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Post-fire vegetation succession in *Taxandria linearifolia* swamps in the northern jarrah forest of Western Australia

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ABSTRACT

The structural and floristic changes occurring with time since fire in *Taxandria linearifolia* swamps were investigated using chronosequence analysis. Sixty-six swamps in the northern jarrah forest of south-western Australia were investigated and the effect of fire on them was quantified. Habitat units were mapped from aerial photographs that were imported into a geographic information system. Field surveys were then conducted at each site to ground-truth mapped habitat units. Habitat units were differentiated using factor analysis. The vegetation within the swamps remained relatively open for the first five years following a fire while being largely dominated by three or four species. Thereafter, vegetation density increased to a peak between 20 and 24 years (>90%) and species richness from 10 to 14 (mean = 5.7 ± 0.4). Long unburnt *Taxandria* swamp shrubland habitat returned to intermediate vegetation density levels, although becoming increasingly woody, as relatively few species dominated. Such a response to fire probably reflects adaptations to the frequent, low intensity fire regimes utilised by Aborigines prior to European colonisation.

Keywords: chronosequence, fire regimes, floristics, succession, swamp shrubland, vegetation structure

INTRODUCTION

The effect of fire on jarrah (*Eucalyptus marginata*) forest communities has been studied in detail (Bell 1995; Burrows et al. 2003; Grant & Loneragan 1999; Hatch 1959; Wallace 1966). Jarrah is recognised as one of the most fire resistant eucalypts and is highly adapted to a fire-prone environment (Burrows et al. 1987). Low intensity fires assist in opening seed capsules and in minimising seed competition (Wallace 1966). Seedlings develop lignotubers and then lie dormant for ten to 20 years until an opening in the canopy, possibly caused by fire, enables a single shoot to develop (Wallace 1966). Adult trees develop bark up to four centimetres thick (Wallace 1966). Jarrah also exhibits dormant budding, epicornic shooting and a surge in growth rate in the first five years following a fire (Wallace 1966).

The *Taxandria linearifolia* swamp shrublands of Western Australia's jarrah forest are distinct communities (Havel 1975; Mattiske & Havel 1998) that form on alluvial soils in the broad, gently-sloping, upper reaches of creek systems (Mulcahy 1967; Mulcahy et al. 1972) in the wetter, western side of the jarrah forest (DCE 1980). On the basis of the tolerance to fire in the surrounding vegetation communities, we could assume that *T. linearifolia* swamps within the jarrah forest would be similarly tolerant. *Taxandria linearifolia* dominates swamps within the jarrah forest but is burnt back by fire before resprouting again.

Despite the amount of research into the effects of fire on the jarrah forest communities (Burrows et al. 2003), very little is known about the post-fire succession in these swamp shrublands. Consequently, the aim of this study was to examine the effect of fire on the *T. linearifolia* swamps of the northern jarrah forest.

METHODS

The 66 *T. linearifolia* swamps surveyed were situated within the northern half of the jarrah forest bioregion (Thackway & Cresswell 1995) in the south-west of Australia (Fig. 1). Sites were selected based on the presence of *T. linearifolia* across a range of environmental conditions in the region. Once selected, aerial photographs, provided as high-resolution images by the Western Australian Department of Land Administration (DOLA), were geo-referenced to GPS surveyed points and mapped using the MapInfo Professional Version 5.5 computer package (MapInfo Corporation Inc. 1985–1999). Visual examination of mapped vegetation units enabled different age classes within the swamps to be identified.

