of sunrise and the order in which sites were surveyed was randomised between months. We averaged abundances across all seven surveys to derive the dependent variables overall bird abundance and abundance of individual species. We also calculated average bird species richness per survey and total bird species richness across all seven surveys. Area searches provide reliable estimates of relative abundance across sites of differing vegetation densities (Craig and Roberts, 2001) which, as *Banksia* woodlands are an open habitat where birds are detected relatively easily, precluded the need to correct for detectability.

2.5. Analysis

2.5.1. Floristics and habitat structure

To examine plant taxa richness between diseased and healthy *Banksia* woodland sites, we used a paired *t*-test. The composition of plant taxa (using presence/absence data) was compared between diseased and healthy sites using Blocked Multiple Response Permutation Procedure (MRBP; Mielke, 1984). MRBP is a slight variation of Multiple Response Permutation Procedure (MRPP; Mielke et al., 1976) that allows for a blocking variable. MRBP is a multivariate permutation that tests whether there are differences between two or more *a priori* classified groups using an *A* statistic (the chance-corrected within group agreement) and an associated *P*-value (McCune et al., 2002). It is analogous to multivariate parametric tests and the procedure utilizes a permutation distribution and is more robust to violations of parametric assumptions that are common in multivariate ecological datasets (Mielke et al., 1976; McCune et al., 2002). We examined plant taxa richness between diseased and healthy *Banksia* woodland sites using a paired *t*-test. Rare plant taxa (present at <3 sites) were excluded from analyses.

We compared habitat structure (plant taxa richness and the six cover estimates) of diseased and healthy sites using a MRBP on the relativised data. We visually represented site similarities using non-metric multidimensional scaling (NMDS) (Kruskal, 1964), based on a Bray–Curtis similarity matrix; displaying the first two axes and any habitat structure variables correlated ($r^2 > 0.30$) with them. We used paired *t*-tests to compare differences in habitat structure variables between diseased and healthy sites. Cover estimates were arcsine square-root transformed (Zar, 1999), though we display untransformed means to ease interpretation. We compared average flowering scores between diseased and healthy sites using Wilcoxon matched-pair signed-rank tests.

2.5.2. Bird communities, foraging guilds and individual bird species

Bird community composition, based on average abundances of each species, was compared between diseased and healthy sites, using MRBP as described for plant taxa composition (again, rare bird taxa were excluded). We also visually represented site similarities in bird community composition using NMDS based on a Bray-curtis similarity matrix and displayed the first two axes and any bird species correlated ($r^2 > 0.30$) with them. We compared community metrics (overall bird abundance, average species richness and total species richness) between diseased and healthy *Banksia* woodland sites using paired *t*-tests. Bird species were assigned to one of four foraging guilds (carnivore, granivore/frugivore, insectivore and nectarivore) based on published information (Higgins, 1999; Higgins and Davies, 1996; Higgins et al., 2005, 2001; Marchant and Higgins, 1993). The mean abundance of each guild, and each of the eight most common species (>15 bird observations from ≥ 6 sites), were also compared between diseased and healthy sites using paired *t*-tests. Guild and individual species abundances were square-root transformed prior to analyses to improve homoscedascity, although we present untransformed abundances.

2.5.3. Habitat associations between bird assemblages and abundance

To determine if correlation existed between the bird community composition and habitat structure matrices were correlated, we used a Mantel test (Mantel, 1967), which is a non-parametric method of assessing the relationship between two similarity matrices (McCune et al., 2002). We employed the Mantel test using a Monte Carlo randomisation option and obtained standardised Mantel statistics (r_m) and associated *P*-values. We used Pearson's correlation coefficients (*r*) to examine relationships between habitat structure variables and plant taxa richness and square-root transformed abundances of the eight most common bird species. Relationships between flowering scores (*B. attenuata*, *B. menziesii*, *B. ilicifolia* and understory) and square-root transformed abundances of commonly occurring bird species were explored using Spearman's rank correlation coefficient (r_s). Multivariate analyses were conducted using PC-Ord (McCune and Mefford, 1999) and univariate analyses and correlations were performed in R3.2.1 (R Core Team, 2013). All values are presented as mean \pm SE.

