Manuscript Number:

Title: Floristic patterns and disturbance history in karri forest, south-western Australiua: 1. Environment and species richness

Article Type: FLA Full Length Article

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Floristic patterns and disturbance history in karri forest, south-western Australia: 1. Environment and species richness.

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Abstract

We examined the influence of disturbance history on interactions between floristic composition and environmental factors in a single community type in karri forest (site type 10, after Inions et al., 1990) in south-western Australia. The relationship of six disturbance and site-based environmental variables, and three plant species richness variables (native, introduced and total vascular plant species) were compared using numerical taxonomic,

regression and correlation approaches. Disturbance and site variables were highly intercorrelated, limiting the opportunity to directly attribute causes to observed floristic patterns. Nevertheless, management practices in karri forest are based on interrelated disturbances (e.g. high intensity slash burns were used to initiate regeneration for timber production), limiting the necessity to separate effects. Community types in karri forest have both, low α diversity (quadrat-based species richness) and species richness of the community in comparison with neighboring vegetation types. For community type 10, α diversity was negatively correlated with time-since-fire ($P < 0.002$) and time-since-regeneration ($P < 0.004$), but was lowest at intermediate times since disturbance (11-20 years). Although ordination revealed no discernable pattern of sites based on floristic composition, four plant assemblages defined a priori according to time-since-disturbance were significantly different from one another ($P < 0.01$ by ANOSIM). Time-since-fire (and other disturbance) influenced floristic composition more than the number of recent past fires in contrast to the more species-rich, but drier and nutrient-poor neighboring jarrah forest communities where the number of past fires is more influential. Under the current climatic regime, karri forest communities are likely to undergo less long-term change in floristic patterns following disturbance than neighboring vegetation types. This is primarily because of the greater intervals between disturbance events, the few transformer weeds in the area and the rapid recovery of native plant cover following disturbance. This study has demonstrated the resilience of karri forest to various discrete disturbances currently associated with these environments, although more profound changes are likely following continuing disturbance intervention such as clearing and grazing.

1. Introduction

The forested ecosystems of south-western Australia cover about 4.25 million hectares in three biogeographic regions (IBRA bioregions <u>sensu</u> Thackway and Cresswell, 1994) of mild Mediterranean climate: Swan Coastal Plain, Jarrah Forest and Warren. Substantial tracts of these forests have been cleared for agriculture and the remainder is managed either as conservation reserves or as the basis of a range of extractive industries including mining, logging, cut flower and honey production. These multiple use forests also supply a range of secondary services including water catchment protection and nature conservation (Dell <u>et al</u>., 1989).

Forest dominated by karri (<u>Eucalyptus diversicolor</u>) is circumscribed by the Warren Bioregion, excepting inland and north-eastern outliers at The Porongurup Range and Mt. Manypeaks. Some 180 500 ha of karri forest exists on publicly owned lands, administered primarily by the Department of Conservation and Land Management; approximately 90 % of this area is in conservation reserves. In this fire-prone landscape, regular prescribed burning is used widely to reduce fuel loads and lower the risk of more intense wildfires, as well as to manage habitat for particular species and communities (see Christensen and Abbott, 1989; Burrows and Wardell-Johnson, 2003).

There has been contention regarding the effects of disturbances such as logging and burning on the flora and fauna of the karri forest (e.g. Abbott and Christensen, 1994; Wardell-Johnson and Horwitz, 1996; Calver et al., 1998). Some of this debate concerning the effects of disturbance reflects different spatial and temporal scales of assessment, different assessment methodologies, and different interpretations of historical and biological evidence. The debate also reflects changes both in community expectations and land tenures implemented before the introduction of The Forest Act in 1918 (Calver and Wardell-Johnson, 2004). Regardless, ecologically sustainable forest management (ESFM) is a key issue for continued timber production in WA's native forests (Lindenmayer, 1999; Calver and Wardell-Johnson, 2004).

The concept that forests can sustain both resource production and maintenance of biodiversity is considered an untested hypothesis and a major management challenge (Lindenmayer, 1999; Wardell-Johnson et al., 2004a). Lindenmayer (1999) identified the key research issues for ESFM as (1) the reliability of indicator species and their value in forest conservation and management, (2) the value of impact studies in quantifying changes in biodiversity, and (3) the role of long term monitoring in achieving sustainability. Accordingly, an understanding of the response of the biota to disturbance is a fundamental requirement of ESFM. Determining pattern and process of secondary succession is therefore required to inform management priorities and operations that satisfy ESFM of karri forest.