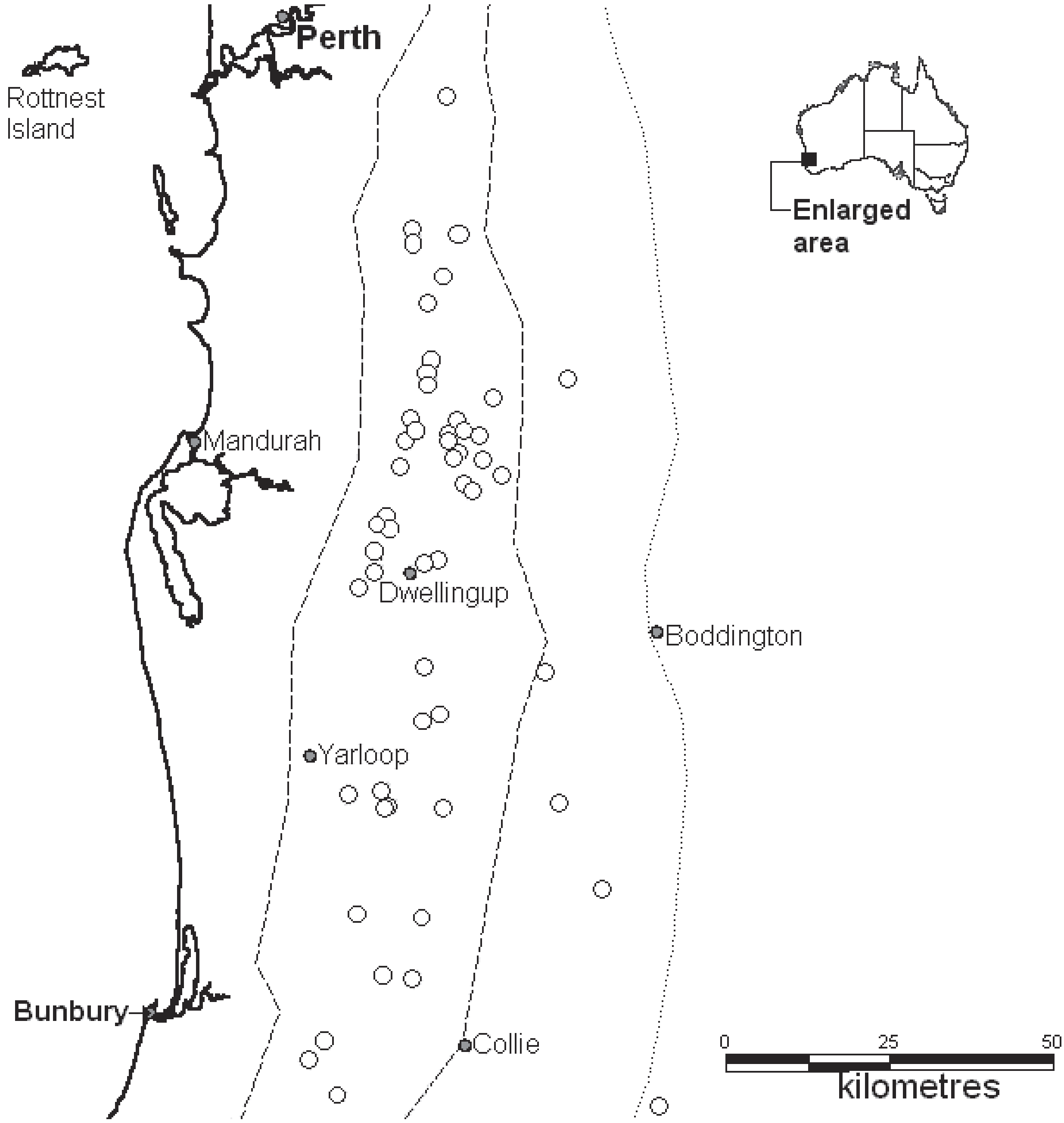

Figure 1. Map of the northern jarrah forest study region with the 66 study sites shown as open circles. The dashed line represents the 1,000 mm rainfall isohyet and the dotted line represents the 700 mm isohyet.

Vegetation units at each site were delineated, 'typed' and subsequently ground-truthed. Each 'typed' habitat unit was representatively sampled with between 5 and 40 quadrats which were determined by the frequency of each habitat units' occurrence (Fig. 2). Quadrats were located in the centre of each unit to minimise the influence of ecotonal features. The structure of each unit was determined by estimating the vegetation density at 0.1, 0.3, 0.5, 1.0, 1.5, 2.0, 3.0 and 5.0 m about ground level. Vegetation density was estimated using the Braun-Blanquet scale of stems covering a 1 m x 0.2 m coverboard held vertically (Braun-Blanquet 1932; Gauch 1986). Floristics at these sites were determined using a 2 m x 1 m quadrat for shrubs, sedges and grasses and a 10 m x 10 m quadrat for trees that was centred in the smaller quadrat. The percent cover of each species within and overhanging the quadrats was categorised according to the Braun-Blanquet scale. Species were identified according to Marchant et al. (1987a; 1987b) and nomenclature was based on the Western Australian Department of Environment and Conservation (DEC) FloraBase web site (http://www.naturebase.net/content/view/2452/1322/)

