Anthropogenic disturbance impacts stand structure and susceptibility of an iconic tree species to an endemic canker pathogen

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Highlights

- The incidence of an endemic canker pathogen increased with anthropogenic disturbance.
- Disturbed edges showed significantly different composition from forest transects.
- Increased tree species diversity was associated with decreased canker incidence.
- We demonstrate the impact of global change and anthropogenic drivers on forest health.

Abstract

Forest ecosystems characterised by higher tree species diversity have been linked to a reduced susceptibility to pathogens. Conversely, endemic pathogens contribute to forest ecosystem dynamics and process. In the face of global change, however, negative impacts arising from more frequent and severe forest disturbances are increasingly observed. An increase in the susceptibility of *Corymbia calophylla,* a keystone tree species of southwest Western Australia, to cankers caused by the endemic fungus *Quambalaria coyrecup,* has emerged in recent decades. Landscape scale assessment of disease incidence has implicated the predisposing role of anthropogenic disturbance, indicating a need for this to be examined at a finer resolution. We assessed the effects of anthropogenic disturbance on the incidence of canker disease caused by *Q. coyrecup* across a disturbance gradient at 17 forest sites. In addition, we determined the impact of disturbance on tree community composition and stand level structural traits including stem density and stand basal area, and investigated the role of these factors as drivers of canker presence. Canker incidence and associated mortality of *C. calophylla* increased with anthropogenic disturbance. Disturbed edges showed significantly different overstorey composition from the forest transects. Total stem density increased with increasing disturbance, and disturbed edges contained greater numbers of *C. calophylla* stems compared to forest transects. There was a much increased basal area of *C. calophylla* on disturbed edges. Regardless of transect position, an increased incidence of canker resulted on sites with increased *C. calophylla* basal area. Lastly, increased tree species diversity (as measured by species richness) was associated with decreased canker incidence. We demonstrate that anthropogenic disturbance has altered stand structure and led to an increased susceptibility of *C. calophylla* to *Q. coyrecup,* resulting in high disease incidence and mortality of trees on disturbed road edges. Our results highlight the complexity of addressing tree health issues in the presence of multiple global change factors.

Key-words *Corymbia calophylla*; *Quambalaria coyrecup*; tree decline; southwest of Western Australia; disease emergence; fungal forest pathogen

Introduction

Endemic fungal pathogens are an important component of many forest processes and when in equilibrium with forest ecosystems, contribute to shaping the dynamics and diversity of forests (Hansen, 1999; Holdenrieder *et al.*, 2004; Ostry and Laflamme, 2008). However, the impacts of global environmental changes in combination with local anthropogenic drivers are changing how forest diseases are being expressed, leading to increased forest and woodland tree decline and mortality (Pautasso *et al.*, 2015). While many studies have focused on the impact of non-native pests and pathogens under these scenarios, elucidating the role of damaging endemic pests and pathogens, global change drivers and their interactions, are now regularly recognised as important areas requiring further research (Burdon *et al.*, 2006; Desprez-Loustau *et al.*, 2007; Tubby and Webber, 2010; Sturrock *et al.*, 2011; Pautasso *et al.*, 2012; Ghelardini *et al.*, 2016).

The southwest of Western Australia (SWWA), a unique ecoregion with a Mediterranean-type climate, is recognised as a 'biodiversity hot spot' (Klausmeyer and Shaw, 2009; Mittermeier *et al.*, 2011). The region has undergone extensive clearing of native vegetation resulting in a highly fragmented landscape (Shepherd *et al.*, 2002), and there has been a persistent trend of declining annual rainfall and increasing temperatures since the mid-1970s (Bates *et al.*, 2008) which is projected to continue into the future (CSIRO & BOM, 2007; IPCC, 2013). Furthermore, introduced pests and pathogens such as the soil borne plant pathogen *Phytophthora cinnamomi* Rands, have had a devastating effect on the native flora and forest ecosystems in the region (Shearer *et al.*, 2007). Over the last 30 years, declines in the health of a number of dominant tree species in SWWA have been observed, likely in association with these factors (Scott *et al.*, 2009; Brouwers *et al.*, 2012; Barber *et al.*, 2013; Matusick *et al.*, 2013; Brouwers and Coops, 2016; Paap *et al.*, 2017a).

Open sclerphyllous eucalypt forest is the most widely distributed forest type in southern Australia, and in SWWA these forests are generally dominated by *Eucalyptus marginata* Donn ex Sm. (jarrah) and *Corymbia calophylla* (R. Br. ex Lindl.) K.D. Hill & L.A.S. Johnson (marri) (Churchill, 1968). Historically, *C. calophylla* has been more tolerant of disease and disturbance than other tree species in SWWA; e.g. *C. calophylla* is field resistance to *P. cinnamomi*, thus continues to survive in infested areas long after *E. marginata* have been killed (Shearer and Tippett, 1989). *Corymbia calophylla* may also be more locally dominant where *E. marginata* has been removed by selective logging (McCaw, 2011). *Corymbia calophylla* provides many economic, social and ecological services in forests and woodlands of SWWA, and as a remnant tree on road verges, parklands and private properties. It is an important habitat tree and provides food resources for native wildlife, including the threatened Carnaby's black cockatoo (*Calyptorhynchus latirostris* Carnaby), Baudin's (*C. baudinii* Lear) and Forest red-tailed black cockatoo (*C. banksia naso* Gould) (Johnstone and Kirkby, 1999; Lee *et al.*, 2013).

In recent years there has been a decline in the health of *C. calophylla* associated with the putative endemic canker pathogen *Quambalaria coyrecup* Paap (Exobasidiomycetes: Microstromatales: Quambalariaceae) (Paap *et al.*, 2017b). A temporal study identified that canker incidence is significantly greater on *C. calophylla* in anthropogenically disturbed sites compared to forest sites, though the number of study sites was limited (Paap *et al.*, 2017b). A subsequent landscape scale survey showed the influence of climate and anthropogenic disturbance on disease incidence (Paap *et al.*, 2017a), highlighting the need to examine the role of anthropogenic disturbance at a finer resolution. This study examines the link between anthropogenic disturbance, stand structure and canker incidence of *C. calophylla*, by establishing transects across a disturbance gradient at 17 forest sites in SWWA.