Species diversity of plants (α diversity after Whittaker, 1977) has been shown to change following disturbance (e.g. Groves and Burdon, 1986; McIntyre and Lavorel, 1994; Wapstra et al., 2003), although it is important to consider native and introduced taxa separately (see

McIntyre and Lavorel, 1994; Wardell-Johnson et al., 2004b) in examining changes in diversity. Although some studies in karri forest have included a floristic component (e.g. Bridgewater, 1981; Wardell-Johnson and Williams, 1996), few have examined disturbance effects on the biota using quadrat-based assessment. In addition, management planning of karri forest has largely focused on studies of vegetation structure and growth (e.g. Stoneman et al., 1989; Borg and Stoneman, 1991; Wardell-Johnson and Williams, 2000; Bradshaw and Rayner 1997a, b) rather than on disturbance and biotic change.

Experimental studies of forest disturbance tend to be limited by the long time frame involved and the confounding variables of site and disturbance history. Space-for-time substitution (retrospective) studies can reveal patterns and processes otherwise neither readily interpretable within a management timeframe nor easily obtainable without data from a broad geographic coverage. The 13 stable community types (site types) of regrowth karri forest defined by Inions et al. (1990) provide a framework of sites that limit variation between sample locations. The regional distribution of karri forest is largely determined by climatic factors (Churchill, 1968), while local variation in community types is also a response to edaphic and geomorphic factors (Inions et al., 1990). By focusing on a relatively extensive and prevalent karri forest type, that is restricted to a single site type but exhibits a range of disturbance histories, this study seeks to separate the effects of site and disturbance impacts. The specific aims are to quantify an age series of floristics in secondary succession using quadrat data, and to determine the influence of particular disturbance regimes on different components of diversity based on origin.

2. Methods

2.1. Study areas

Inions <u>et al</u>. (1990) used 204 long-term monitoring plots established as part of the permanent inventory program in karri forest as the basis for their classification of karri sites. Site type 10 (50 quadrats) was the most prevalent of the site types defined, and occurred generally in the central and northern parts of the main karri range, particularly in relatively gravelly sites (see Inions <u>et al</u>., 1990; Fig. 1). We based our quadrat selection on the 50 permanent inventory plots used in the original sampling regime, supplemented with 41 sites of a variety of known disturbance histories in the same landform/soils units in the same general areas (selected after Churchward <u>et al</u>., 1988). Quadrats were interspersed throughout the landscape associated with the original 50 quadrats defining the site type. Thus, no major riparian sites were included, although some quadrats included minor first order gullies.

The locations of sampling sites were selected to give coverage of disturbance history while keeping community and site type constant. This included sites that were in relatively close proximity to private property (although none within 100 m), as well as areas that had experienced a variety of burning, silvicultural and logging activity. Thus, we located quadrats within vegetation that had not been transformed by agricultural clearing, or by the construction of log landings, or roads. These activities have the capacity to substantially change community type by influencing hydrological and other functions (Breidahl and Hewett, 1992; Wapstra <u>et al</u>., 2003). All quadrats were located at least 20 m from road verges to avoid the edge effects associated with such sites.

2.2. Floristics and quadrat assessment

Detailed studies have recognized that an appropriate sample area is about 400 m^2 in forested areas (Wardell-Johnson and Williams, 1996). This allows a representative floristic list for the site, and minimizes the influences of individual large trees or logs within a quadrat. Quadrats larger than this area may include ecotones, and are problematic for complete floristic assessment if vegetation is dense. All quadrats in this study were 20 m x 20 m and were permanently marked. The sites were assessed at least twice (and up to five times), including at least once during the main flowering period in spring to enable accurate identification of all vascular plants. The cover-abundance of each plant species was recorded using a modified Braun Blanquet scale (i.e. 3 <1 %, 4 1-5 %, 5 5-10 %, 6 10-25 %, 7 25-50 %, 8, 50-75%, 9 > 75 %). Species nomenclature follows Paczkowski and Chapman (2000). A list of vascular plants encountered in the study (along with their origin) is available from the corresponding author.

2.3. Environmental and species-group variables

Six site and disturbance variables were recorded in all quadrats (Table 1), and association between these variables was examined using Chi-squared analysis (Table 2). Species richness of vascular plants and of the species-groups of plants based on origin (introduced or native) was derived from the complete lists for each quadrat. Data were the total list of taxa of each site (α diversity after Whittaker, 1977). We also compared overall species richness for this community with other communities in karri forest and elsewhere in the region. In this case, data were the total list of species occurring in at least one quadrat in site type 10. The

relationship of species-groups of plants with time-since-fire and time-since-regeneration was examined using regression and correlation analysis.