3. Results

3.1. Floristics and habitat structure

We identified 150 plant taxa in floristic quadrats. Plant community composition differed significantly between diseased and healthy sites (A = 0.09, P = 0.004), as did the habitat structure (A = 0.32, P = 0.005). Diseased sites had more bare ground and less litter, small shrub, tree and canopy cover than healthy sites (Fig. 3c; Table 1). Plant taxa richness was lower in diseased (44.29 ± 2.31, range 40–57) compared to healthy (58.43 ± 2.23 range 52–70) sites (Table 1).

3.2. Flowering scores

Flowering scores were lower in diseased, compared to healthy sites, for both *B. menziesii* (0.60 ± 0.40 vs 1.27 ± 0.09 : *P* < 0.05) and *B. attenuata* (0 ± 0 vs 0.30 ± 0.05 : *P* < 0.05). There was no significant difference in *B. ilicifolia* flowering scores between diseased and healthy sites (*P* > 0.05), but there was significantly less understorey flowering in diseased, compared to healthy, sites (0.41 ± 0.07 vs 0.91 ± 0.12 : *P* < 0.05).

3.3. Bird assemblage composition

We detected 520 birds of 36 species (see Table A1 for complete list) across all surveys, with the eight most common species being white-cheeked honeyeater (n = 72), brown honeyeater (n = 59), splendid fairy wren (n = 51), western spinebill (n = 45), yellow-rumped thornbill (n = 35), western wattlebird (n = 32), silvereye (n = 22) and tawny-crowned honeyeater (n = 17) (see Table 2 for scientific nomenclature). The MBRP on the 24 species detected in ≥ 3 sites, indicated bird community composition differed significantly between diseased and healthy sites (A = 0.087, P = 0.010) with clear separation of sites based on disease status (Fig. 3b). Tawny-crowned honeyeaters, yellow-rumped thornbills and white-winged fairy-wrens (*Malurus leucopterus*) were associated with diseased sites with brown honeyeaters, western spinebills, silvereyes and Australian ravens associating with healthy sites (Fig. 3d). Average bird species richness was lower in diseased (2.14 ± 0.25) compared to healthy, sites (3.27 ± 0.42 ; $t_6 = -2.63$, P = 0.039), however, disease status did not influence total bird

species richness (diseased: 10.57 ± 1.00 , healthy: 12.71 ± 1.34 ; $t_6 = -1.43$, P = 0.200) or overall bird abundance (diseased: 4.41 ± 0.65 , healthy: 6.20 ± 0.91 ; $t_6 = -2.07$, P = 0.080).

3.4. Foraging guilds and individual species

Abundance of the four foraging guilds did not differ significantly between diseased and healthy sites, although there was a trend towards more nectarivores in healthy sites (Table 2; P = 0.080). Four of the eight most common species differed significantly in abundance between diseased and healthy sites with more brown honeyeaters, western spinebills and silvereyes in healthy sites and more tawny-crowned honeyeaters in diseased sites (Table 2).

3.5. Habitat associations between bird assemblage and abundance

There was a positive association between bird community composition and habitat structure of sites $(r_m = 0.251, P = 0.011)$, indicating habitat structure influenced bird community composition (Fig. 3). The abundance of four of the eight common species was associated with at least one habitat structure variable (Table 3). Brown honeyeater abundance was positively associated with litter, shrub and tree cover, but negatively associated with bare ground (Table 3). Similarly, western spinebill abundance was positively associated with tree and canopy cover but negatively associated with bare ground (Table 3). Silvereye abundance was positively associated with litter cover while tawny-crowned honeyeater abundance was negatively associated with plant taxa richness and tree cover (Table 3).

Silvereye abundance was positively associated with *B. attenuata*, *B. menziesii* and understory flowering scores while brown honeyeater abundance was positively associated with *B. menziesii* and understory flowering scores (Table 3). In contrast, tawny-crowned honeyeater abundance was negatively associated with both *B. attenuata* and *B. menziesii* flowering scores (Table 3).

