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Tuart (*Eucalyptus gomphocephala*) decline is not associated with other vegetation structure and composition changes

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Abstract

Tree decline affects forests and woodlands on most continents. The loss of canopy species from these landscapes has marked impacts on the surrounding environment. Understanding the consequences of tree mortality on vegetation structure and composition will contribute to developing management strategies for these ecosystems. The tuart (*Eucalyptus gomphocephala*), once the dominant tree species on the coastal plain in southwest Western Australia, has been cleared extensively and today occurs over less than a third of its former range. Compounding the effects of this clearing, dramatic declines in tree health over the past two decades has been recorded. We examined whether *E. gomphocephala* decline is reflected in changes to overall vegetation structure and composition. Using Landsat Thematic Mapper satellite data, we identified 12 sites with stable or improving vegetation vigour over the previous 15 years ('healthy' sites) and 12 sites with declining vegetation vigour over this time ('declining' sites). Health of *E. gomphocephala* trees, as well as litter, vegetation structure and vegetation composition were compared across these sites. Four health measures indicated that *E. gomphocephala* trees from healthy and declining sites were statistically distinguishable ($p <$ 0.001). Trees at declining sites showed marked epicormic growth (up to 96% of canopy), evidence of crown dieback, reduced crown density and increased foliage transparency. The canopy changes were reflected in marked reduction in leaf litter for declining sites ($p = 0.024$). Despite the changes in *E. gomphocephala* canopy and leaf litter, however, there were no significant differences in vegetation community composition, relative vegetation cover for five height strata, vegetation structural and compositional diversity, presence of coarse woody debris, or overall canopy cover. There were also no differences in soil chemistry between the healthy and declining sites. The agent of tuart decline therefore appears to be specific to *Eucalyptus gomphocephala* at these sites, or alternatively the changes to other plant species have been too subtle to detect at this stage.

Introduction

Widespread tree mortality ('tree declines') mar landscapes globally, with some declines occurring at a continental scale (Jurskis 2005b; Tkacz et al. 2007). Clearing, grazing, salinisation or altered pH influence water and nutrient

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availability for trees (Close et al. 2008; Jurskis 2005a), while greenhouse gases and climate change have escalated the incidence of heat and drought (Allen et al. 2010; Sturrock et al. 2011). Humans have also aided the movement of insect, fungal and other pathogens, which have destroyed large swathes of new host species that lack natural resistance to these challenges (Kliejunas et al. 2009; Pautasso et al. 2010). Atmospheric pollution and nutrient imbalances can further exacerbate tree susceptibility to disease (Cale et al. 2017), while insect vectors can increase the rate of spread (Russin et al. 1984).

Tree declines have major impacts on the physical and biological components of forests and woodlands (e.g. Kizlinski et al. 2002; Weste 2003). As tree canopies dieback and canopy gaps form, sunlight penetration increases, affecting ground-level microclimatic conditions (e.g. Ruthrof et al. 2016). For example, higher ground temperature, and also greater temperature fluctuations

(e.g. Ellison et al. 2005) can result from tree decline. Post-decline, plant succession can result in altered plant species composition as declining tree species are replaced by others (e.g. Oak 2005). Plant species that increase during tree declines are likely to have different biologies from declining species, including modified vegetative and reproductive plant properties (e.g. McDowell et al. 2008; Penuelas et al. 2010). Altered plant species composition may also influence litter characteristics (e.g. Ellison et al. 2005). Tree declines therefore alter the environment around them, with consequences for fire regimes and other biota in the local vicinity.

The distribution of the iconic tuart (*Eucalyptus gomphocephala*) tree has been drastically reduced due to clearing for agriculture, industry and urbanisation, and today its distribution is restricted to 30,300 ha, less than a third of its former range (Government of Western Australia 2003). The health of the remaining *E. gomphocephala* population has declined dramatically since 1975, resulting in large-scale mortality in many parts (Fig. 1). Although the exact causes still need to be elucidated, it is suspected that multiple factors are responsible for the decline of *E. gomphocephala*. Changes to ground water chemistry and levels may have predisposed *E. gomphocephala* to decline (Edwards 2004; Longman and Keighery 2002), while reduced soil microbial diversity and functioning (Cai et al. 2010; Ishaq et al. 2013, 2018), reduction in fire frequency together with increased understorey density (Archibald et al. 2010), micronutrient deficiency (Close et al. 2011), and a plant pathogen (*Phytophthora multivora*) (Scott et al. 2009) are also implicated. Together with these putative predisposing factors, drought and heat also contribute to the severe dieback being observed in *E. gomphocephala* (Matusick et al. 2012). To date there has been no sign of improving condition of *E. gomphocephala* within declined sites, so the loss of these trees is having a permanent and dramatic effect upon the environment. The aim of this study was to determine whether tuart decline is reflected in changes to overall vegetation structure and composition. We compared *E. gomphocephala* health measures and overall vegetation structure and composition for 12 sites characterised by declining canopy vigour and 12 sites characterised by stable/increasing canopy vigour.