2.4. Numerical analysis

Patterns derived from the 224 species by 91-site matrix were examined using numerical analysis approaches (Sneath and Sokal, 1973; Belbin, 1985). Dissimilarity between sites based on overall floristic composition was quantified using the Bray Curtis Metric, a method that has performed consistently well in a variety of tests and simulations on different types of data (Faith et al., 1987). The resulting dissimilarity matrix was visually presented through semi-strong hybrid multidimensional scaling ordination (SSH MDS with dissimilarity cut level at 0.9, Shepard, 1962; Belbin, 1991), using the package WinPATN (Belbin, 1995a, b; Belbin et al., 2003). SSH MDS is widely used in the study of relationships between species assemblages (Kent and Peddy, 1992; Digby and Kempton, 1991) and seeks to provide, in few dimensions, an accurate representation of the relationship between samples (i.e. sites) on the basis of their attribute (i.e. species) profiles.

The relationship of species-groups of taxa based on origin, and disturbance and site variables, with the ordination pattern was explored using principal axis correlation (PCC procedure in WinPATN, Belbin, 1995a). The significance of correlation of each group of taxa, and each disturbance and site variable were assessed using Randomization tests (with 100 permutations) and the MCAO procedure of WinPATN, Belbin, 1995a; Belbin et al., 2003). The statistical significance of differences in the species composition between various disturbance and site

categories was tested with analysis of similarity (ANOSIM - WinPATN, Belbin, 1995a; Belbin et al., 2003), with 100 permutations.

3. Results

3.1. Species richness, disturbance and site

Overall total species richness averaged 29.1 ± 1.1 (mean $\pm$ standard error) per 400 m^2 quadrat. There were significant differences ($P < 0.05$, Tukey HSD) between total species richness and three of six disturbance and site variables (Table 3). Thus, species richness varied according to time-since-fire, time-since-regeneration and the number of past fires. Three of six disturbance and site variables were continuous. Thus, total species richness varied according to time-since-fire ($P < 0.002$, $r^2 = 0.105$), declining with age (log (SR Total) = 3.42 (± 0.05) – 0.01 (± 0.003) * t, Fig. 2). However, there was an increase in species richness many years after fire (Table 3). Thus species richness was highest within the first three years after fire and lowest at intermediate ages. There was no trend for total species richness to change with time-since-regeneration. However, if mature plots were removed, total species richness declined with age (log (SR all) = 3.40 (± 0.06) – 0.005 (± 0.002) * t, $P < 0.004$, $r^2 = 0.121$).

Native species richness varied as with total species richness for time-since-fire, time-since-regeneration and number of fires (Table 3). However, introduced species richness varied with time-since-fire, time-since-regeneration and distance to private property. Interestingly, introduced species richness was negatively associated with distance from private property, possibly due to most recently regenerated sites being distant to private property, and the lack

of sites within immediate proximity (i.e. less than 100 m) of private property. Landscape position and fire intensity provided no general trend in regard to species richness for either introduced or native taxa. Significant differences between categories of distance to private property were found only with respect to introduced species.

When treated as continuous variables, species richness of native, and introduced plants both followed a trend toward fewer species with time-since-fire (log (SR native) = 3.3 (± 0.05) – 0.01 (±0.00) * t, $P < 0.002$, $r^2 = 0.09$, log (SR introduced) = 1.15 (± 0.11) – 0.01 (± 0.01) * t, $P < 0.052$, $r^2 = 0.042$). Introduced species richness and native species richness both declined with time-since-regeneration (log (SR native) = 3.29 (± 0.06) – 0.004 (± 0.002) * t, $P < 0.01$, $r^2 = 0.101$, log (SR introduced) = 1.34 (± 0.13) – 0.011 (± 0.003) * t, $P < 0.002$, $r^2 = 0.143$) when mature sites were not included.

3.2. Karri floristic assemblages, disturbance and site

Although no clear pattern emerged in the three dimensional ordination based on the total floristic composition (Fig. 3), floristic assemblages differed significantly between all categories of LFIRE ($p < 0.01$, Table 1) and all categories of RGENC ($p < 0.001$). There were also some differences between assemblages according to LAND and PPC. Thus, greatest differences in assemblages were between sites far from private property and those in close proximity, with sites within three km of private property not being significantly different from one another. Greatest differences in assemblages were between sites high in the landscape profile with sites low in the profile. However, no assemblages were significantly different from one another based on FIRES and FIREINT (Table 1).

Four extrinsic disturbance and site factor variables, RGENC, LFIRE, LAND, and PPC were each strongly associated with the three dimensional ordination based on floristic composition ($P < 0.05$, MCAO, Fig. 3), while FIREINT and FIRES were not. LFIRE and RGENC were similar, as they are strongly associated in the disturbance regimes prevailing in the karri forest used for timber production. The vector for PPC was almost opposite to those of LFIRE and RGENC, suggesting that most recently logged and regenerated sites were distant from private property. The vector for LAND was perpendicular to those of disturbance (LFIRE and RGENC), with a relatively high proportion of sites in the 11-20 years-since-disturbance categories being highest in the landscape.