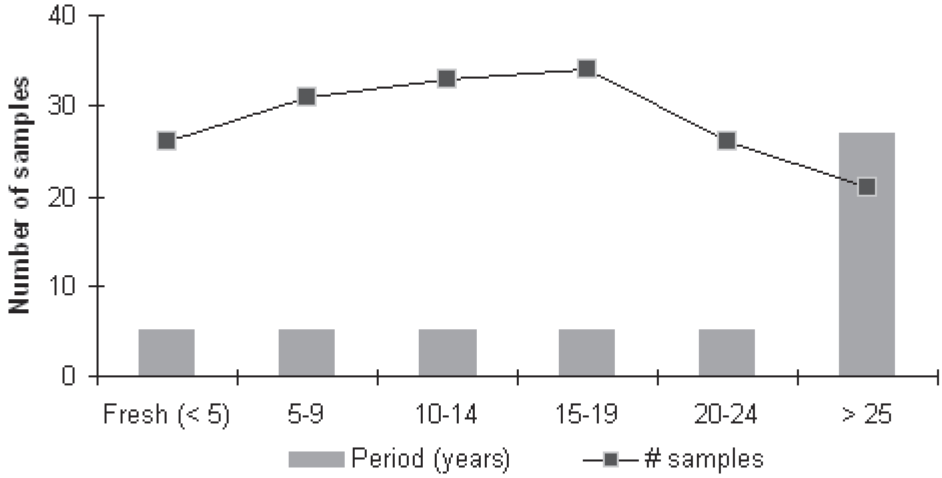

Figure 2. Number of samples and the period of years which they span for each age class within the Taxandria *swamp shrubland.*

Leaf litter depth was measured using a standard DEC litter depth gauge at three places within the 10 m x 10 m quadrat. We also recorded the number of stags (dead trees or shrubs); percent cover of bare earth and open water; the number of cut stumps and logs. The stags, cut stumps and logs were counted in 10 m x 10 m quadrats and the remainder were recorded in the smaller 2 m x 1 m quadrats. These habitat components are grouped hereafter as 'other habitat variables'.

The number of years since the last fire burnt each habitat unit (termed here as the age of the habitat unit) was estimated by counting growth rings on the *T. linearifolia* which has only one growth period per year (L. McCaw *pers comm.*[1]; Hayward 2002). A 240 mm straight pruning saw was used to cut the stems to provide a surface without the need for further preparation. These growth rings were validated by comparison with the known fire history of three sites (Hayward 2002). Growth rings at three sites were used for the comparison: the recently burnt Findlay Brook site (one growth ring in six months since a fire); the older Victor Road site (three to four rings in the three and a half years since a fire) and the Kesners site (ten to 12 rings in the 12 years since a fire). Where growth rings indicated more than one age present within a quadrat, the oldest age (largest ring count) was used.

Data analysis

Factor analysis was conducted on structural, floristic and other variables to differentiate *T. linearifolia* swamp age classes using the Statview Version 5.0 computer program (SAS Institute 1992–1998). Other habitat units within the swamps were differentiated using TWINSPAN (Hayward et al. 2005b), but are described here in more detail. Variables not conforming to the assumptions of normality and heterogeneity were normalised using square-root transformations (small counts) and arcsine transformations (percentages). Analysis of variance was used to determine the significance of differences between the factor scores of each habitat unit. Age classes that could not be differentiated in this manner were plotted on two dimensional factor plots to allow differentiation.

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RESULTS

The flora of the *T. linearifolia* swamp shrublands studied in the northern jarrah forest comprised 57 plant species including one exotic weed species. The eight heights at which vegetation density was measured were reduced to four factors that explained 82.9% of the variation in the data (Table 1). The ten plant species used to differentiate the age classes of *T. linearifolia* swamps were reduced to five factors that explained 62% of the variation (Table 2). The six 'other habitat factors' were reduced to three factor scores that explained 52% of the variation in the data (Table 3).

Taxandria swamp shrubland habitat units were largely differentiated using individual factors with significant differentiation occurring on 13 out of 15 habitat type comparisons (Tables 4 and 5). Plotting of two factor scores from most structural and floristic factors allowed the separation of the two *Taxandria* age class comparisons that could not be statistically differentiated using individual factors. For example, structural factors two and three and floristics factors one and two differentiated between the 5 – 9 and 10 – 14 and the 20 – 24 and > 25 year old *Taxandria* swamp shrubland habitat units (Fig. 3 and Table 5).