Fig. 1 **a** Healthy tuart (*Eucalyptus gomphocephala*) tree with full canopy, **b** tree showing crown dieback, **c** trees with different stages of epicormic regrowth, and **d** a dead *E. gomphocephala* (central) with unaffected *Agonis flexuosa* in the foreground

Methods

Site selection

Twenty-four long-term monitoring sites (each 100 m × 100 m) were established in 2006 across the Yalgorup region, on the Swan Coastal Plain south of Mandurah, Western Australia. The 24 sites had high *E. gomphocephala* density, similar land use and fire history. The 24 sites were identified based on changing trends in vegetation vigour over the preceding 15 years (1991–2005) derived from Landsat Thematic Mapper satellite data (Caccetta et al. 2000), with 12 declining sites (characterised by declining vegetation vigour over time) and 12 healthy sites (characterised by stable or improving vegetation vigour over time). Soils from a subset of these sites have also been analysed for bacterial (Cai et al. 2010) and mycorrhizal fungi (Ishaq et al. 2013, 2018) functionality and diversity, and the crown condition for these sites analysed using multispectral imagery (Evans et al. 2012). The decline results in death of *E. gomphocephala* on a massive scale, but we only measured sites where there were still living trees so that we were sure we were capturing the present decline and not trees that had potentially died due to other (previous) causes (e.g. senescence, wind damage).

Various measurements were made in 2006 to quantify average habitat characteristics for each site:

Measures of *Eucalyptus gomphocephala* 'health'

The health of individual *E. gomphocephala* in the 24 sites was quantified. The extent of crown dieback (estimated percentage of crown affected by branch mortality) and epicormic growth (quantified as the percentage contribution of secondary shoot and foliar growth in the overall canopy) were measured using a modified version of the Crown Dieback Ratio and Epicormic Index Crown density (Kile et al. 1981). Crown density (the amount that crown branches, foliage and reproductive structures block light visibility through the crown, as an estimated percentage), and foliage transparency (the amount of skylight visible through the live, normally foliaged part of the tree, expressed as percentage) were recorded based on the method developed by the U.S. Department of Agriculture Forest Service (2002). Each of these parameters was simultaneously assessed by two observers from two aspects (standing at right angles to each other) for four randomly chosen *E. gomphocephala* within each site.

Litter and coarse woody debris

The amount of leaf litter present at each site was determined using three approaches. Litter cover (quantified as a percentage) was visually estimated using a 1m² frame placed randomly 25 times at each site. Litter cover data were not normally distributed and were subsequently square root transformed for statistical analyses. Litter depth (mm) was measured with a marked metal rod placed perpendicular to the soil at 50 random locations for each site. All visible organic litter material was collected for five 0.3 m × 0.3 m sample plots per site, and dried in a 60 °C oven for 2 days to obtain litter mass (g).

The number of logs (mean diameter of >0.1 m) was counted for a 30 m × 40 m rectangle in the centre of each of the 24 sites; logs were individually measured (length, diameter at mid-point) and total log volume estimated (length x cross-sectional area).

Plant species structure and composition

Samples of all the woody plant species growing in the study area were collected (Department of Biodiversity, Conservation and Attractions, licence SW012162) and 30 species were identified and confirmed by a botanist. Each of the 1 ha sites was systematically surveyed on foot and then subjective visual estimates were made of the percentage cover of each of these woody species at five height classes: <1 m, 1-2 m, 2-3 m, 3-10 m and > 10 m. These values were converted to a Braun-Blanquet scale (Wikum and Shanholtzer 1978, codes detailed in Fig. 4). A Shannon-Wiener Diversity Index (SWDI) (Zar 1999) was calculated as a measure of the diversity of the vegetation community composition using the percentage composition for each species. A second Shannon-Wiener Diversity Index (SWDI) was calculated as a measure of the vertical structural vegetation diversity, using the vegetation structure cover over each height class as the measures.

