ORIGINAL ARTICLE

Evidence for the equal resilience of *Triodia* spp. (Poaceae), from different functional groups, to frequent fire dating back to the late Pleistocene

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Species with different regenerative responses to fire are hypothesised to coexist by utilising the different temporal and spatial niche opportunities created by the stochasticity of the fire regime. This is strongly supported by observations of instability of species' presence and abundance at the local scale while these are stable at the community scale. However, observations of species coexistence in fire-prone communities are limited to several decades only. To improve the robustness of this hypothesis, coalescent analysis, using chloroplast microsatellites, was undertaken on three sympatric species of *Triodia* from different functional groups in the fire-prone Kimberley region of Western Australia. The results inferred that

T. bitextura, an obligate resprouter, *Triodia* sp., an obligate seeder, and *T. epactia*, a facultative resprouter, had mean T_{mrca} values of 65k, 40k and 111k generations, respectively. Using a mutation rate of 3.2×10^{-5} and a generation time of 5 years gave T_{mrca} values of 436k, 203k and 556k years, respectively. These results provide evidence for the coexistence of these species to the same fire regime dating back to the late Pleistocene. It also demonstrates the long-term resilience of an obligate seeder, *Triodia* sp., in a frequently burnt environment at the community scale.

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Introduction

Plant functional groups are defined by a common set of physiological or phenological responses to environmental conditions or disturbances (Hooper and Vitousek, 1997). Applicable over a range of scales, the concept distinguishes annual from perennial, tree from herb or resprouter from obligate seeder, among many others. As such, using functional groups to classify plants provides a tractable means to study large-scale ecosystem processes (Ustin and Gamon, 2010). Plant functional groups defined by their regeneration strategies are hypothesised to differ in their resilience (*sensu* Holling, 1973) to the same fire regime. This is due to differential allocation of resources to vegetative or sexual reproduction, which determines the probability of persisting through the fire return interval (Verdu, 2000). If the time taken to return to reproductive maturity is not achieved before the next fire event, populations will decline and suffer localised extinctions (Bradstock *et al.*, 1996; Russell-Smith *et al.*, 2002). Slow-growing obligate seeding species, those that rely entirely on seed germination after fire for regeneration, are considered to be the most vulnerable to this scenario (Hoffmann, 1998) and localised reductions and extinctions have been observed (Russell-Smith *et al.*,

2002; Prior *et al.*, 2007). However, the temporal and spatial scale and the reasons for which this occurs differ across plant structural groups meaning there is no single fire frequency that favours all species in a community (Pausas and Lloret, 2007). Tree species that require decades to reach maturity will be far more vulnerable than grasses to subdecadal fire intervals (Genries *et al.*, 2009). The impact of the fire regime can therefore be species specific and variable across functional and structural groups. However, coexistence of both groups is widespread, with disturbance, particularly fire, hypothesised to mediate fluctuations in dominance of particular groups over time (Chesson, 2000; Clarke and Dorji, 2008).

The stable coexistence of species from different functional groups is possible owing to the covariance between environmental and competitive responses among species, which is known as the storage effect (Sears and Chesson, 2007). Empirical evidence for this has been shown across a range of fire-prone habitats on different continents for periods of up to several decades (Williams *et al.*, 2003; Andersen *et al.*, 2005; Thuiller *et al.*, 2007). Thuiller *et al.* (2007) showed that although presence and abundance of species was highly unstable at the local scale, it was stable at the meta-community scale. These results help resolve contradictions that arise in regard to the vulnerability of particular functional groups to fire, that is, obligate seeders vs obligate resprouter, depending on the spatial and temporal scale of the observation. Given global changes in fire regimes across the world due to climate change and changes in

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land-use practices (Beerling and Osborne 2006; Shlisky *et al.*, 2007), the ability to generalise and therefore predict long-term responses of functional groups to the fire regime is important for conservation-management practices. If the resilience of different functional groups in a community could be resolved over historical time periods, this would provide a much more robust analysis than studies spanning years or even decades.

Coalescence (Kingman, 1982) provides a technique for such an analysis, enabling the demography of a species to be inferred over times beyond that available from direct observation (see Kuhner, 2009 for a recent review). The ideal system to test the comparative historical resilience between plants from different functional groups would be in a region with high fire frequency using plants in which reproduction is initiated by fire.