High values in structural factor two relate to dense vegetation 2 – 3 m tall while high factor values in structural factor three relate to high density 1 – 2 m above ground level (Fig. 3 and Table 5). High factor values for floristics factor one relate to a high species cover of *Astartea fascicularis* while negative values relate to low cover of *Lepidosperma tetraquetrum* (Fig. 3). High factor score values for floristics factor two relate to high cover of *T. linearifolia* (Fig. 3).

The *Taxandria* swamp shrubland habitat units are

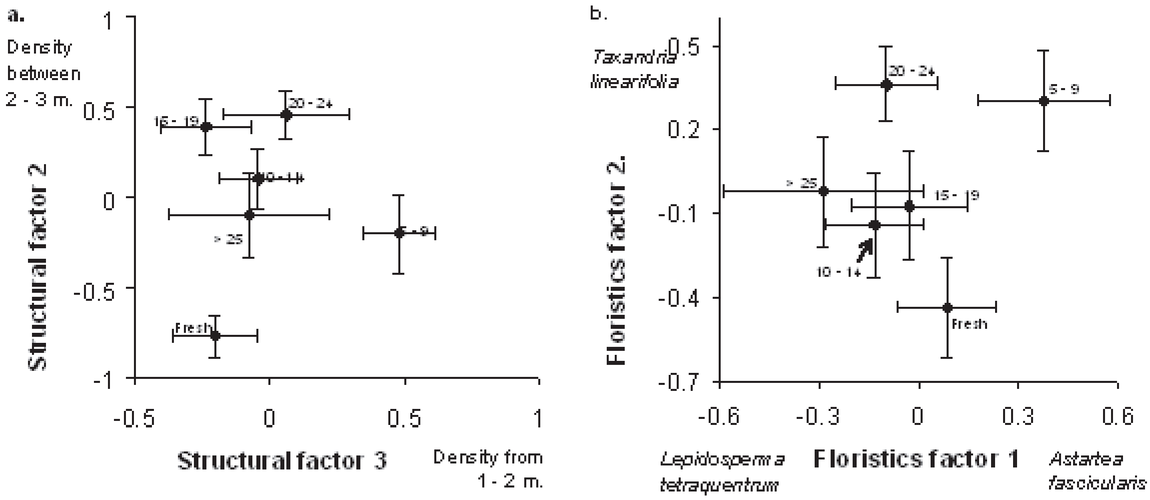

Figure 3. Factor score plots highlighting the differentiation between the 5–9 and the 10–14 year old and the 20–24 year old and long unburnt (>24 year old) Taxandria *swamp shrubland habitat units. a) Positive values of factor 2 relate to high vegetation density between 2–3 m above ground level while high values of factor 3 relate to high vegetation density between 1–2 m. b) Positive values of factor 1 relate to a high cover of* Astartea fascicularis *and negative values relate to a high cover of* Lepidosperma tetraquetrum. *High values of factor 2 relate to high cover of* Taxandria linearifolia.

generally similar in their species composition, all being dominated by *Taxandria linearifolia* with *Lepidosperma tetraquetrum* almost always dominating the ground layer. Other plant species present in these habitat units include *Hypocalymna cordifolium*, *Xyris lacera*, *Thomasia* species and the sedge *Gahnia decomposita*.

The early post-fire seral stage of the *Taxandria linearifolia* swamp was characterised by relatively low vegetation density (Figs 3 and 4) and dead stems (stags) of *T. linearifolia* (Fig. 5) that resprouted from lignotubers at the base of the plant. Very little leaf litter remained following the recent fire and the proportion of bare ground was high (Fig. 5). Species richness was very low. For the first four years following a fire *Lepidosperma tetraquetrum* and *Astartea fascicularlis* were among the few species that coexisted with *T. linearifolia*.