Total canopy cover was recorded for four densiometer readings taken at breast height in the main compass directions at each of 10 points (each 25 m apart) located along three lines through the centre of the site (i.e. total 40 readings per site).

Soil collection and chemical analyses

A 12 cm diameter soil corer was used to collect undisturbed, intact soil samples at 0–10 cm depth, at locations 5 m north, south, east and west from the trunk of each of four randomly chosen trees per site in December (summer) 2006. The samples were combined for each tree into plastic bags and transported in a cooler to the laboratory the same day, where they were sieved (<2 mm) and stored at 4°C for a maximum of 2 days before soil chemical analysis. Soil samples (for each of the four trees sampled at each site; total 48 samples) were sent to a commercial laboratory (CSBP Soil and Plant Analysis Laboratory, Bibra Lake-Perth) for chemical soil properties. Subsamples of sieved soil were air-dried at 25 °C, and pH was measured in a soil-water or soil-CaCl$_2$ mixture (Rayment and Higginson 1992). Other subsamples were ground with a mortar and pestle and analysed for organic carbon (g kg^{-1}) (Walkley and Black 1934), nitrate nitrogen and ammonium nitrogen (mg kg^{-1}) using KCl extractant, phosphorus and potassium (mg kg^{-1}) using the Colwell method, sulphur using the KCl-40 method, and exchangeable

calcium (mequiv. 100 g^{-1}) according to Rayment and Higginson (1992). Micronutrients (Fe, Cu, Zn, and Mn) were extracted with diethylenetriaminepentaacetic acid (DTPA), exchangeable cations with $NH_4Cl/BaCl_2$.

Statistical analyses

Health of *E. gomphocephala* was compared by multi-dimensional scaling (MDS) (PAST 3.15) (Hammer et al. 2001) using a Euclidian similarity index between healthy or declining sites. The input measures were the mean-standardised values for the amount of epicormics, dieback, crown density, and foliage transparency. The MDS coordinates were compared between healthy and declining sites by PERMANOVA. This was followed by similarity percentage (SIMPER) analysis to determine which measure of *E. gomphocephala* health contributed the most to the differences between healthy and declining sites.

MDS analyses were similarly carried out to determine whether there were differences in other vegetation parameters between healthy and declining sites, independently of *E. gomphocephala* health. Mean-standardised values for the three litter variables (litter mass, litter cover, litter depth) were compared in one analysis, the percentage cover for 30 plant species in a second, the relative vegetation cover for each of the five height classes in a third, vegetation structural and compositional diversity in a fourth, and the number and volume of logs in a fifth. Average canopy cover (densiometer reading) was compared between healthy and declining sites by PERMANOVA.

A final MDS was used to compare the 14 soil measures for the 24 sites: pH_H_2O, pH _$CaCl_2$, organic carbon, nitrate nitrogen, ammonium nitrate, phosphorus (P), potassium (K), ferrous (Fe), Copper (Cu), Zinc (Zn), Manganese (Mn), sulphur, iron, and conductivity.

Values are presented as means ±1SD throughout.

Results

Eucalyptus gomphocephala health measures varied dramatically over the 24 study sites (Fig. 2; Table 1) and