4. Discussion

Our study indicates that plant pathogens can have significant indirect effects on faunal communities by altering habitat structure and, potentially, resource availability. Although bird community composition differed between sites, as did the abundance of some bird species, all of the commonly occurring species were present in diseased sites. The patches of *Phytophthora*-diseased habitat in our study were smaller than the home ranges of many bird species we detected, and occurred amongst a matrix of healthy Banksia woodland. The spatial scale of infestation from the pathogen and the degree of habitat specificity of fauna species may be critical determinants of the magnitude of impacts on biodiversity from this plant pathogen.

4.1. Does P. cinnamomi dieback change bird community composition, abundance of foraging guilds or individual species?

Although we recorded significantly fewer birds per survey in diseased sites, overall species richness was not reduced. Our finding contrasts with Armstrong and Nichols (2000) who recorded a net decrease in bird species richness in *Phytophthora*-diseased areas of jarrah (*Eucalyptus marginata*) forests. Similarly, the limited amount of research on the responses of other fauna to *Phytophthora* indicates that species richness is often reduced in diseased areas e.g. invertebrates (Nichols and Burrows, 1985); reptiles and frogs (Nichols and Bamford, 1985).

Coupled with our findings, research indicates that *P. cinnamomi* infestations may significantly impact avian biodiversity and community composition. We found that the bird community composition differed between diseased and healthy *Banksia* woodland with brown honeyeaters, western spinebills and silvereyes more abundant in healthy sites and tawny-crowned honeyeaters more abundant in diseased sites. Armstrong and Nichols (2000) also found western spinebills to be at higher densities in healthy compared to diseased jarrah forest. Although the abundance of feeding guilds did not differ between diseased and healthy sites in our study, the altered abundances of the individual species are likely to be in response to modified food or habitat resources. Previous research has indicated that diseased sites may support higher densities of more generalist and omnivorous bird species, often associated with partially cleared or thinned habitat (Armstrong and Nichols, 2000) whereas the abundance of insectivorous bird species considered typical of healthy forest (Armstrong and Nichols, 2000) may be reduced. There are few comparative global studies that have investigated the impacts of plant pathogens, such as *P. cinnamomi*, on fauna. Forest insects can mimic the canopy loss caused by invasive plant pathogens and may have similar impacts on fauna. Tingley et al. (2002) studied birds in eastern hemlock forests and recorded a distinct difference in community composition between areas subject to attack by hemlock woolly adelgid (*Adelges tsugae*) and pristine areas. Those species that disappeared from insect-infested areas were sensitive to the removal of the hemlock overstorey. Similarly, Rabenold et al. (1998) found that canopy and sub-canopy bird species declined in spruce-fir forest following balsam woolly adelgid (*Adelges piceae*) attacks. Research on other types of disturbance that similarly alter vegetation, such as fire, forest clearing and subsequent regrowth, consistently indicate modified bird communities in response to the disturbance agent (Borges and Stouffer, 1999; Easton and Martin, 1998; Valentine et al., 2012a).

4.2. Are changes in the bird community related to changes in habitat structure from P. cinnamomi dieback?

Our results indicate that changes in habitat structure caused by *P. cinnamomi* are mediating differences in bird community composition. Similarly, other authors have reported that the changes in habitat structure caused by *P. cinnamomi*, (such as reduced litter and log availability), influence small mammal abundance and community composition (Laidlaw and Wilson, 2006; Newell and Wilson, 1993). In our study, the most profound difference in diseased *Banksia* woodland sites was the almost complete absence of the defining *Banksia* spp. overstorey. No studies involving disease-induced loss of overstory are available for comparison, but similar studies on forest insect attack have indicated the importance of canopy, with canopy-dependent species declining due to the loss of habitat (Matsuoka et al., 2001; Rabenold et al., 1998; Tingley et al., 2002).

Clear-cutting, and other forestry activities that remove overstorey canopy vegetation typically have negative impacts on bird species richness and abundance. Hingston and Grove (2010) observed that the highest species richness of canopy-utilising bird species occurred in 150-year-old forest and that young forest with reduced canopy contained few of these species. The loss of overstorey vegetation may also affect understorey bird species that make use of forest overstorey trees (Talbott and Yahner,

2003). In Australia, woodland bird species of conservation concern were more likely to occur in woodlands with good canopy cover and a low incidence of eucalypt dieback (Montague-Drake et al., 2009). Thus, it is likely that the loss of canopy will have significant effects on the bird community of *Phytophthora*-affected *Banskia* woodlands.