3.3. Design

A total of 13 of the 15 possible associations between the six explanatory variables yielded significant results (Table 2). Only for the FIRES/LAND combination was there no suggestion of interaction. Thus, sites of younger regeneration had not been burnt since the slash fire prescribed to facilitate regeneration; such fires almost always being in summer or autumn, and of high intensity. Distance to private property was also strongly associated with each of these variables. Similarly, sites distant from private property were more likely to have been recently burnt or regenerated than sites in close proximity to private property.

4. Discussion

4.1. Species richness, disturbance and site

More species were detected in this study than in studies elsewhere in karri forest, reflecting the increased α diversity often associated with recently disturbed areas (e.g. Purdie and Slatyer, 1976; Groves and Burdon, 1986; McIntyre and Lavorel, 1994; Wapstra <u>et al</u>., 2003). Thus, most sites in the Tingle Mosaic study of Wardell-Johnson and Williams (1996) had not been recently disturbed, and few introduced taxa were encountered. High α diversity was encountered in comparison with other studies in karri forest, although low when compared to that found in surrounding vegetation types in the same region (Wardell-Johnson and Williams, 1996). In addition, species richness of the community is also low in comparison with neighboring communities due to many species occurring throughout karri forest but with limited distribution beyond. Thus karri forest communities have much in common throughout the distribution of karri (Inions <u>et al</u>., 1990; Wardell Johnson and Williams, 1996), and are most notable for their differences with other community types regardless of disturbance history.

It is likely that site type 10 has relatively high α diversity and community species richness in comparison with other site types in karri forest because it is widespread, and occurs in more gravelly terrain than the most highly productive stands of karri. For karri forest communities in general, highly productive stands on deep loams (i.e. site types 11, 12 and 13) are typically also lowest in floristic diversity (Inions <u>et al</u>., 1990). Resources are a major factor influencing

the diversity and species composition of plant communities (Tilman, 1982), although the most highly productive stands are not always the least diverse (see Kinzig et al., 2001).

Native species dominate all sites in this study despite the variety and timing of disturbance regimes. Some sites were assessed within one year following disturbance, but were among the most species-rich; and most of these species were native to the area. Previous studies in karri forest have demonstrated an abundance of introduced species soon after logging, particularly if the regeneration burn is delayed before replanting (Breidahl and Hewett, 1992). However, we found no introduced species dominating quadrats in this study. Furthermore, only one introduced species encountered (blackberry Rubus discolor), has been accorded environmental weed status. This species is infrequent in site type 10, being most strongly associated with moist, riparian systems, areas notable for dominance by introduced plants (Fox and Fox, 1986; Malanson, 1993). Although introduced species were most numerous in recently disturbed sites, most are ephemerals that do not remain at the site following the natural restoration of dense cover by native species (Wardell-Johnson et al., unpublished data), a situation also encountered by Wapstra et al., (2003) in wet eucalypt forest in Tasmania (Australia).

4.2. Floristic assemblages, disturbance and site

The lack of observable trends and a relatively high stress value (0.22 in three dimensions) in the floristic ordination reflected a lack of outliers among the quadrats, due to the ubiquitous nature of many of the dominating species in this community type. The lack of association of fire intensity and number of fires, with the floristic ordination contrasts with recent studies of community composition which have demonstrated their importance (e.g. Burrows and

Wardell-Johnson, 2003; Watson and Wardell-Johnson, 2004). Thus, time-since-fire is more influential in karri forest than the number of fires in determining floristic composition, while the number of fires is more important in nutrient-poor sites such as the jarrah forest community reported by Burrows and Wardell-Johnson (2003), and in granitic terrain in Girraween National Park, south-eastern Queensland, Australia (see Watson and Wardell-Johnson, 2004). By contrast to the present study, proportionately less of the flora consists of fire ephemerals in these latter studies where long-lived resprouting shrubs comprised most of the understorey biomass.

4.3. Design implications

Many of the confounding interactions between disturbance and site variables were of sufficient practical importance that they need to be considered in interpreting the results. Because of the strong interactions between disturbance and site variables, it is not possible to ascribe causation to the variables recorded. Thus separation of effects of logging and of fire on floristic composition has not been possible in this study. Environmental management in the karri forest (as in all environments) is associated with interrelated disturbances. For example, high intensity slash burns that are prescribed following logging are part of an interrelated pattern with respect to time-since-fire, time-since-regeneration and fire intensity. The link with number of fires and these other variables is also strong because of the difficulty of prescribing fire in regenerating stands that are less than about 16 years old (McCaw et al., 1994). Thus the interaction between numbers of fires and fire intensity (Table 2) is not unexpected, as fire

intensity is likely to be greater in areas of greatest accumulation of fine biomass (in other words increasing with time-since-fire, Wardell-Johnson, 2000).