Fig. 2 Measures of tuart (*Eucalyptus gomphocephala*) health for 12 sites with stable or improving vegetation vigour ('healthy' sites; H) and 12 sites with declining vegetation vigour ('declining' sites; D). **a** Epicormic growth, **b** crown density crown density, **c** crown dieback (branch mortality as % of crown), and **d** foliage transparency. Data are the means (horizontal line), quartiles (box) and standard error (whisker)
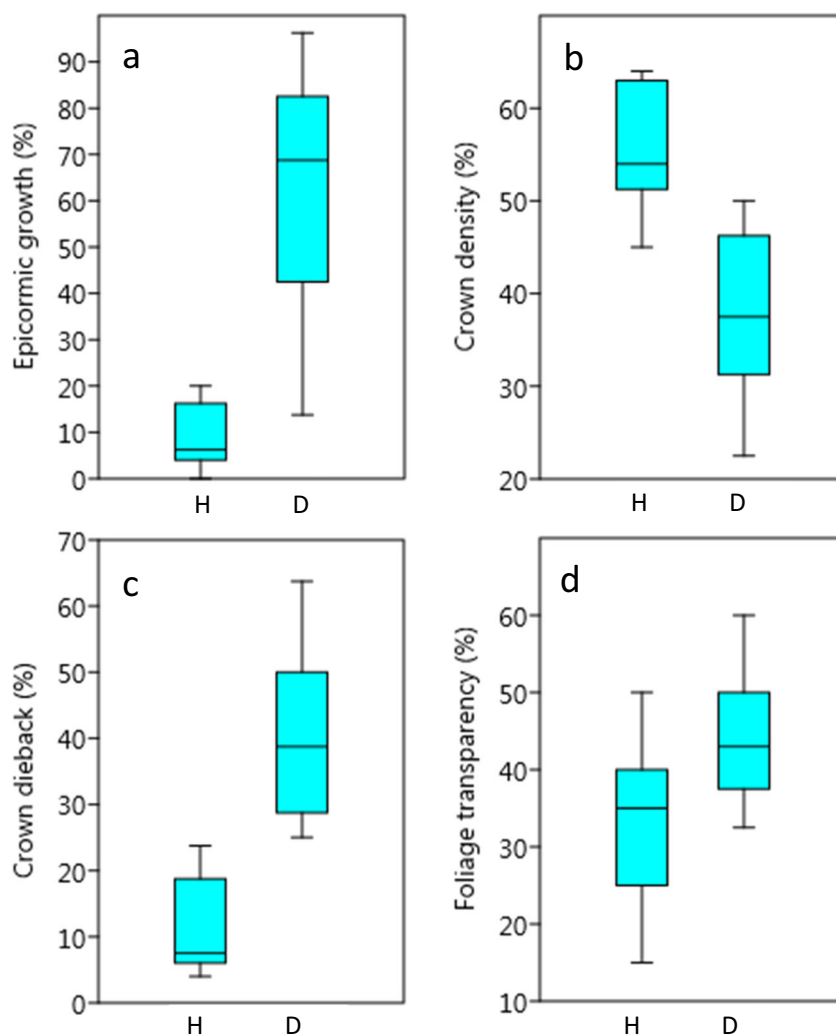
Table 1 Summary of statistical analyses, showing breakdown of significant results. Values are the means ±1SD (range)

Measure	'Healthy'	'Declining'
Tuart (*Eucalyptus gomphocephala*) health measures (PERMANOVA: $Pseudo\text{-}F_{1,22} = 28.18$, p < 0.001		
Epicormic growth	8.8 ± 7.1 (0–20) %	61.7 ± 26.1 (13.8–96.3) %
Crown density	56.1 ± 6.5 (45.0–63.8) %	37.7 ± 9.0 (22.5–50.0) %
Crown dieback	11.0 ± 6.7 (3.8–23.8) %	40.7 ± 12.2 (25.0–63.8)%
Foliage transparency	33.9 ± 10.5 (15.0–50.0) %	44.4 ± 7.8 (32.5–60.0) %
Litter measures (PERMANOVA: $Pseudo\text{-}F_{1,22} = 4.45$, $p = 0.024$)		
Litter mass	175 ± 83 (58–348) $g \cdot m^{-2}$	91 ± 57 (35–197) $g \cdot m^{-2}$
Litter cover	91 ± 15 (50–100) %	80 ± 24 (35–100) %
Litter depth	19.2 ± 8.4 (6.4–32.8) mm	13.6 ± 5.9 (5.6–22.4) mm
Vegetation composition - relative cover of woody species (PERMANOVA: $Pseudo\text{-}F_{1,22} = 1.38$, $p = 0.200$)		
Vegetation structure - relative cover for each of five height classes (PERMANOVA: $R = 0.24$, $Pseudo\text{-}F_{1,22} = 1.22$, p = 0.293)		
Vegetation structural and compositional diversity SWDI (PERMANOVA: $R < 0.01$, $Pseudo\text{-}F_{1,22} = 0.40$, p = 0.663)		
Volume or number of logs present (PERMANOVA: $R < 0.01$, $Pseudo\text{-}F_{1,22} = 0.19$, p = 0.786)		
Overall canopy cover (PERMANOVA: $Pseudo\text{-}F = 0.25$, p = 0.623)		
Soil chemistry - 14 soil measures (PERMANOVA $R = 0.22$, $Pseudo\text{-}F = 1.95$, p = 0.060)		

was significantly different between the 12 healthy and 12 declining sites (PERMANOVA: $Pseudo\text{-}F_{1,22} = 28.18$, $p < 0.001$). Epicormic growth was the strongest determinant of the difference between *E. gomphocephala* at healthy and declining sites (SIMPER: 33.8%) (Table 1). The next strongest factor was *E. gomphocephala* crown density (SIMPER: 27.1%), with a marked range in values for declining sites (Table 1). Foliage transparency (SIMPER: 14.22%) ranged from 15 to 60% and was more marked for the declining sites (Table 1).