Between five and nine years following a fire the vegetation density at the ground layer increased (Fig. 4), as did species richness and litter depth (Fig. 5). The dead stags found in freshly burnt habitat were no longer present (Fig. 5). Between years 10 and 14 post-fire, species richness per quadrat reached a peak, leaf litter continued to develop and the amount of bare earth and number of stags declined (Fig. 5). Vegetation density at ground level reached an intermediate level, however vegetation density between 2 and 3 m increased substantially (Figs 3 and 4). By 15 to 19 years post-fire, species richness began to decline which continued until the long unburnt stage (Fig. 5). Vegetation density (Fig. 4) and leaf litter depth continued to increase (Fig. 5). Vegetation at ground level and between 2 – 3 m attained its highest density (Figs 3 and 4).

In long unburnt swamps (> 24 years since fire), vegetation density returned to a more intermediate level, akin to that between five and 14 years post-fire (Figs 3 and 4). Long unburnt swamps were almost completely dominated by a canopy of *Taxandria linearifolia,* which may reach up to 10 to 15 m, and *Lepidosperma tetraquetrum* in the ground layer. *Astartea fascicularis* is also occasionally present.

Also within the *Taxandria* swamp shrublands are habitat units dominated by bullich (*Eucalyptus megacarpa*) overstorey with the shrubs *T. linearifolia*, *Hypocalymna cordifolium*, *Thomasia* species and *Boronia molloyiae* interspersed with the sedge *Lepidosperma tetraquetrum.* This habitat unit has a high species richness (mean = 7.6 ± 0.7 s.e.).

Lepidosperma – Hypocalymna swamps are also found within *Taxandria* swamps and are low but densely vegetated (below 1.5 m) areas that lack the *T. linearifolia* dominated canopy. Instead *L. tetraquetrum* and *H. cordifolium* dominate these areas. Nonetheless, they are also relatively species rich with a mean number of species recorded per quadrat of 6.3 (± 0.7 s.e.).

Also within the *Taxandria* swamp are small pockets dominated by the swamp paperbark (*Melaleuca rhaphiophylla*). These areas exhibit relatively high floristic richness (m = 6.1 ± 0.5 s.e.) and the deep leaf litter implies they may require long periods without fire to develop.

Flooded gum (*Eucalyptus rudis*) woodland occurs in seasonally inundated areas when topography changes from the broad, flatter areas where the *Taxandria* swamps dominate to slightly steeper, narrower, more deeply-incised valleys along larger watercourses on the drier eastern side of the jarrah forest. To the more mesic western side of the jarrah forest, the steep-sided banks of larger rivers are dominated by *Grevillea diversifolia* and *Banksia littoralis.* The *Taxandria linearifolia* swamp shrublands in the northern jarrah forest are generally surrounded by open forest dominated by bullich and/or Western Australian blackbutt or yarri (*Eucalyptus patens*) on the lower slopes