Materials and methods

Study species and area

The SWWA has a Mediterranean climate characterised by warm to hot, dry summers, and mild to cool, wet winters (following Peel *et al.*, 2007). *Corymbia calophylla,* a tall bloodwood tree endemic to the SWWA, has a restricted range between 28° 51'S, 114° 58'E in the north and 34° 36'S, 118° 44'E in the south (Fig. 1), occurring in areas receiving between 360 - 1150 mm annual rainfall with average annual temperatures ranging between 14°C - 21°C (averages for 1981-2010, derived from the Australian Water Availability Project (AWAP) dataset, see Jones *et al.*, 2009; Raupach *et al.*, 2009, 2011).

Field survey and study sites

A field survey was undertaken during April and May of 2015 to determine the incidence of cankers on *C. calophylla* across a disturbance gradient at 17 sites in the SWWA (Fig. 1). The following criteria were required to be met for sites to be considered suitable: 1. a remnant roadside stand of vegetation containing *C. calophylla* adjacent to anthropogenic disturbance (including agriculture, horticulture, plantation, viticulture or grazing land); 2. an area of relatively undisturbed forest containing *C. calophylla* present across the road. Site selection

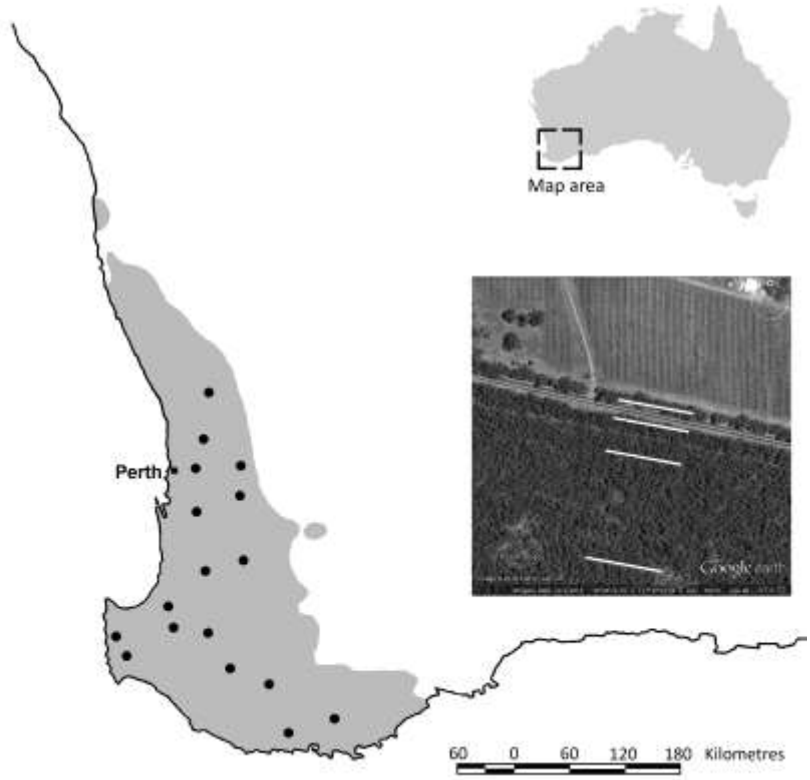

Fig. 1. The *Corymbia calophylla* (marri) distribution across the southwest of Western Australia (grey) and location of sites assessed for canker incidence across a disturbance gradient (transect layout detail in inset).

was guided by the results from a previous survey of canker disease incidence across the *C. calophylla* range (Paap *et al.*, 2017a). A desktop study was then carried out using Google Earth to find potential sites in regions with known disease incidence that met the two criteria. Potential sites were visited and visually assessed to confirm suitability. Seventeen sites within the *C. calophylla* range were found to be appropriate locations for the field study.

At each site, four 3 x 100 m transects were established. These were run parallel to each other and positioned 1. along the disturbed roadside vegetation; 2. the forest edge adjacent to the road; 3. 50 m into forest and 4. 200 m into forest (Fig. 1). A handheld Garmin Colorado (GARMIN International, Kansas, USA) with an accuracy of 8 m was used to record GPS coordinates at the start and end point of each transect and together with a 5 m tape measure and 100 m length of builders line to ensure accurate positioning of transects.

Canker incidence and estimates of stand density and basal area

All trees within each transect with a diameter at breast height (DBH) > 5 cm were measured, and the species identity recorded to determine tree species composition and relative importance for each transect. Canker presence or absence was noted for *C. calophylla*. Assessment of cankers was based on the presence or absence of the symptoms and signs associated with *Q. coyrecup* infecction, including excessive bleeding (gummosis) staining the trunk or limb dark red, splitting and eventual shedding of the bark to reveal perennial cankers, and sporulation of the pathogen visible as powdery white masses within the cankered area (Paap *et al.*, 2008; Paap *et al.*, 2017b). Occurrence of dead trees, their DBH and species identity were also recorded, and for *C. calophylla*, cause of death was determined as canker (evidenced by clearly visible stem girdling cankers) or a cause other than canker.

For each transect, the number of *C. calophylla* trees with cankers was converted into a proportion by dividing it by the total number of surveyed *C. calophylla* trees present on the transect. Total stem density was calculated as number of stems per hectare. Total stand basal area (m^2 ha^{-1}) was calculated as the sum of the basal area of all trees within each transect divided by transect area and multiplied out to a hectare. Stand level proportion of the stem density and basal area of *C. calophylla* relative to other species were calculated as density of *C. calophylla* stems divided by total stems and *C. calophylla* basal area divided by total basal area.