There were also marked differences in leaf litter between healthy and declining sites (Fig. 3; Table 1) (PERMANOVA $Pseudo\text{-}F_{1,22} = 4.45$, $p = 0.024$). Declining sites had less litter mass, which translated into less litter cover and depth.

Despite the changes in *E. gomphocephala* canopy and leaf litter, there were no significant differences in other habitat measures between healthy and declining sites. *Eucalpyptus gomphocephala* dominated the sites, with an average of 18% cover over the 24 sites. This was followed, in descending order, by *Spyridium globulosum* (9.5%), *Agonis flexuosa* (7.6%) and *Banksia sessilis* (7.4%). The average cover of the other woody plant species varied from <0.1 to 4.2%. There was no significant difference in the relative cover for the 30 plant species between healthy and declining sites (Table 1; $p = 0.200$). There were also no differences in relative vegetation cover for each of the five height classes (Fig. 4; $p = 0.293$), for vegetation structural and compositional diversity indices (Fig. 5; $p = 0.663$), the
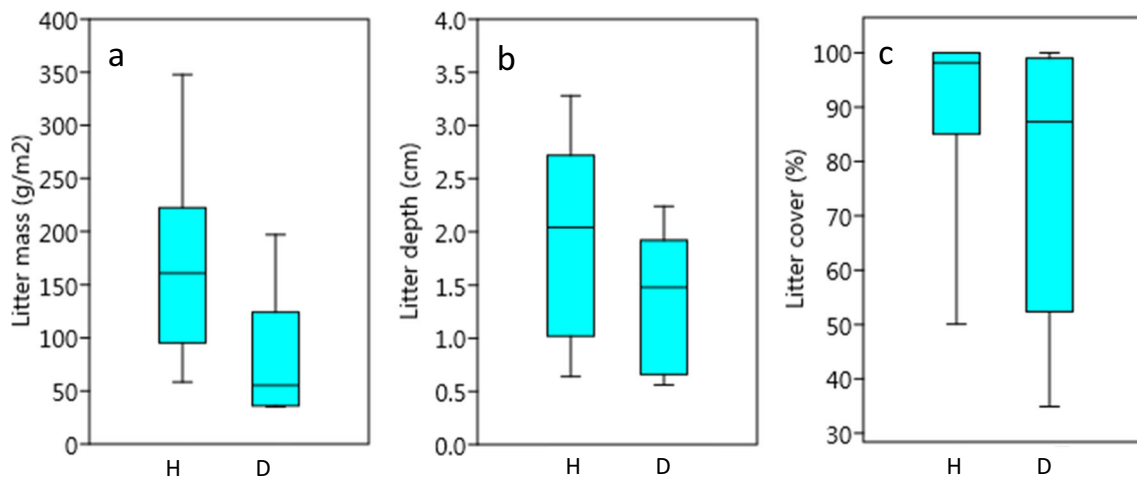
Fig. 3 Three measures of leaf litter **a-c** for 12 sites with stable or improving vegetation vigour ('healthy' sites; H) and 12 sites with declining vegetation vigour ('declining' sites; D). Data are the means (horizontal line), quartiles (box) and standard error (whisker)
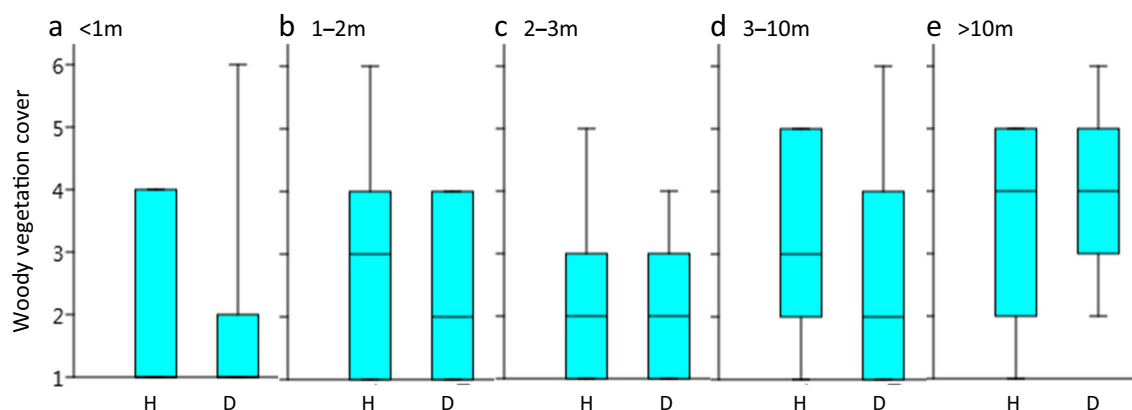
Fig. 4 Measures of woody vegetation cover at five height strata for 12 sites (a-e) with stable or improving vegetation vigour ('healthy' sites; H) and 12 sites with declining vegetation vigour ('declining' sites; D). Data are shown for Braun-Blanquet scale (Wikum and Shanholtzer 1978), where 0 = absent, 1 = few individuals, 2 = <5% cover but numerous individuals, 3 = 5–25% cover, 4 = 25–50% cover, 5 = 50–75% cover, and 6 = 75–100% cover. Data are the means (horizontal line), quartiles (box) and standard error (whisker)