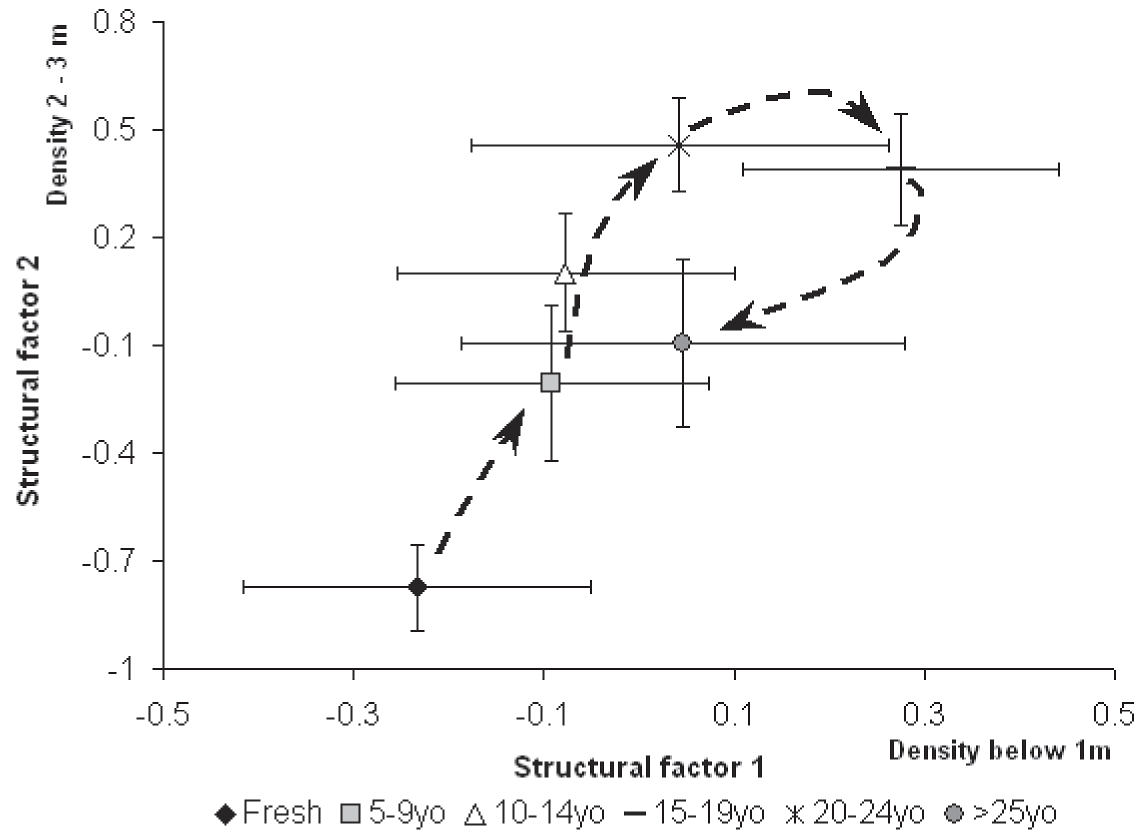

Figure 4. Relationship between structural factors one and two and the differentiation of Taxandria *swamp shrubland habitat units. The mean point is shown along with standard error bars. Positive values of factor one relate to dense vegetation below one m and high positive values of factor two relate to high density between two and three m. The arrows show the increase in vegetation density for both structural factors as time since fire increases until the 20–24 year age class, after which the vegetation structure returns to a more intermediate level.*

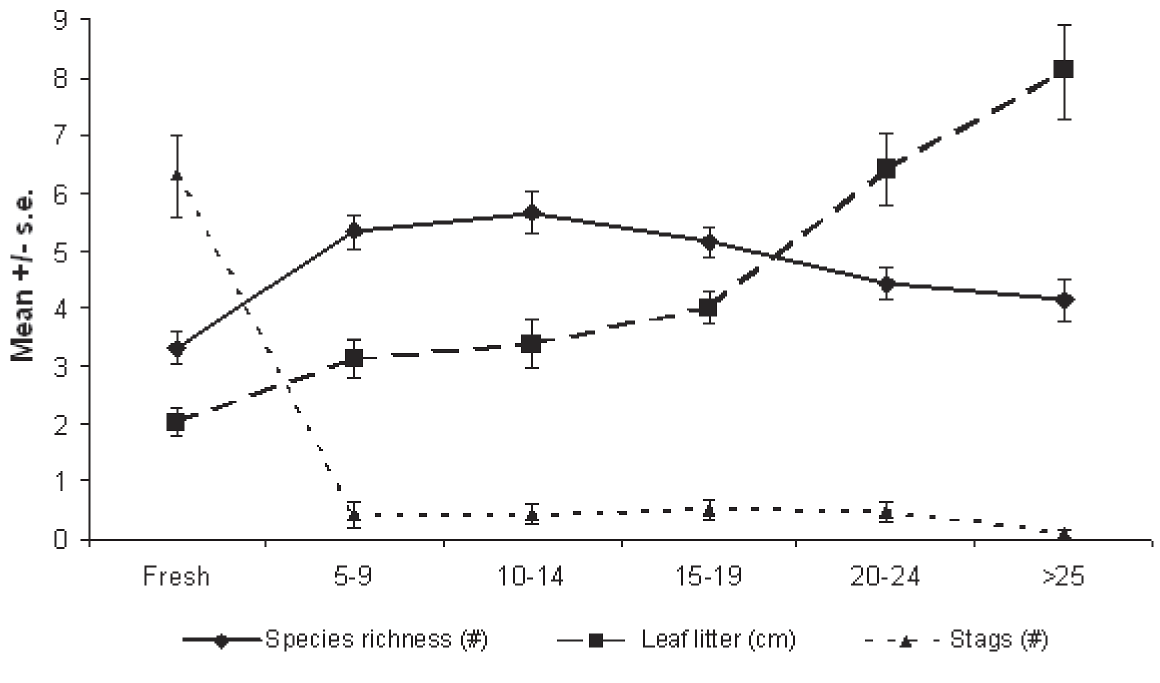

Figure 5. Relationship between mean (± s.e.) species richness per quadrat, leaf litter depth (cm) and the number of dead stems (stags) for each age class of the Taxandria *swamp shrubland habitat units.*

which give way to jarrah forest communities on the upper slopes and ridge tops.