Statistical analysis

To quantify the effect of anthropogenic disturbance on stand level structural traits and canker incidence, we compared total stem density, total basal area, *C. calophylla* stem density and basal area, proportion of stem density and basal area of *C. calophylla* relative to other tree species, incidence of cankered *C. calophylla* and mortality in each of four transects (showing different levels of anthropogenic disturbance) for 17 sites. To model structural traits as a function of anthropogenic disturbance, linear mixed models including anthropogenic disturbance as fixed effect and site as random effects was used. To model canker incidence, the proportion of cankered *C. calophylla* was compared to the proportion of *C. calophylla* without cankers, and we looked at the incidence of *C. calophylla* mortality of cankered and non-cankered trees separately. To model canker incidence we used a binomial generalized mixed model including anthropogenic disturbance as fixed effect and site as random effect. Mortality models had the same structure as the canker incidence model but using a poisson distribution. We included the total number of individuals per transect in the mortality models as an offset to account for differences in tree density along the anthropogenic disturbance gradient (Zuur *et al.*, 2009)

To determine differences in tree species community composition and relative abundance between each transect we used the Bray-Curtis dissimilarity index to calculate dissimilarity values from tree species abundance data. Relative abundances were calculated based on basal area. Bray-Curtis dissimilarity values were calculated with the vegdist function in package vegan (Oksanen *et al.*, 2013). We then performed unconstrained ordination of plots using non-metric multidimensional scaling (NMDS) with function metaMDS in vegan. We used the Bray-Curtis index as it includes the abundance information which is an important aspect of community structure (Anderson *et al.*, 2011). Permanova was performed on Bray-Curtis dissimilarity values between transects using function adonis in vegan which is shown to be unaffected by heterogeneity in balanced designs (Anderson and Walsh, 2013). Pairwise comparisons of the dissimilarity between each transect used function adonis with p-adjust method 'holm' in vegan to adjust for multiple comparisons. We fitted the proportion of cankered *C. calophylla* onto the NMDS ordination using the envfit function in package vegan. Equality of variance between the transects was investigated using function betadisper in package vegan to calculate multivariate dispersion.

To investigate driving factors of canker presence, the number of *C. calophylla* trees with canker as a proportion of the number of *C. calophylla* trees was used as the response variable. Predictor variables were identified *a priori* and consisted of tree diversity on each transect (Shannon diversity index and species richness), *C. calophylla* basal area, stem density and average stem DBH. Data exploration was carried out according to Zuur *et al.* (2010). To model canker incidence as a function of covariates, a binomial generalized linear mixed model was used. All covariates were standardized (i.e. substracting the mean and dividing by the standard deviation) before fitting the model, to ease the comparison of model coefficients and avoid model fitting problems. To incorporate the dependency among observations, site was used as a random intercept.

To verify that the models complied with underlying model assumptions, residuals were plotted against fitted values (Zuur *et al.*, 2009). The optimum model was chosen via AIC values. For models, we report standardized estimates and their standard errors, Z and *P* values. All analyses and figures were performed and created in R (R Core Team, 2015). Plots were created in ggplot2 (Wickham, 2009) and models were fit with lme4 (Bates *et al.*, 2015)

Results

Stand level structural traits

The DBH of individual trees of all species within the study transects ranged from 5.0 cm to 159.0 cm. Total stem density ranged from 567 to 2967 stems ha^{-1} and total basal area ranged from 27.06 to 230.76 m^2 ha^{-1}. Total stem density was significantly (F = 5.98, df = 3, P = 0.001) different across the disturbance gradient, with higher total stem density within the disturbed gradient (Fig. 2, Table 1, Table S1). *Corymbia calophylla* stem density ranged from 167 to 1867 stems ha^{-1}, and as for total stem density, was significantly (F = 21.32, df = 3, P < 0.001) different across the disturbance gradient with transects on disturbed edges containing higher numbers of *C. calophylla* stems compared to forest transects. The relative abundance of *C. calophylla* across the gradient also varied significantly F = 47.41, df = 3, P < 0.001), with transects on disturbed edges comprised of a greater proportion of *C. calophylla* stems compared to other transects (Fig. 2, Table 1, Table S1).

Table 1. LMM and GLMM results of the effect of anthropogenic disturbance (fixed effect) on stand level structural traits, stem density (SD) (stem ha^{-1}) and basal area (A_b) (m^2 ha^{-1}), and proportion of cankered *C. calophylla* , number of dead *C. calophylla* with and without canker of a transect, including site as a random effect. Goodness of fit statistics include Akaike information criterion (AIC) and the coefficient of determination (R^2).

	Anthropogenic disturbance		Site	Goodness of fit	
	F-value	*P*-value	Stan. Dev	AIC	R^2
SD *C. calophylla*	21.3	< 0.001	115.8	949.9	0.57
SD total	5.9	0.001	276.7	999.9	0.52
% SD *C. calophylla*	15.1	< 0.001	0.08	34.0	0.41
A_b *C. calophylla*	47.4	< 0.001	12.73	626.9	0.69
A_b total	29.9	< 0.001	14.6	657.3	0.67
% A_b *C. calophylla*	28.2	< 0.001	0.10	13.5	0.65
% canker incidence	62.6	< 0.001	0.14	1526.6	0.38
mortality (canker)	7.1	< 0.001	0.87	93.2	0.01
mortality (other)	0.2	0.90	0.46	81.6	0.13