Changes in the habitat structure of vegetation in diseased areas is likely to contribute to the altered abundances of individual bird species, depending on habitat requirements. In our study, the tawnycrowned honeyeater was the only species significantly associated with diseased sites and was negatively associated with tree cover. Tawny-crowned honeyeaters typically prefer proteaceous heathland habitats, with complex floristic composition, as opposed to the woodland or forest habitat that the brown honeyeater and western spinebill frequents (Higgins et al., 2001). The higher abundances of tawny-crowned honeyeaters in the diseased areas may have been influenced by the heath-like structure of the diseased sites. The higher amounts of canopy cover in the healthy sites are likely to be more suitable habitat for the brown honeyeaters and western spinebills. In addition, the western spinebill rarely occurs in disturbed habitats and is strongly associated with natural bushland areas in the Perth region (Davis et al., 2013). In contrast, the brown honeyeater is often recorded utilising disturbed areas and urban gardens more than native bushland (Davis et al., 2013). The lower abundance of this species in the diseased areas may reflect reduced foraging opportunities, through reduced *Banksia* flowering, in addition to structural changes.

4.3. Are changes in the bird community related to dieback-induced changes in floristics and flowering?

Nectar availability is a key driver of population dynamics in bird communities dominated by nectarivores such as in south-western Australia (McFarland, 1986; Newland and Wooller, 1985) and South Africa (Symes et al., 2008). Although previous studies have suggested a potential impact of *P. cinnamomi* on nectar availability (Cahill et al., 2008; Armstrong and Nichols, 2000), none have examined the flow-on consequence of this to birds; although the abundance of small mammals, such as the agile antechinus *Antechinus agilis* and the bush rat *Rattus fuscipes* have previously been correlated with floristic factors associated with non-diseased vegetation (Laidlaw and Wilson, 2006).

Of the four bird species most indicative of healthy sites in our study, three species (brown honeyeater, western spinebill and silvereye) are fully or partially nectarivorous (Higgins et al., 2001) and occurred in higher abundances in healthy sites. The abundance of brown honeyeaters and silvereyes was also positively associated with flowering score. The diseased sites clearly showed that there was an almost complete loss of the dominant overstorey *Banksia* (a very important source of nectar for birds in these woodlands) and a reduction in the flowering of understory plants. Although we did not measure actual nectar content, it is a reasonable assumption that flower availability is strongly correlated to nectar availability (McFarland, 1986). Given the importance of *Banksia* species for nectarivorous birds in our study system (Newland and Wooller, 1985; Ramsey, 1989), and that seasonal flowering events can lead to densities of nectarivorous birds that are much higher than surrounding areas (Newland and Wooller, 1985), the ongoing loss of *Banksia* species due to *P. cinnamomi* is a major concern.

4.4. Landscape context, interactions and limitations

The disturbance to native habitats by *P. cinnamomi* is complex and requires consideration of its interactions with other disturbances, including fire. Fire is an important disturbance agent in numerous ecosystems, especially the Mediterranean-type environments in south-western Australia (Burrows and Abbott, 2003). Although fire management for multiple purposes (e.g. human safety, conservation) is challenging (Penman et al., 2011), prescribed burning is widely employed as a land management tool in these regions. *Banksia* woodlands are considered one of Australia's most flammable ecosystems (Burrows and Abbott, 2003) and the time since last fire is a key component in structuring flora and faunal communities (Valentine et al., 2012b). Fire can reduce structural complexity and reduce canopy cover, vegetation cover and litter (Fisher et al., 2009; Valentine et al., 2012b). Fire is also known to alter resources available to birds and can result in lower abundances of insectivores and frugivores in more frequently burnt habitats (Valentine et al., 2012a). These changes from fire have complex and as yet, poorly understood, interactions with *Phytophthora* dieback since the response of individual plant species to fire and *Phytophthora* are also poorly understood. For example, fire has been shown to influence the survival and dispersal of *P. cinnamomi* on the south coast of Western Australia and to further reduce post-fire establishment of plant species (Moore, 2005). Further

research on the complex interactions between these two forms of disturbance on fauna species, would be worthwhile.