Changes with age since fire within the Taxandria swamp shrubland

Increased time since fire results in a continuum of increased vegetation density below 1 m and between 2–3 m until 24 years when the structure opens out to a more intermediate level (Fig. 4). Initially the structural change reflected by increased density was detected at heights of 2–3 m but after 14 years the density below 1 m also increased.

DISCUSSION

The jarrah forest is susceptible to wildfire during the six hotter months of the year in normal conditions, however during drought it is considered possible for wildfires to occur throughout the year (Wallace 1966). Under Aboriginal fire regimes, much of the jarrah forest is thought to have burnt at low intensity every three to four years (but see Miller et al. 2007), except for wet areas such as swamps that escaped fire for longer periods (Burrows et al. 1995; Wallace 1966; Ward & Sneeuwjagt 1999). Jarrah is considered well adapted to fire (Wallace 1966) in conjunction with the surrounding flora (Gardner 1957). The *Taxandria* swamps also show characteristics that suggest they too have evolved to cope with such regimes.

The immediate impact of a fire on the vegetation within a swamp is major, but short-term and often unburnt patches result in a mosaic of age classes (Abbott 2000; Burrows & Friend 1998). Within a month, the *Taxandria linearifolia* resprouts and vegetation density increases. Plant species richness peaks between five and 19 years after a fire but is highest between ten and 14. There is a 3–5 year peak in species richness occurring after fires in the wider jarrah forest communities (Bell & Koch 1980), which is twice as frequent as that of the swamps, and is thereby illustrating evolution for a lower frequency of fire in the swamps. This pattern of species richness is not restricted to the jarrah forest and occurs in coastal woodland in eastern Australia where richness peaks around five years after a fire (Fox 1988). Floristically, as well as being species rich, the swamps less than 14 years after a fire appear more diverse (although not quantified) in that they have non-dominant plant species exhibiting higher percentage cover than older swamps which are dominated by one or two species.

Species richness in *Taxandria* swamps declines 14 years after a fire and this decline may begin to plane after 25 years. Again this pattern has been observed in other areas, however elsewhere there is an increase in species richness in long unburnt sites (Fox 1988). This reduction in species richness may reflect the long history of Aboriginal burning and lightning-caused fires in the jarrah forest.

Swamps over 25 years of age are characterised by a few, large *Taxandria* shrubs with a canopy at least 5 m high. The vegetation returns to a more intermediate density similar to 5–14 years post-fire. Species richness is also low with older swamps dominated by *T. linearifolia* and *Lepidosperma tetraquetrum* while any other species present generally occur at very low levels.

The trajectory of succession within the swamp based on structural density (Fig. 4) reflects similar trajectories occurring in other ecosystems (Fox 1988). Such trajectories have been applied to small mammal community succession in those same areas and these show similar behaviour where the community exhibits a circuit before returning to similar compositions at intermediary ages (Fox 1990). The mammal community inhabiting the *T. linearifolia* swamps probably behave in a similar fashion with variation in abundance caused by the succession of their habitat (Hayward et al. 2005b; Hayward et al. 2007). It may be such habitat requirements are a response to both predator-avoidance in the dense vegetation (Hayward et al. 2005a) and dietary requirements (Hayward 2005) but the frequent and low intensity fire regimes adopted by the Noongar Aboriginal people of south-west Western Australia (Abbott 2000; Burrows *et al.* 1995; Ward *et al.* 2001; Ward and Sneeuwjagt 1999) were probably conducive to maintaining a mosaic of successional stages.

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Table 1

Factor scores for the vegetation structural factors used to differentiate age classes within *Taxandria linearifolia* swamps and the variance they explained. Variables explained by each factor are illustrated in bold.