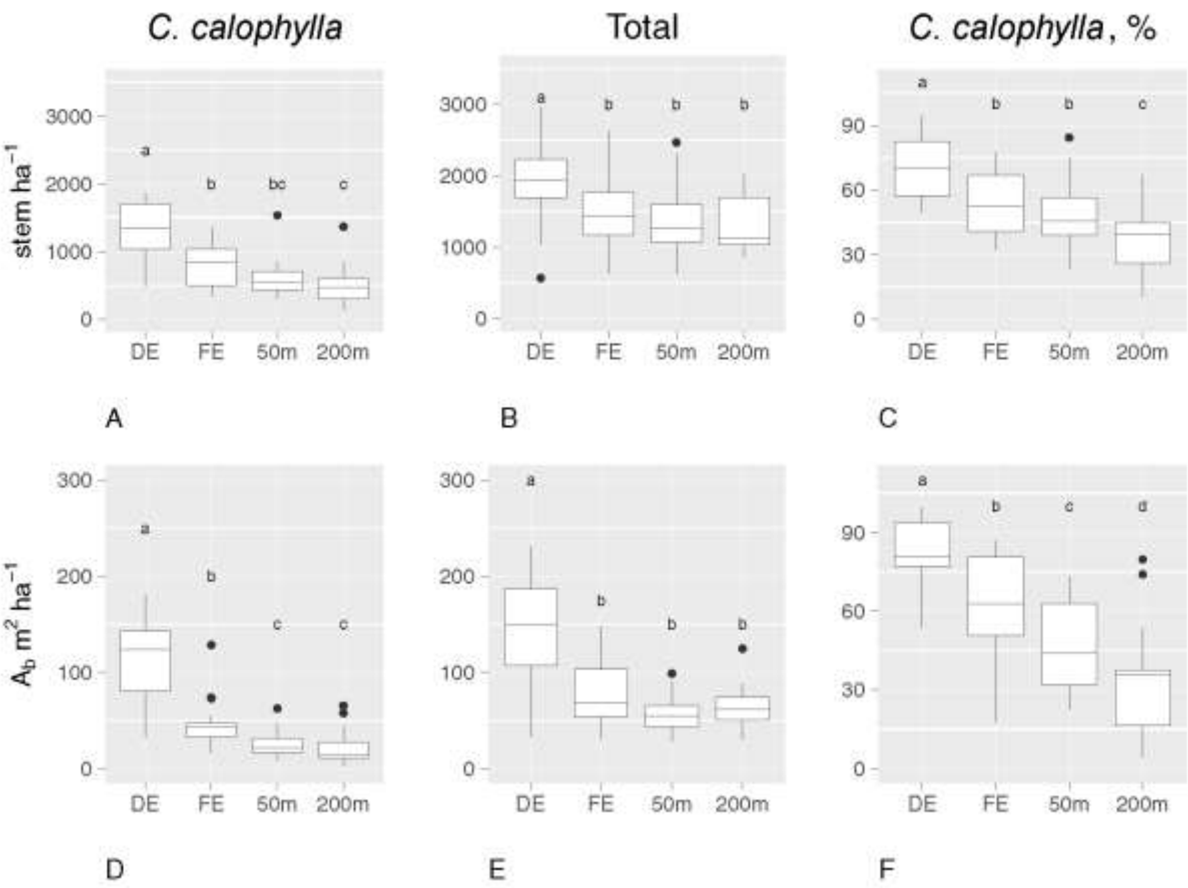

Fig. 2. Stand structural traits across a disturbance gradient at 17 southwest Western Australia study sites on (A) number of *Corymbia calophylla* stems per hectare, (B) total number of stems per hectare, (C) proportion of stems per hectare comprised of *C. calophylla*, (D) *C. calophylla* basal area (A_b), (E) total $A_{b,}$ and (F) proportion of A_b contributed by *C. calophylla*. DE: Disturbed edge; FE: Forest edge; 50 m: 50 m into forest; 200 m: 200 m into forest. Different letters indicate significantly ($P < 0.05$) different values.

Total basal area varied significantly ($F = 29.98$, df = 3, $P < 0.001$) across the disturbance gradient (Fig. 2, Table 1, Table S1). *Corymbia calophylla* basal area was also significantly ($F = 47.41$, df = 3, $P < 0.001$) different across the disturbance gradient (Fig. 2, Table 1, Table S1). This was a result of a much increased *C. calophylla* basal area on disturbed transects in comparison to all other transects. Consequently, *C. calophylla* made up a significantly ($F = 28.19$, df = 3, $P < 0.001$) greater proportion of total basal area on disturbed transects compared to other transects (Fig. 2, Table 1, Table S1). In addition, *C. calophylla* basal area and the proportion of basal area consisting of *C. calophylla* were both significantly (*P* < 0.001, respectively) greater on the forest road edge than the forest transects (Fig. 2, Table 1, Table S1).

Composition of stands

Eucalyptus marginata was the most frequent codominant tree species, present in transects of all 17 forest sites. *Eucalyptus wandoo* Blakely co-occurred at two forest sites, while *E. patens* Benth. was present at one forest site. Woody species occasionally contributing to stem densities and basal areas included *Allocasuarina fraseriana* (Miq.) L.A.S.Johnson, *Banksia grandis* Willd., *B. sessilis* (Knight) A.R.Mast & K.R.Thiele, *Hakea amplexicaulis* R.Br., *Persoonia elliptica* R.Br. and *P. longifolia* R.Br.

Based on Bray-Curtis NMDS ordination transects across the disturbance gradient differed significantly (stress = 0.104, R^2 = 0.40, PERMANOVA, F = 141, *P* = 0.001) in species composition (Fig. 3). Adonis pairwise comparisons of the dissimilarity between each transect found the disturbed road edge differing significantly (*P* = 0.01) from the three forest transects, with significant dissimilarity also found between the forest edge and 50 m and 200 m into the forest (*P* = 0.015 and *P* = 0.003, respectively). *Corymbia calophylla* was the main species present in the disturbed road edge. By contrst, species such as *A. fraseriana*, *B. grandis* or *P. elliptica* were mostly associated to the transect 200 m into the forest. The proportion of *C. calophylla* individuals with canker was significantly correlated to the ordination scores (R^2 = 0.51, *P* = 0.001), being associated to the disturbed road edge.