An important consideration in our study is that we examined patches of diseased woodland in an area of continuous woodland, where there are high rates of long-term disease infestation in some areas (Wilson et al., 2012) but from an avifaunal perspective the landscape remains well connected to surrounding areas of healthy woodland. It is likely that impacts on fauna will be greatly exacerbated in large landscape-level disease fronts or in fragmented landscapes. In Western Australia, some national parks are already over 60% diseased, equating to nearly 700 km² of affected habitat (Shearer et al., 2007). In these situations, *P. cinnamomi* may create barriers to dispersal for some animal species due to changed habitat structure and lack of resources such as nectar. This could have cascading effects on biodiversity, by impacting on plant pollination, seed dispersal and other ecosystem services.

Barringer et al. (2012) documented an example of this in the whitebark pine forests (*Pinus albicaulis*) of the USA. Whitebark pines infected by exotic disease and attacked by mountain pine beetles (*Dendroctonus ponderosae*) produced fewer cones and were then visited less by the Clarke's nutcracker (*Nucifraga columbiana*) on which they depend for seed dispersal. Consequently forest disturbance had a cascading effect, causing a decline in food resources for the nutcracker, a loss of seed dispersal and ultimately a loss of population viability for the pine. The potential impacts of *P. cinnamomi* are clearly severe and extensive and are likely to increase with time unless broadscale measures to control or limit the spread of this forest disease are taken.

Our study suggests that birds may be somewhat resilient to the short-medium term impacts of *Phytophthora* dieback in continuous landscapes, as long as the spatial extent of diseased areas remains small and embedded within extensive healthy areas. However, the ongoing modification of vegetation structure and floristics associated with *P. cinnamomi* infestation may have a significant long-term impact on the habitat utilised by the bird communities in *Banksia* woodlands. We provide evidence that *P. cinnamomi* drives changes in bird community composition through changes to both habitat structure and floristics. Given the broad range of plant species that are susceptible to dieback (Shearer et al., 2007) it is a difficult problem to manage. Management actions, such as hygiene, quarantine measures, track closures, and application of phosphite (a weak solution of phosphoric acid that gives susceptible plants resistance to *P. cinnamomi*) need to be implemented to reduce dieback extent and impacts. Although eradication of the pathogen remains unachievable at the moment, there is an urgent need to identify and protect those areas that remain free of *P. cinnamomi* infestation.

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Fig. 1. Location of study sites in relation to Perth, Western Australia.



Fig. 2. Photographs showing structural changes between diseased (a) and healthy (b) *Banksia* woodland.



A: Infested Banksia Woodland



B: Healthy Banksia woodland

Fig. 3. NMDS ordination (Bray-Curtis distance measure) on (a) habitat structure (n = 8, threedimensional stress = 0.06, axis 1 $r^2 = 0.36$ and axis 2 $r^2 = 0.31$; A = 0.32, P = 0.005) and (b) bird community composition (n = 24 species; three-dimensional stress = 0.09, axis 1 $r^2 = 0.57$ and axis 2 $r^2 = 0.24$; A = 0.087, P = 0.010) of *Phytophthora*-diseased and healthy *Banksia* woodland sites. Numbers next to each site indicate the number of years since last fire and the site pair (a-g in brackets). Correlations of the variables ($r^2 \ge 0.3$) (c) habitat structure and (d) bird species used in each NMDS are also provided. Note: bfcs = black-faced cuckoo-shrike.



Table 1. Paired *t*-test values of numbers of plant taxa and arc-sine transformed proportion of habitat structural cover estimates in diseased and healthy *Banksia* woodland. Mean number of plant taxa and untransformed habitat percentage cover estimates ($\% \pm SE$) for diseased and healthy sites are shown.

	<i>t</i> 6	Means (±SE)			
		Diseased	Healthy		
Plant taxa richness	-10.89***	44.29 ± 2.31	58.43 ± 2.23		
Canopy cover (%)	-4.00**	5.24 ± 2.44	37.96 ± 8.40		
Tree cover (%)	-4.37**	$\boldsymbol{0.86 \pm 0.70}$	37.14 ± 8.15		
Shrubs (1–2 m) (%)	0.66	11.00 ± 3.21	6.29 ± 2.38		
Small shrubs (<1 m) (%)	-2.53*	13.57 ± 2.61	39.29 ± 9.16		
Litter cover (%)	-6.68***	10.29 ± 4.12	40.00 ± 6.64		
Bare ground (%)	3.48*	$\textbf{35.00} \pm \textbf{6.07}$	18.57 ± 4.97		

Significant values are highlighted in bold.