volume or number of logs present (Fig. 6; $p = 0.786$), or overall canopy cover (Fig. 7; $p = 0.623$) (full details of statistical analyses are shown in Table 1).

There was also no measurable difference in the 14 soil measures between healthy and declining sites (Table 1; $p = 0.060$).

Discussion

Healthy tuart are a thing to behold. These tall (10–40 m and 1–2 m dbh) trees make a significant mark on the landscape due to their massive size and dense canopies. Iconic trees are often retained in urban parks and as shade for livestock in agricultural landscapes. Therefore, there has been deep community and scientific concern regarding the progress and aetiology of *E. gomphocephala* decline. As their health declines, more dead branches appear as the trees drop leaves; the worst-affected living trees that we recorded had 64% of their

total canopy affected by crown dieback. To recover photosynthetic capacity, the trees invest heavily in epicormic growth, with the worst affected trees we recorded having 96% of their total canopy composed of epicormics. Leaf thinning in declining *E. gomphocephala* results in higher levels of foliage transparency, which can be as high as 60% in affected trees. These symptoms reflect tree declines in other eucalypt species (e.g. Close and Davidson 2004) in response to a range of abiotic and biotic challenges. Dieback of tuart has been occurring since the mid-1990's (Archibald et al. 2005), and subsequent to our study, a severe dieback event occurred in 2010/ 2011 associated with a significant hot period together with a record dry summer, and an estimated 500 ha of tuart woodland died-back (Matusick et al. 2012). Tuart have continued to decline.

The most marked differences in *E. gomphocephala* trees between healthy and declining sites was due to the abundance of epicormic growth on declining trees. Epicormic growth is a