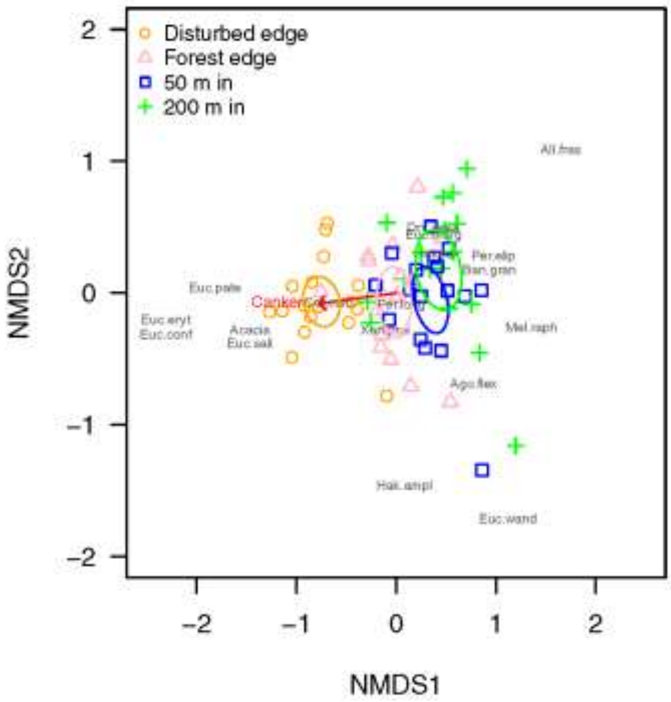

Fig. 3. NMDS plots based on Bray-Curtis dissimilarities of tree community composition across a disturbance gradient. Ellipses represent 95% confidence intervals around transect centroids. The arrow depicts the association between the proportion of *Corymbia calophylla* individuals with canker and sites. Abreviated species names are depicted in grey.

Variation and drivers of canker presence

Canker incidence of *C. calophylla* was significantly (F = 62.67, $P < 0.001$) different among the anthropogenic disturbance gradient (Fig. 4, Table 1, Table S2). *Corymbia calophylla* mortality resulting from cankers was similarly positively correlated with anthropogenic disturbance, with the disturbed road edge experiencing a significantly (F = 7.14, $P < 0.001$) higher number of trees killed by girdling cankers than the forest transects (Fig. 5, Table 1, Table S2). Very few recorded deaths of *C. calophylla* were attributable to causes other than canker across all sites and transects, and mortality levels due to other causes did not differ significantly (F = 0.17, $P = 0.902$) across the disturbance gradient (Fig.5, Table 1, Table S2).

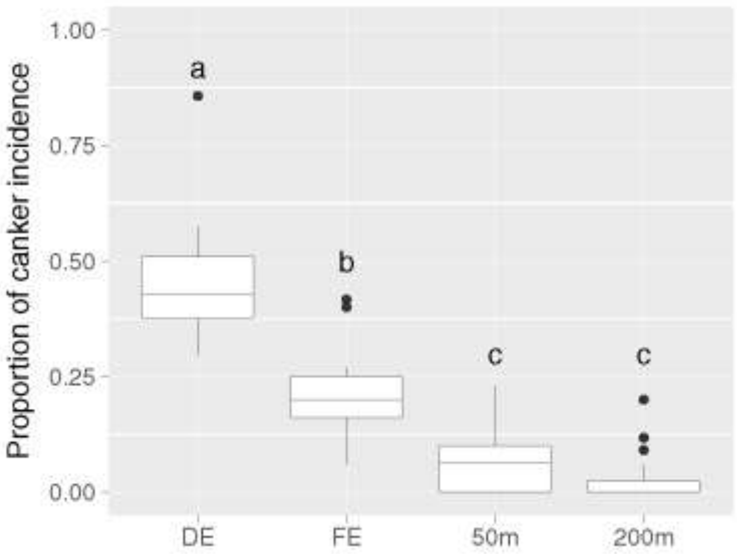

Fig. 4. Proportionof *Corymbia calophylla* with canker across a disturbance gradient at 17 southwest Western Australia study sites. DE: Disturbed edge; FE: Forest edge; 50 m: 50 m into forest; 200 m: 200 m into forest. Different letters indicate significantly (P < 0.05) different values.