4.4.Implications for Ecologically Sustainable Forest Management

Burrows and Wardell-Johnson (2003) argued that impacts resulting from complex interactions between various agents of disturbance may be of greater importance than the impacts resulting from any particular event. There are numerous examples of interactive effects of disturbance in forest ecosystems, particularly following transformative change (e.g. Clarke and Schedvin, 1999; Schefler et al., 2001). Thus, human associated disturbances generally favor introduced species (Denslow, 1985; McIntyre and Lavorel, 1994), and artificially increased nutrient and moisture levels are important causal factors of exotic species incursion in low nutrient Australian environments (Clements, 1983; Hobbs, 1989; McIntyre and Lavorel, 1994; Prieur-Richard and Lavorel, 2000). Alterations of disturbance regimes result in shifts in species composition, with the loss of less tolerant native species, a decrease in native diversity, and increased exotic diversity (McIntyre and Lavorel, 1994; Prieur-Richard and Lavorel, 2000). Under certain disturbance regimes some introduced species are capable of fundamentally altering the structure and function of ecosystems (Groves and Burdon, 1986; Bridgewater, 1990; Michael, 1994). We did not find evidence for such change in this study, despite the relatively high (for south-western Australia) fertility and moisture status (Inions et al., 1990) of this community type.

The relatively low dominance (despite relatively high species diversity) of introduced taxa in this study can be attributed to the rapid recovery of native taxa following disturbance, leading

to very high levels of cover within four years (Stoneman et al., 1989; Wardell-Johnson and Williams, 2000). We also argue that the lack of transformative effects is the result of relatively infrequent disturbance events in association with a limited pool of transformative species (cf rainforest restoration of eastern Australia – Wardell-Johnson, et al., 2004b). By contrast, dominance by introduced species has occurred in nearby areas subject to frequent disturbance such as streamlines and road verges, and areas bared of native plant cover for prolonged periods, such as agricultural clearings or abandoned settlements. This has sometimes led to the development of unstable synthetic vegetation (Bridgewater, 1990) in such sites.

Neither the intensity of fire nor the number of fires was as strongly associated with community composition as time-since-disturbance in this study. This does not imply a similarity in effect regardless of the intensity of fire or the number of fires in a community over a given time frame. Rather, the intensities and number of fires examined in this study relate to a broad-scale managed landscape, rather than an experimental context. Furthermore, the range of intensities and number of fires examined were well within the extremes possible within karri forest environments. However, this study does provide a general demonstration of resilience (Holling, 1973) of the present floristic assemblages to the variety of disturbances currently associated with publicly managed karri forest. Wapstra et al., (2003) also noted this pattern in community types in wet eucalypt forest in Tasmania (Australia), although these authors also found that certain species-groups of plants (particularly ferns) were vulnerable to disturbances associated with particular logging approaches.

Observed patterns suggested that disturbance history influenced not only floristic composition, but also the form of the plant assemblage at a site. Time-since-disturbance (where the disturbance is a discrete event such as a fire, rather than a continuing disturbance intervention such as grazing – see Saunders and Hobbs., 1991) was found to influence floristic composition more than the number of recent past fires. By contrast to this study, the number of past fires is more influential in species-rich, nutrient-poor sites such as neighboring jarrah forest communities. This may be due to the longer intervals between when fires occur in karri forest (despite more rapid fuel accumulation there). Under the current climatic regime, karri forest communities are likely to undergo less long-term change in floristic patterns following disturbance than neighboring vegetation types. This is primarily because of naturally greater intervals between disturbance events, few transformative species in the immediate area, and rapid return of cover of native karri communities following disturbance.

5. Conclusion

This study demonstrates the resilience of karri forest floristic assemblages following various disturbances currently associated with these environments. However, the effects of similar disturbance history variables on other components of the biota such as structure and fauna assemblages may be worthy of investigation. Other components of the biota may be more strongly associated with the history of disturbance (see Wardell-Johnson and Williams, 2000) than is floristic composition Resilience demonstrated to discrete events, such as those investigated in this study may not prevent more profound changes following continuing disturbance intervention such as clearing and grazing. However, most of the karri forest

present at the time of European settlement has not been cleared or grazed and occurs in a relatively intact environment. Hence, despite the dramatic visual impacts of clear felling and occasional high intensity fires, recent management regimes in karri forest may have had less impact on floristic assemblages than commonly perceived.

Although this study has demonstrated some resilience in this community type, it is possible that some taxa remain vulnerable to particular regimes. We suggest that an examination of the life history attributes of the taxa in this study may be fruitful in assessing whether site type 10 in karri forest includes species-groups that are more vulnerable than others to particular disturbance regimes. Such an assessment may identify appropriate regimes for particular groups and also provide evidence of historical disturbance regimes in this community type (and possibly elsewhere in the south-west). Furthermore, comparisons with neighboring community types may allow understanding of factors associated with differential resilience in relation to disturbance.