Fig. 5 Measures of the diversity of **a** woody vegetation structure and **b** plant species composition for 12 sites with stable or improving vegetation vigour ('healthy' sites; H) and 12 sites with declining vegetation vigour ('declining' sites; D). Diversity is captured as Shannon Weiner Diversity Index (SWDI) values. Data are the means (horizontal line), quartiles (box) and standard error (whisker)
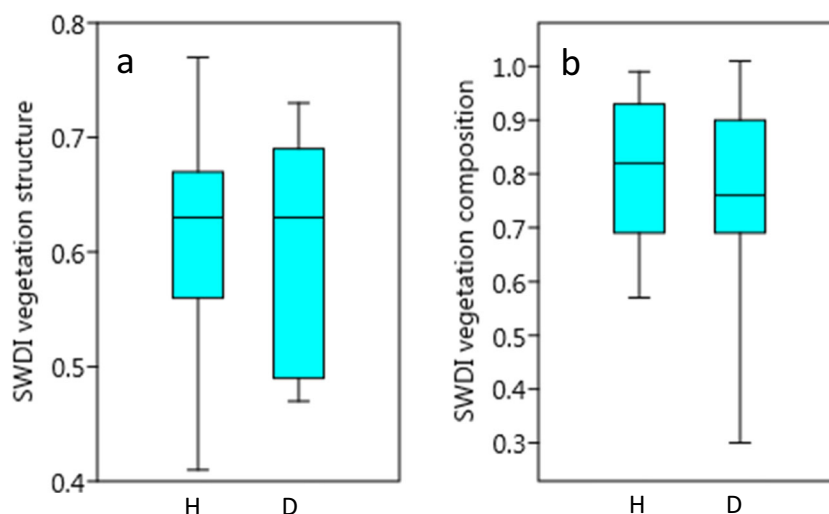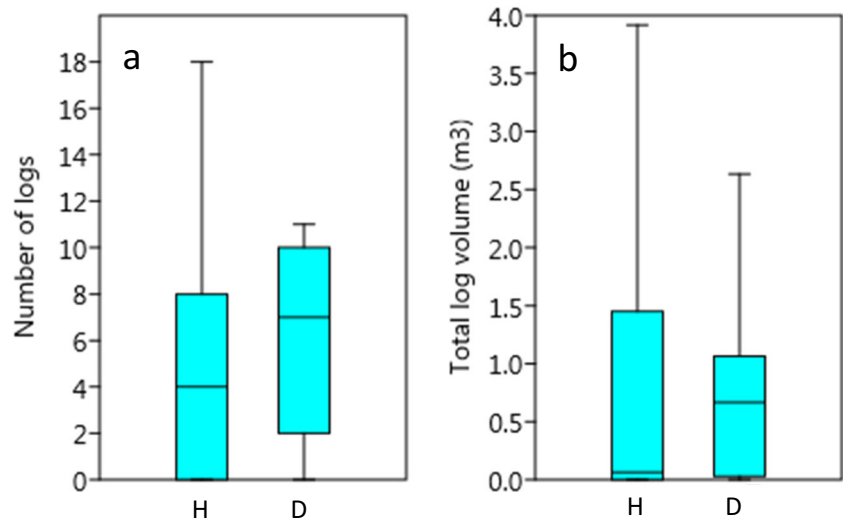
Fig. 6 Measures of logs for a 30 × 40 m sampling grid, showing **a** the numbers of logs and **b** total volume of logs for 12 sites with stable or improving vegetation vigour ('healthy' sites; H) and 12 sites with declining vegetation vigour ('declining' sites; D). Data are the means (horizontal line), quartiles (box) and standard error (whisker)

common response of *Eucalyptus* species as they attempt to recover their canopy (e.g. lost due to water stress, disease or fire). Canopy dieback resulted in reduced crown density and increased foliage transparency, which also translated into reduction in leaf litter (mass, cover and depth) at these sites. A similar loss of litter has been recorded for hemlock affected by the hemlock woolly adelgid (*Adelges tsugae* Hemiptera: Adelgidae) in north-eastern USA (Kizlinski et al. 2002) and jarrah forest in southwest Western Australia infected with *Phytophthora cinnamomi* (Anderson et al. 2010; Armistead 2008; Postle et al. 1986). Although there had not been sufficient time for a similar accumulation of coarse woody debris,

as the decline progresses further and only dead stags are left, these would eventually decay and fall, contributing to an increase in woody debris, as has been noted in other decline syndromes (Hennon et al. 2002; Kearney et al. 2005; Spetich 2005; Tempel and Tietje 2006).

Despite these differences in *E. gomphocephala* health and leaf litter, there were no significant differences for other plant community measures: plant species composition, vegetation cover, or diversity of vegetation community and structure. Understorey vegetation changes have often been recorded accompanying tree declines. For example, shrub development often increases as a consequence of the loss of the overstorey (Adams and Hammond 1991; Alsop and Laughlin 1991) and resultant increasing light levels (Jenkins et al. 1999) from which other plant species may benefit (Elliott and Swank 2008; Small et al. 2005). Alternatively, the structure of plant communities can be dramatically altered where other plant species are similarly susceptible to the underlying cause (Kennedy and Weste 1986; Weste 2003). For example, plant species diversity is reduced in the presence of *Phytophthora cinnamomi* dieback (e.g. Newell 1998; Shearer and Dillon 1996).