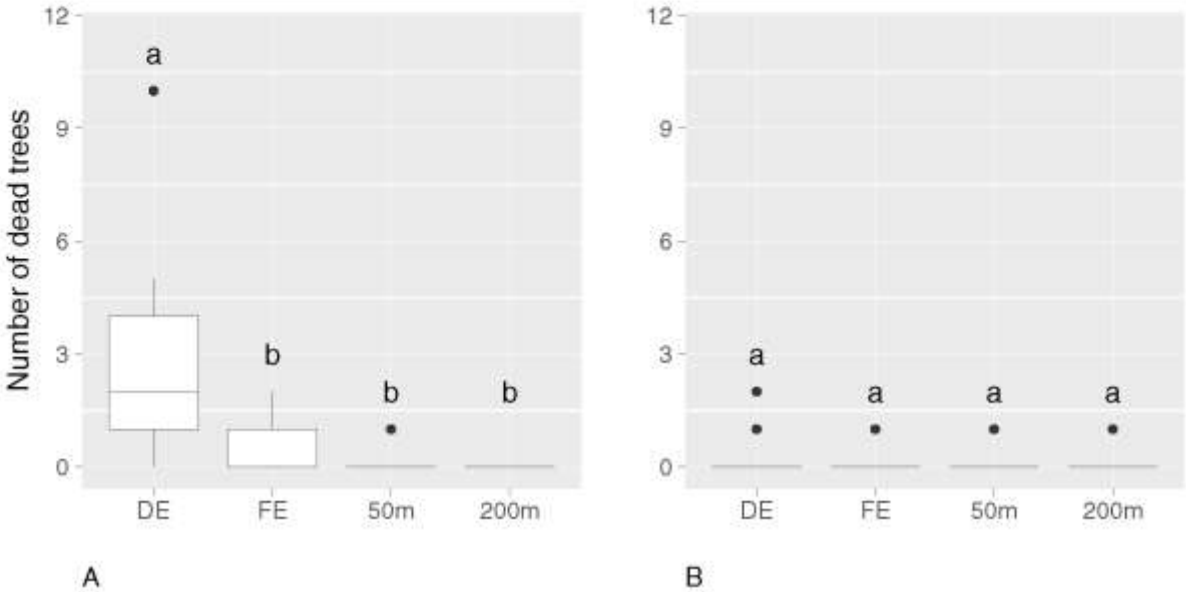

Fig. 5. *Corymbia calophylla* mortality across a disturbance gradient at 17 southwest Western Australia study sites (a) death caused by canker, (b) death by cause other than canker. DE: Disturbed edge; FE: Forest edge; 50 m: 50 m into forest; 200 m: 200 m into forest. Different letters indicate significantly (P < 0.05) different values.

Investigation of factors driving canker presence using the binomial model found that regardless of where trees were on a site, canker incidence was associated to structural and diversity variables (Fig. 6, Table 2). Increased canker incidence was associated with higher stand *C. calophylla* stem density and average individual DBH for the stand. These results suggest that a high incidence of canker occurs in high density stands with large trees. On the other hand, canker incidence decreased with greater tree species, indicating that stands with a higher number of species were less likely to have canker presence.

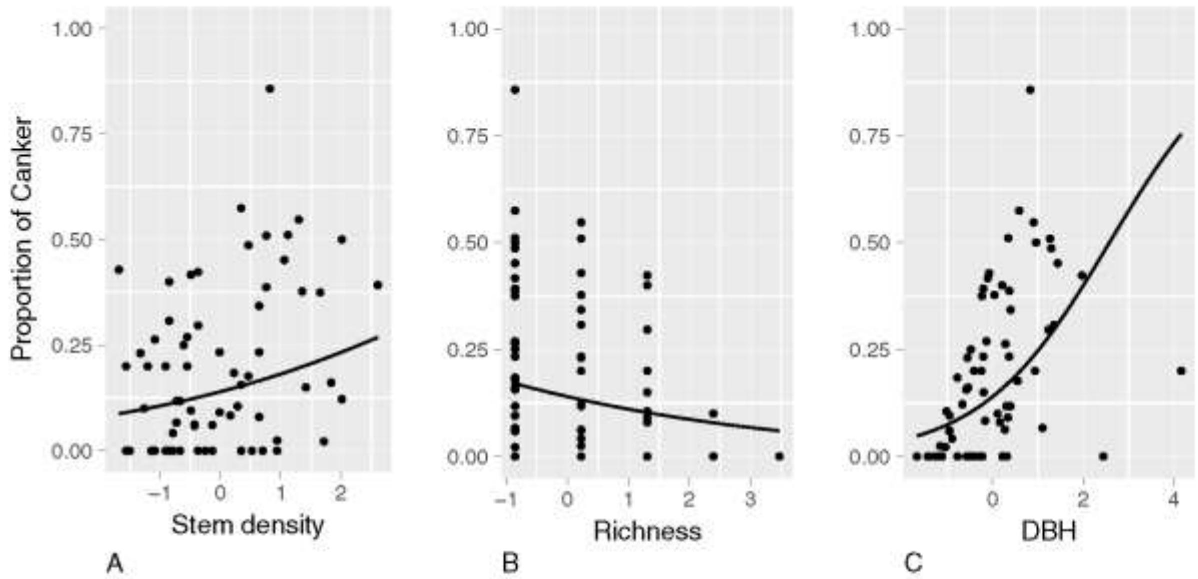

Fig. 6. Proportion of canker presence as a function of total stem density (stems ha^{-1}), richness of tree species and average DBH of *Corymbia calophylla* (cm). Lines depict predictions of GLMM binomial model. Note that covariates are standardized values.

Table 2. Estimated regression parameters, standard errors, z-values and P-values for binomial GLMM; proportion of canker incidence modelled against covariates: Richness of tree species, total stem density (stems ha^{-1}) and average DBH for *Corymbia calophylla* (cm).

Fixed effects				
	estimate	Std error	z-value	*P*-value
Intercept	-1.81	0.09	-3.52	< 0.001
Stem density	0.31	0.07	4.21	< 0.001
Richness	-0.26	0.09	-2.85	< 0.001
DBH	0.70	0.07	9.75	< 0.001
Random effect				
	Std Dev			
Site	0.22			
Goodness of fit				
AIC	307.6			
R^2	0.16			

Discussion

This study clearly demonstrates the impact of anthropogenic disturbance on stand structure and the incidence of canker disease of *C. calophylla.* Alarmingly high rates of canker presence, resulting in mortality, were recorded for trees located on road edges adjacent to anthropogenic disturbance. Disease incidence and mortality significantly decreased in road edges bordering forest, and continued to decrease with increased distance from the road, confirming results from previous studies implicating the role of anthropogenic disturbance in canker incidence of *C. calophylla* (Paap *et al.*, 2017a; Paap *et al.*, 2017b).

NMDS ordination demonstrated significant differences between tree community composition of the disturbed road edge and forest transects, in addition, forest edge composition differed from that at 50 m and 200 m into the forest. *Corymbia calophylla* dominated disturbed road edges, while species such as *A. fraseriana, B. grandis* or *P. elliptica* were mostly associated to the transect 200 m into the forest. The proportion of *C. calophylla* individuals with canker was significantly correlated to the ordination scores, being associated to the disturbed road edge.