Acknowledgements

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Figure captions

Fig. 1. Distribution of 91 study sites, major towns, and the main distribution of the karri forest in south-western Australia.

Fig. 2. Species richness of vascular plants compared to time-since-fire for 91 quadrats in community type 10 in karri forest, south-western Australia.

Fig. 3. Sites, floristics and disturbance history
  a) Ordination of 91 sites in community type 10 in karri forest, south-western Australia based on floristic composition (stress = 0.22). For each site, time since last fire fire is shown by different symbols (open square = 1-3 years, closed square = 4-10 years, open triangle = 11-20 years, closed triangle = greater than 20 years).

  b) Principal axis correlation showing vectors of site and disturbance variables significantly associated (P < 0.05) with MDS ordination, and centroids of four a priori site-groups shown in figure 3a.
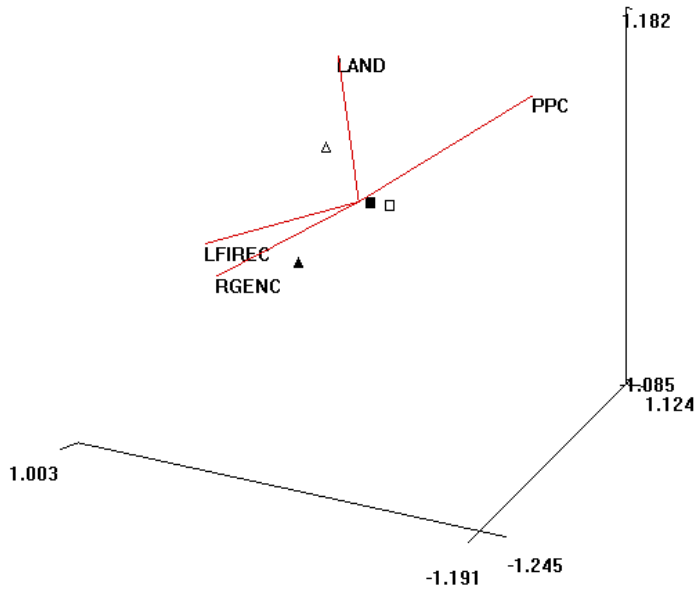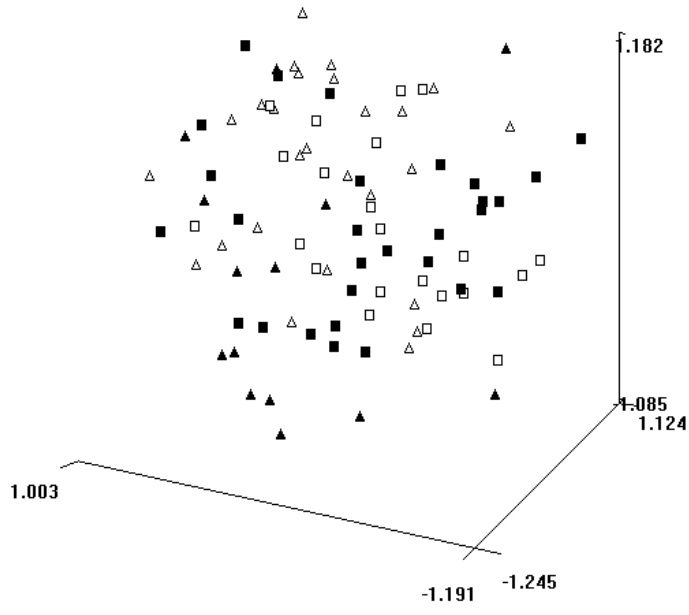
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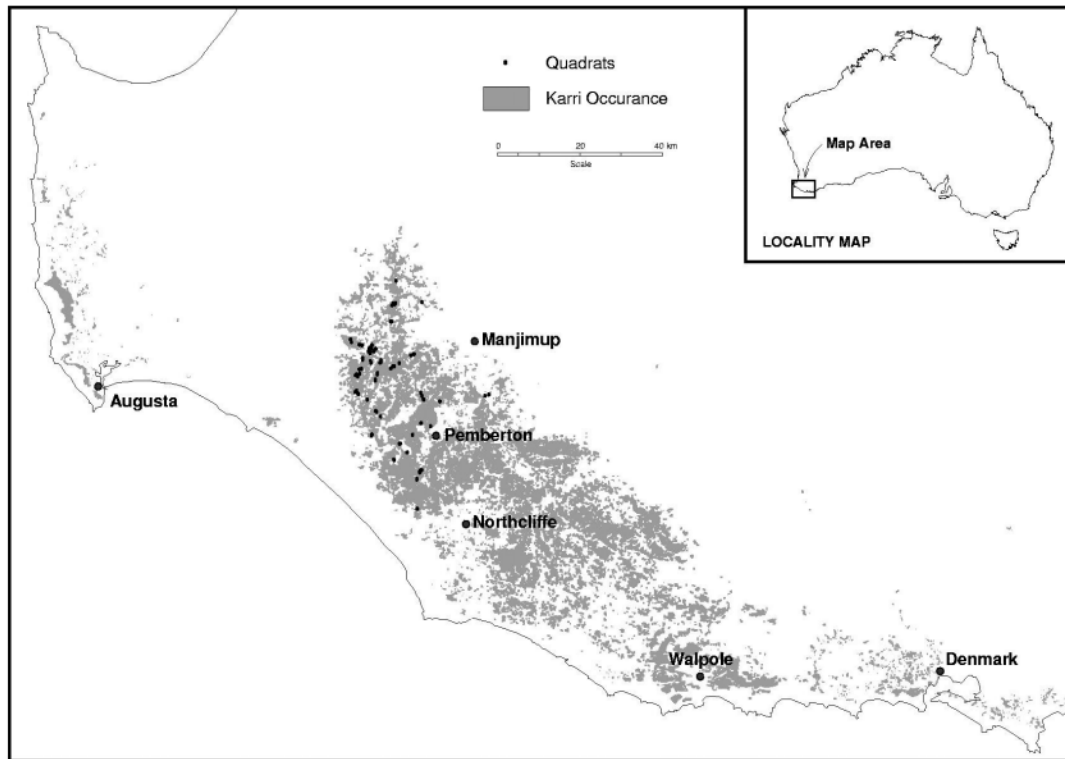
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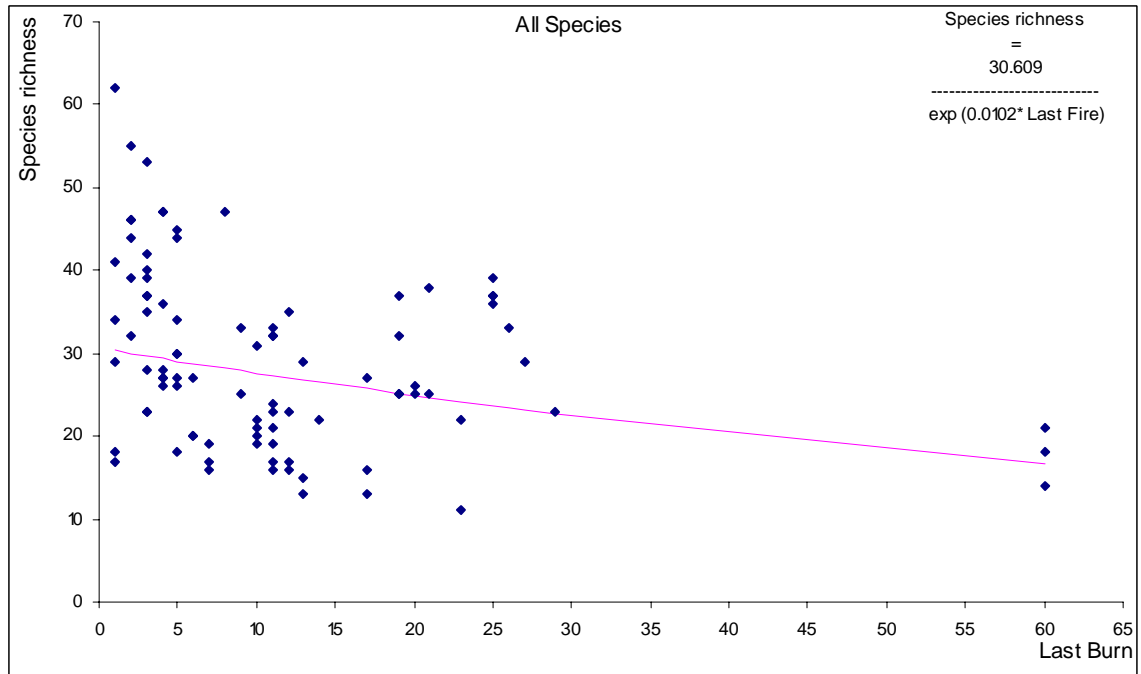
Figure