Variable	Factor 1	Factor 2	Factor 3	Factor 4
Density at 10 cm	**0.870**	0.080	-0.023	0.097
Density at 30 cm	**0.934**	0.025	0.175	0.043
Density at 50 cm	**0.772**	-0.035	0.475	-0.010
Density at 1 m	0.333	0.016	**0.856**	0.061
Density at 1.5 m	0.046	-0.095	**0.877**	-0.116
Density at 2 m	-0.024	0.445	0.427	**-0.557**
Density at 3 m	0.076	**0.938**	-0.110	0.017
Density at 5 m	0.090	0.068	0.037	**0.943**
Variance explained	37.5%	20.2%	14.9%	10.3%

Table 2

Factor scores for the floristic factors used to differentiate age classes within *Taxandria linearifolia* swamps and the variance they explained. Variables explained by each factor are illustrated in bold.

Variable	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Agonis linearifolia	0.010	**0.800**	0.068	0.010	-0.046
Aotus cordifolia	-0.053	-0.075	-0.095	**0.653**	-0.187
Astartea fascicularis	**0.877**	0.037	-0.009	-0.047	-0.011
Boronia molloyiae	0.209	-0.419	0.031	-0.102	**0.559**
Dampiera hederacea	0.307	0.290	**0.629**	-0.203	0.041
Hypocalymna cordifolium	-0.160	0.056	-0.133	-0.051	**0.720**
Lepidosperma tetraquentrum	**-0.493**	0.392	0.114	-0.247	0.360
Thomasia paniculata	-0.237	-0.063	**0.719**	-0.081	-0.243
Thomasia pauciflora	0.021	0.117	**-0.496**	**-0.562**	-0.313
Xyris lacera	0.135	0.425	-0.245	**0.639**	-0.020
Variance explained	15.0%	13.7%	12.6%	10.7%	10.0%

Table 3

Factor scores for the other habitat factors used to differentiate age classes within *Taxandria linearifolia* swamps and the variance they explained. Variables explained by each factor are illustrated in bold.

Variable	Factor 1	Factor 2	Factor 3
Species richness	0.066	**-0.858**	-0.016
Leaf litter	**-0.719**	0.060	0.301
Stags	**0.651**	0.364	-0.034
Logs	-0.075	-0.083	**0.900**
Open water	0.160	**0.612**	-0.010
Bare earth	0.678	-0.022	0.242
Variance explained	22.9%	15.8%	13.3%

Table 4

Comparisons between the various age classes of the *Taxandria* swamp shrubland habitat types based on ANOVA. The individual comparisons using Scheffe's test are shown in Table .

Factor	$F_{5, 165}$	Probability
Structural factor 1 (SF1)	0.914	0.4736
Structural factor 2 (SF2)	6.491	< 0.0001
Structural factor 3 (SF3)	2.148	0.6230
Structural factor 4 (SF4)	21.098	< 0.0001
Floristics factor 1 (FF1)	1.453	0.2080
Floristics factor 2 (FF2)	2.509	0.0321
Floristics factor 3 (FF3)	3.345	0.0066
Floristics factor 4 (FF4)	0.385	0.8589
Floristics factor 5 (FF5)	8.597	< 0.0001
Other habitat factors 1 (OF1)	31.108	< 0.0001
Other habitat factors 2 (OF2)	6.962	< 0.0001
Other habitat factors 3 (OF3)	1.228	0.2718

Table 5

Identification of the factors used to differentiate between the *Taxandria* swamp shrubland habitat units. The factor that differentiated each habitat unit is presented along with the Scheffe's post-hoc test significance level. The factors used were structural (SF1, SF2, SF3, SF4), floristic (FF1, FF2) and other habitat variables (OF1, OF2). A cross (X) signifies there was no direct differentiation possible between habitat units and so plots of two factor scores were subsequently used (Fig. 3).

Habitat unit	Fresh	5–9 years old (y.o.)	10–14 y.o.	15–19 y.o.	20–24 y.o.	> 25 y.o.
Fresh	–					
5–9 year old	OF1 [%] OF2 [%]	–				
10–14 year old	SF2 * OF1 * OF 2 *	X	–			
15–19 year old	SF2 [%] FF5 [%] OF1 [%] OF2 [%]	SF4 [%] FF5 [%]	SF4 [%] FF5 [%]	–		
20–24 year old	SF2 [%] OF1 [%]	SF4 * OF1 [%]	OF1 *	FF5 *	–	
> 25 year old	SF4 [%] OF1 [%]	SF4 [%] OF1 [%]	SF4 [%] OF1 [%]	SF4 [%] FF5 [%] OF1 [%]	X	–

* significant at less than 0.05 level.
[%] significant at less than 0.01 level.