Further examination of stand level structural traits found disturbed edges showed a significant reduction in tree diversity, and increased stem density and basal area of *C. calophylla.* The construction of roads may introduce invasive species to the landscape, alter flows of materials and change levels of available resources including water, light and nutrients (Coffin, 2007). Forest edges experience higher wind and solar radiation levels, and greater moisture and temperature fluctuations (Crockatt, 2012). Where adjacent to agricultural or urban areas, increased deposition of nitrogen and other fertilisers, pesticides and other pollutants are likely to further impact edges (Sapsford *et al.*, 2017). Mycorrhizal fungi, through their mutualistic relationship with plant roots, play an integral role in tree health and a range of biotic and abiotic stress factors negatively affecting tree health have also been shown to impact mycorrhizal communities, though the relationships between forest tree declines and changes in associated mycorrhizal fungal communities are complex (Sapsford *et al.*, 2017). All these factors may contribute to the disturbance experienced by edges in the current study and underpin the observed differences in stand structure and canker disease incidence.

Pekin *et al.* (2009) examined eucalypt forest structure of mixed *E. marginata* and *C. calophylla* forest stands in SWWA, finding total stem densities ranging from 467 - 3467 stems ha^{-1}. These results are congruent with our stem density for forests sites ranging from 633 – 2633 stems ha^{-1}. Total stem densities on disturbed edges were significantly greater (ranging from 567 – 2967 stems ha^{-1}). Increased stem densities on forest edges compared to forest interiors have been reported previously for temperate and tropical forest types (Palik and Murphy, 1990; Williams-Linera, 1990), along with increased tree mortality (Williams-Linera, 1990; Nascimento and Laurance, 2004). Pekin *et al.* (2009) found *E. marginata* was more abundant than *C. calophylla* throughout the region, with results from the current study also finding *E. marginata* more abundant than *C. calophylla* in the interior forest transects. In contrast to this, however, disturbed roadside transects were dominated by *C. calophylla* with a five-fold increase in mean basal area of *C. calophylla* on disturbed edges compared to interior forest transects. This is most likely attributal to a combination of edge effects including increased light availability, altered hydrology, fertiliser inputs from adjacent agricultural land and the loss of co-dominant overstorey species. Remy *et al.* (2016) found prominent edge effects along edge-to-interior forest transects in Belgium and Denmark. Nitrogen stocks of wood, roots and mineral soil were higher on edges, as were stem density and wood volume, all of which decreased with distance from the edge (Remy *et al.*, 2016). Air temperature, moisture and nitrogen deposition typically have edge effects of ca. 50 m (Crockatt, 2012), which may explain observations for a number of stand structural traits in the current study that were similar between the forest edge and the transect at 50 m, while at 200 m were significantly different from forest edges.

There are a number of possible explainations for the dominance of *C. callophyla* on disturbed edges. McCaw (2011) suggests *C. calophylla* may be more locally dominant on mesic sites, or where *E. marginata* has been removed by selective logging. *Corymbia calophylla* may also persist where *E. marginata* has been killed by *P. cinnamomi*. *Eucalyptus marginata* has been shown to be substantially less tolerant of waterlogging than other SWWA forest species (Davison, 1997). Disturbed road edges may be more prone to soil moisture variability and inundation, which may be an additional contributing factor to the loss of *E. marginata* from these sites. To our knowledge this is the first study that documents the extent of change in stand structure and composition of remnant roadside vegetation and forest road edges in SWWA.

Investigation of factors driving canker presence found that regardless of where trees were on the site, stands with greater tree diversity showed reduced canker frequencies, while stands with higher *C. calophylla* stem density and average stem DBH showed higher levels of canker disease. In fragmented landscapes, the mortality of large trees is greater near forest edges than in forest interiors, leading to a reduced tree diversity in edge-affected vegetation with potential consequences on ecosystem functions (Rolo *et al.*, 2018). Decreases in tree species diversity and increased density of a single species may lead to levels of pathogen pressure above those which the host is adapted to in natural forest settings, potentially resulting in increased damage by pathogens (Ennos, 2015). This link between tree species diversity and a forest's susceptibility to fungal pathogens confirms the 'insurance hypothesis,' where biodiversity insures ecosystems against declines in their functioning, because many species provides a greater guarantee that some will maintain functioning, even if others fail (Yachi and Loreau, 1999). Burdon and Chilvers (1982) review of host density as a factor in disease ecology introduces the idea of a critical host population density, below which disease will not occur. Pautasso *et al.* (2005) expand on this, proposing the concept of critical host diversity- a level of species richness which limits a particular disease to a silviculturally acceptable level.

A reduction in damage in forests with higher species diversity compared to single species forests has been observed for numerous pathogens. For example, increasing tree species diversity of neighbouring trees resulted in decreasing foliar fungal infestations on two common tree species (*Tilia cordata* Miller and *Quercus petraea* (Mattuschka) Lieblein) in the Kreinitz tree diversity experiment in Germany (Hantsch *et al.*, 2014). Studies of the invasive pathogen *Phytophthora ramorum* Werris, De Cock & Man in't Veld in Californian coastal forests found diverse forests showed lower *P. ramorum* infection incidence compared with less diverse stands (Haas *et al.*, 2011), while Cobb *et al.* (2012) determined that low densities of tanoak in a matrix of non-susceptible neighbouring species slowed disease transmission enough to retain overstorey tanoak, supporting the existence of host density thresholds. In addition to the concept that forest susceptibility is dependent on tree diversity, Pautasso *et al.* (2005) also propose 'reversing the terms,' where the question becomes whether susceptibility leads to diversity i.e. 'pathogen driven diversity'. Hawkins and Henkel (2011) present an example of native forest pathogens as important determinants of forest structure and composition in the absence of fire, where *Armillaria* species and *Pseudoinonotus dryadeus* (Pers.) T. Wagner & M. Fisch. enhanced mortality of *Abies concolor* var. *lowiana* (Gord. & Glend.) Lemmon (white-fir) (approximating the role of fire) resulting in canopy gap formation, enabling the regeneration and persistence of *Pseudotsuga menziessii* var. *menziessii* (Mirbel) Franco (Douglas-fir). These studies all support our observations of increased canker in *C. calophylla* stands. There is however contradictory evidence suggesting the causal agent *Q. coryecup* is an endophyte, and that it is increased stress that leads to disease development.