These data suggest that the aetiology of the decline is specific to *E. gomphocephala*. *Phytophthora multivora* is pathogenic to *E. gomphocephala* under glasshouse conditions (Scott et al. 2012) and has been isolated from rhizosphere soils and *E. gomphocephala* roots in declining sites (Scott et al. 2009). This newly described *Phytophthora* species has also been recovered from a diverse range of dying urban tree species (Barber et al. 2013). Although we know little about the host range of *Phytophthora multivora*, it appears to show less damage on understorey plant species compared with its effect on *E. gomphocephala* trees. If the mid-storey dominant *Agonis flexuosa* increases in the wake of tuart decline (Archibald 2006), the alternative dominant vegetation type would have a completely different canopy structure, flowering
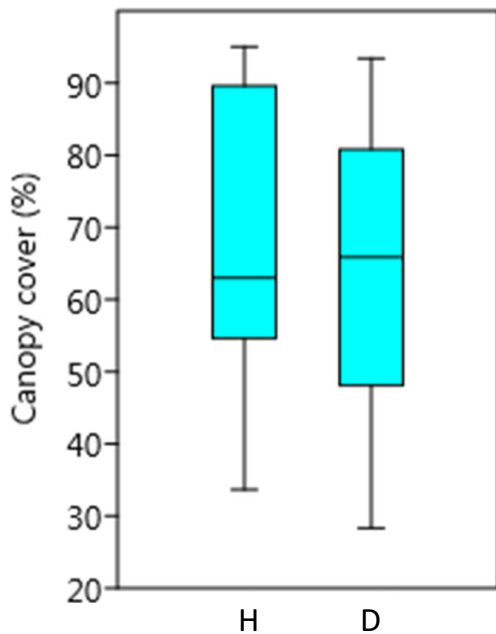

Fig. 7 Measures of canopy cover for 12 sites with stable or improving vegetation vigour ('healthy' sites; H) and 12 sites with declining vegetation vigour ('declining' sites; D). Data are the means (horizontal line), quartiles (box) and standard error (whisker)

phenology, pattern of leaf growth and turnover, biochemical composition and response to fire (Archibald 2006; Barrett and Tay 2005; Boland et al. 2006; Keighery 2002). However, if *Agonis flexuosa* is similarly vulnerable to this pathogen (as we suspect), then changes in vegetation structure or composition are therefore likely to become more exaggerated in the future.

Arguably, we are still too early in the decline aetiology to have started to see significant changes in understorey communities, composition and structure. However, in other semiarid and Mediterranean ecosystems, reduced seedling recruitment, long-term shift in vegetation composition, reduced radial growth and increased crown defoliation have been observed (Allen et al. 2010; Breshears et al. 2005; Carnicer et al. 2011). It is likely, with the loss of tuart trees from stands, seedling recruitment of tuart will be reduced, as its seed does not survive in the soil for long and the species requires fire and associated ash beds to successfully germinate and establish in the absence of competition (Ruthrof et al. 2011). Consequently, with the continuing predicted drying and warming climate (Bates et al. 2008) together with the other causes of tuart decline (e.g. *P. multivora*) we are likely to see a shift in species composition and structure in the tuart forest in the future. These changes will impact on vertebrate and invertebrate fauna.

We also recorded no statistically significant differences in soil analyses between healthy and declining sites ($p = 0.060$). The decline in health is therefore not directly attributable to soil chemistry changes, although reduced leaf litter would contribute to reduced organic matter available for soil bacteria, which would consequently reduce nutrient cycling and therefore nutrient availability for plants. Potential increases in soil temperature due to canopy loss and consequent reduced soil moisture would similarly result in reduced microbial activity. Declining sites have lower soil bacterial functional diversity and activity (Cai et al. 2010). Furthermore, *E. gomphocephala* seedlings grown in soil from healthy and declining sites develop different mycorrhizal fungi associations, with more ectomycorrizal fungi associated with seedling roots grown in soil collected from healthy sites, and more arbuscular mycorrhizal fungi from seedling roots grown in soil collected from declining sites (Ishaq et al. 2013, 2018). *Eucalyptus gomphocephala* health will no doubt reflect their rhizosphere environment, but the differences in microbial functionality could also suggest responses to a common underlying cause (Sapsford et al. 2017).

In conclusion, we identified study sites based on long-term (15-year) vegetation vigour as reflected in their spectral reflectance (Caccetta et al. 2000). It is noteworthy that the site differences identified through remote sensing translated into different *E. gomphocephala* health; decreases in leaf litter were also recorded for declining sites. Despite the dramatic loss of the canopy for decline-affected sites, understorey vegetation structure and composition were not significantly different for these study sites, although future changes are likely with plant succession. In addition to improving our understanding of the aetiology of this decline, impacts on habitat for fauna is also an important consideration.

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