**P* < 0.05.

**P < 0.01.

***P < 0.001.

Table 2. Paired *t*-tests values of the square-root transformed abundances of commonly occurring species (>15 bird observations from ≥ 6 sites) and foraging guilds in diseased and healthy *Banksia* woodland. Untransformed mean abundances (individuals survey⁻¹ ± SE) for diseased and healthy sites are shown.

	<i>t</i> 6	Means (±SE)		
		Diseased	Healthy	
Carnivore	0.24	0.33 ± 0.18	0.18 ± 0.07	
Granivore	-1.02	0.20 ± 0.08	0.43 ± 0.21	
Insectivore	-0.56	2.06 ± 0.36	2.37 ± 0.37	
Splendid fairy-wren, Malurus splendens	1.12	0.61 ± 0.14	0.43 ± 0.13	
Yellow-rumped thornbill, Acanthiza chrysorrhoa	-0.86	0.29 ± 0.18	0.43 ± 0.21	
Silvereye, Zosterops lateralis	-2.99*	$\boldsymbol{0.08 \pm 0.08}$	0.37 ± 0.13	
Nectarivore	-2.10	1.82 ± 0.62	3.22 ± 0.73	
Brown honeyeater, Lichmera indistincta	-3.73**	0.31 ± 0.14	0.90 ± 0.26	
White-cheeked honeyeater, Phylidonyris niger	-0.16	0.71 ± 0.39	0.76 ± 0.40	
Western wattlebird, Anthochaera lunulata	-1.60	0.16 ± 0.07	0.49 ± 0.29	
Tawny-crowned honeyeater, Gliciphila melanops	3.73**	0.31 ± 0.12	$\textbf{0.04} \pm \textbf{0.02}$	
Western spinebill, Acanthorhynchus superciliosus	-3.91**	0.18 ± 0.06	0.73 ± 0.19	

Significant values are highlighted in bold.

*P < 0.05.

**P < 0.01.

Table 3. Results of the analyses on the correlations between the square-root transformed abundances of commonly occurring bird species and number of plant taxa, structural variables (Pearson's correlation coefficients [*r*]) and flowering scores for *B. attenuata*, *B. menziesii*, *B. ilicifolia* and understorey vegetation.

Bird species	Plant taxa ^a	Habitat cover (%) ^a					Flowering score ^b			
		Bare ground	Litter	Small shrubs	Trees	Canopy	B. attenuata	B. menziesii	B. ilicifolia	Understorey
Splendid fairy-wren	0.012	0.219	-0.008	0.038	-0.331	-0.419	-0.092	-0.062	-0.374	0.06
Yellow- rumped thornbill	0.109	0.294	-0.208	0.101	0.038	0.073	0.144	0.106	-0.012	-0.220
Silvereye	0.434	-0.186	0.653*	0.52	0.484	0.326	0.588*	0.706**	-0.321	0.736**
Brown honeyeater	0.392	-0.655*	0.793***	0.576*	0.615*	0.44	0.497	0.573*	0.137	0.873***
White- cheeked honeveater	-0.147	-0.307	0.244	0.025	-0.142	-0.076	-0.077	0.156	0.36	0.132
Western wattlebird	0.073	-0.087	0.3	0.141	0.232	0.243	-0.034	0.287	0.412	-0.132
Tawny- crowned honeveater	-0.618*	0.033	-0.464	-0.344	-0.556*	-0.437	-0.730**	-0.639**	0.336	-0.469
Western spinebill	0.265	-0.775**	0.514	0.254	0.625*	0.695**	0.524	0.492	0.389	0.51

Significant values are highlighted in bold.

$$*P < 0.05.$$

**P < 0.01.

****P* < 0.001.

^aAnalysed used Pearson's correlation coefficient.

^bAnalysed using Spearman's rank correlation coefficient.