Originally described from cankers of *C. ficifolia* (von Muller) Hill & Johnson, it has been proposed that *Q. coyrecup* has a SWWA origin (Cass Smith, 1970). At the time the disease ravaged amenity planted *C. ficifolia* throughout the region but was not observed on natural stands within its restricted range of the Walpole-Nornalup area on the south coast of SWWA (Cass Smith, 1970). Later surveys found these natural stands remained disease free, while amenity planted *C. ficifolia* in nearby towns were heavily diseased (Paap *et al.*, 2008). It has been suggested that the disease originated on *C. calophylla,* as early reports found that while it was widespread across the *C. calophylla* range the disease was very slow to develop on this host (Cass Smith, 1970). Up until the 1980s there were limited reports of decline and mortality of *C. calophylla* resulting from *Q. coyrecup* infection (Kimber, 1981), however, in recent decades the disease has become increasingly serious and widespread, raising questions of what is driving disease development (Shearer, 1994; Paap *et al.*, 2017b). Early studies on *C. ficifolia* found cankers were frequently associated with bark injuries e.g. arising from pruning or breaking of branches, and that canker surfaces could be covered with masses of spores which when transported by wind, rain splash etc., would spread the disease (Cass Smith, 1970). The more recent outbreak of the canker disease in anthropogenically disturbed areas, roadsides and parks, has been attributed to increased stress.

A previous landscape scale study of *C. calophylla* found the presence of pathogenic *Phytophthora* spp. and climate, together with anthropogenic disturbance, influenced the probability of canker presence (Paap *et al.*, 2017a). The negative impacts of climate change on forest health have already been observed in SWWA, with drought and heat induced forest dieback and mortality reported in response to extreme climatic conditions (Brouwers *et al.*, 2012; Matusick *et al.*, 2012; Matusick *et al.*, 2013). Mantyka-Pringle *et al.* (2012) found the effects of landscape fragmentation on vegetation were greatest in regions with high maximum temperatures and declining rainfall, with Brouwers *et al.* (2013) also finding a synergistic effect of these factors on *E. wandoo* health in SWWA. As such, the stresses presented by habitat fragmentation, land use change, stand structure change and the presence of introduced *Phytophthora* spp., under altered climate conditions, will likely continue to contribute to an increasing vulnerability of *C. calophylla* to *Q. coyrecup.*

The current study highlights the impact of anthropogenic disturbance on stand structure, and the impact of both anthropogenic disturbance and altered stand structure on the susceptibility of *C. calophylla* to canker. Specifically, anthropogenic disturbance drives stand composition to a state of reduced tree diversity, leaving *C. calophylla* as the dominant species and increased *C. calophylla* basal area, with the change to these stand traits resulting in increased host susceptibility to the canker causing agent *Q. coyrecup*. Therefore, the implications of the potentially rapid and extensive loss of *C. calophylla* as a result of mortality inducing cankers, particularly from disturbed road edges where they are frequently the only remaining tree species, are especially significant. These will include economic, social and ecological costs associated with tree removal and clean-ups after storms, lost honey and pollen production, loss of wildlife habitats and food resources, as well as the loss of amenity values such as shade, impacts on the control of salinity and erosion, and the conservation of roadside verges.

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Appendix

Table S1. Summary statistics, mean with 95% confidence intervals for stand level structural traits of transects on disturbance gradients (disturbed edge, forest edge, 50 m into forest and 200 m into forest) across 17 study sites.

Structural trait	Disturbed edge	Forest edge	50 m in	200 m in
SD *C. calophylla*	1311.8 (1146.9-1476.6)	790.2 (625.4-955)	613.7 (448.9-778.6)	503.9 (339.1-668.7)
SD total	1890.2 (1636-2144.4)	1478.4 (1224.2-1732.6)	1329.4 (1075.2-1583.6)	1339.2 (1085-1593.4)
% SD *C. calophylla*	0.71 (0.64-0.79)	0.54 (0.46-0.61)	0.48 (0.41-0.56)	0.36 (0.29-0.44)
A_b *C. calophylla*	119.1 (106-132.2)	46.3 (33.2-59.3)	26.2 (13.1-39.3)	21.9 (8.8-35)
A_b total	148.3 (131.4-165.3)	76.1 (59.2-93.1)	56.5 (39.6-73.5)	64.2 (47.2-81.1)
% A_b *C. calophylla*	0.83 (0.74-0.92)	0.62 (0.53-0.71)	0.46 (0.37-0.55)	0.32 (0.23-0.41)

Structural traits include stem density (SD) (stem ha^{-1}) and basal area (A_b) (m^2 ha^{-1})

Table S2. Summary statistics, mean with 95% confidence intervals for % canker incidence, number of dead trees with and without canker (mortality canker and other, respevtively) of *Corymbia calophylla*, for transects on disturbance gradients (disturbed edge, forest edge, 50 m into forest and 200 m into forest) across 17 study sites.

Variable	Disturbed edge	Forest edge	50 m in	200 m in
% canker incidence	0.47 (0.41-0.53)	0.19 (0.15-0.25)	0.05 (0.03-0.09)	0.03 (0.01-0.06)
mortality (canker)	2.59 (1.25-3.92)	0.41 (0.09-0.73)	0.18 (-0.09-0.45)	0 (0-0)
mortality (other)	0.12 (0.03-0.46)	0.14 (0.04-0.5)	0.21 (0.07-0.64)	0.18 (0.05-0.66)