Table

Table 1. Disturbance history and environmental variables collected at each site. The number of sites (n) is given for each category. Overall and pairwise comparisons between each category indicate whether differences exist between the floristic assemblages in each group. (P-values determined using ANOSIM).

Variable name	Description	Categories	Number of sites	Global P	P for pairwise comparisons
REGENC	Time-since-regeneration in four age groups after Bradshaw and Rayner (1997a)	1 - Establishment (1–8 yr) 2 - Juvenile (9–30 yr) 3 - Immature (31–120 yr) 4 - Mature (120 yr and above)	21 21 23 26	0.000	< 0.001 for all comparisons
FIRES	Number of past fires, including stand regeneration since 1961	0 1 2 3	3 53 26 9	0.778	> 0.05 for all comparisons
LFIRE	Time-since-fire, in 4 categories	1 - 1-3 yr 2 - 4-10 yr 3 - 11-20 yr 4 - 21 + yr	22 29 26 14	0.000	< 0.001 for all comparisons except sites 1 & 2 (P = 0.01)
FIREINT	Intensity of most recent fire	1 - Low 2 - Moderate 3 – High	30 13 48	0.580	> 0.05 for all comparisons
LAND	Landscape position	1 - Minor valley 2 - Mid slope 3 - Upper-slope 4 – Crest	7 48 24 12	0.040	3 & 2, P = 0.040 3 & 1, P = 0.000 4 & 1, P = 0.010. For all other comparisons, P > 0.05
PPC	Distance to nearest private property (km) - in 5 categories	1 - < 1 km 2 - 1-2 km 3 - 2-3 km 4 - 3-4 km 5 - > 5 km	23 11 12 25 20	0.010	4 & 5, P = 0.000 4 & 1, P = 0.000 4 & 3, P = 0.000 4 & 2, P = 0.010 5 & 1, P = 0.000. For all other comparisons, P > 0.05

Table

Table 2. Associations between disturbance and site variables, as determined by Chi-squared analysis. Significant (P < 0.05) associations are bolded.

Variable	FIRES	LFIREC	FIREINT	LAND	PPC
REGENC	**.001**	**.001**	**.001**	.062	**.001**
FIRES	-	**.011**	**.001**	.164	**.006**
LFIREC		-	**.018**	**.001**	**.001**
FIREINT			-	**.012**	**.001**
LAND				-	**.009**

Table 3. Vascular plant species richness (SR ± standard error) within categories based on origin (see text for details) in relation to disturbance history and site variables in site type 10 in karri forest, south-western Australia. Means with the same letter are not significantly different (Tukey HSD procedure).

Variable	Category	Origin		
		Total	Native	Introduced
REGENC	Establish	38.19 ± 1.95 a	33.05 ± 1.66 a	5.14 ± 0.53 a
	Juvenile	23.29 ± 1.95 b	21.52 ± 1.66 b	1.76 ± 0.53 b
	Immature	23.83 ± 1.86 b	22.17 ± 1.58 b	1.65 ± 0.50 b
	Mature	31.00 ± 1.75 a	29.00 ± 1.49 a	2.00 ± 0.47 b
FIRES	0	17.67 ± 5.81 b	16.67 ± 4.87 b	1.00 ± 1.55 a
	1	31.81 ± 1.38 a	28.66 ± 1.16 a	3.15 ± 0.37 a
	2	27.59 ± 2.15 a, b	25.18 ± 1.80 a, b	2.41 ± 0.57 a
	3	23.00 ± 2.79 a, b	22.08 ± 2.34 a, b	0.92 ± 0.74 a
LFIRE	1-3 yr	37.27 ± 2.02 a	32.59 ± 1.73 a	4.68 ± 0.53 a
	4-10 yr	28.59 ± 1.76 a, b	26.40 ± 1.51 a, b	2.21 ± 0.46 b
	11-20 yr	23.58 ± 1.86 b	22.42 ± 1.59 b	1.15 ± 0.49 b
	21 + yr	27.36 ± 2.53 b	24.64 ± 2.17 b	2.71 ± 0.66 a, b
FIREINT	Low	28.13 ± 1.94 a	26.00 ± 1.62 a	2.13 ± 0.50 a
	Mod	26.77 ± 2.95 a	24.85 ± 2.47 a	1.92 ± 0.76 a
	High	30.27 ± 1.54 a	27.23 ± 1.28 a	3.04 ± 0.40 a
LAND	Minor valley Mid slope	27.67 ± 3.04 a	26.42 ± 2.52 a	1.25 ± 0.79 a
		28.00 ± 1.52 a	25.02 ± 1.26 a	2.98 ± 0.40 a
	Upper-slope	32.63 ± 2.16 a	29.92 ± 1.78 a	2.71 ± 0.56 a
	Crest	26.57 ± 3.99 a	24.86 ± 3.30 a	1.71 ± 1.04 a
PPC	< 1 km	30.70 ± 2.16 a	27.91 ± 1.83 a	2.78 ± 0.55 a, b
	1-2 km	25.73 ± 3.13 a	24.27 ± 2.64 a	1.45 ± 0.79 b
	2-3 km	24.64 ± 2.77 a	23.64 ± 2.34 a	1.00 ± 0.70 b
	3-4 km	32.88 ± 2.07 a	28.96 ± 1.75 a	3.92 ± 0.53 a
	> 5 km	27.17 ± 2.44 a	24.78 ± 2.07 a	2.39 ± 0.62 a, b