The tropical savannas of northern Australia provide such a model system, as there are many plant species that rely on fire for regeneration and the average fire return interval is 5 years in lower-rainfall areas, increasing to biannual at lower latitudes, which have greater rainfall and therefore greater fuel accumulation (Felderhof and Gillieson, 2006). Taxa within *Triodia* provide ideal model species because they are reliant on fire for reproduction (Burbidge, 1943; Noble, 1989; Rice and Westoby, 1999) and encompass several functional groups, including obligate seeders (Casson and Fox, 1987), facultative resprouters and obligate resprouters (Wells, 1999). As with other species of obligate seeders, the resilience of obligate seedling *Triodia* spp. to short fire return intervals, as occurs in northern Australia, has been questioned (Rice and Westoby, 1999). However, as with all other predictions regarding the resilience of particular functional groups to particular fire regimes, the evidence is based on short-term observations. Here, I use coalescent analysis to determine the minimum time that three *Triodia* species, each from a different functional group, have persisted in the landscape where fire has been present for millennia.

Materials and methods

Site details and sampling

The study was carried out at Mornington Wildlife Sanctuary, in the south central Kimberley of northern Western Australia. The property, owned and managed by the Australian Wildlife Conservancy, covers 325 000 ha within the savanna biome of the wet/dry tropics. It receives 600–800 mm of rain per year, with 90% falling during the summer months: November–April (<http://www.bom.gov.au>). The landscape is dominated by the quartzite sandstone escarpments of the Proterozoic King Leopold Sandstone and low basaltic hills and valleys of the Carson Volcanics (Geol. Survey WA, 1:250 000 Geol. Series). Fires in the area are both temporally and spatially stochastic at a local scale, owing to heterogeneity of stand structure, which is dependent on fuel loads, in turn being dependent on preceding rainfall and ignition from lightning strikes (Allan and Southgate, 2002). This is illustrated by fire scar mapping from remote-sensing data (Supplementary Appendix).

Leaf samples were collected from 16 individuals from each of the three species *T. epactia*, *T. bitextura* (17°30.627'S, 126°6.514'E) and *Triodia* sp., 6 km away at

Figure 1 Representation of sequential sampling method. The black dots represent individual plants and leaf samples were collected from those with white dots. The sequence is counted as the number of individuals between samples: 0,1,1,1,1,4,4 etc. See text for further details.

(17°32.325'S, 126°9.452'E). *T. epactia* is a facultative resprouter with strong regrowth after fire plus some seed germination, *T. bitextura* is an obligate resprouter that has strong regrowth after fire, produces ramets and has virtually no seed production, and *Triodia* sp. is an obligate seeder in which all adults die during fire with total regeneration from the seed bank (unpublished data). Seeds are observed to be dispersed by both wind and surface water during rain events in the wet season.

Plants were sampled along a transect of exponentially increasing inter-plant distances in an attempt to capture potentially autocorrelated samples for which the scale was unknown. Plants were sampled, in the first half of the transect, not by fixed distances, but by the number of individuals between those sampled, following the sequence; 0, 1, 1, 1, 1, 4, 4, 4, 8, 8, 16, 16, with the numbers being the number of plants between those sampled (Figure 1). This was done because plants grow in a labyrinthine pattern with bare ground separating individual 'hummocks' at varying distances (Figure 4). This means any potential spatial autocorrelation would not be based on regular distances, but by the number of individuals that separate those that are sampled. Sampling in the latter half of the transect used predetermined fixed distances at 50, 50, 100 and 100 m because many individuals are included at this scale. Total distances of each transect were therefore slightly different, being 372 m for *T. bitextura*, 366 m for *T. epactia* and 383 m for *Triodia* sp.

Leaf tissue samples, approximately 3 cm long, were stored in Eppendorf tubes in a refrigerator until analysis, whereupon samples were ground in liquid nitrogen and total DNA extracted using DNeasy Plant Mini Kit (Qiagen, Valencia, CA, USA) following the manufacturer's protocol. Chloroplast microsatellites were chosen to determine demographic histories as they are non-recombining, haploid and effectively uni-parentally inherited (Birky, 1995), providing direct evidence of a lineage. The availability of 'universal primers' for highly conserved primer sites on either side of polymorphic repeat regions has made such analyses possible (Provan *et al.*, 2004; McGrath *et al.*, 2006).

Microsatellites

A total of 10 non-coding microsatellites were tested from those developed by McGrath *et al.* (2006) and Provan *et al.* (2004), from which only four, *trnK*, *atpI/atpH*, *atpB/rbcL* and *TeaSSR4* (23S-5S internal transcribed spacer), were able to be amplified. Only the last three had polymorphic alleles and were used in the analysis. PCR amplification was performed with the following parameters for *atpI* and *atpB*: initial denaturation of 72 °C for 3 min followed by 35 cycles of 94 °C for 1 min, 56 °C for 1 min and 72 °C for 1 min with a final extension of 72 °C for 5 min. The parameters for *Tea4* were 95 °C for 1 min with 35 cycles of 95 °C for 1 min, 60 °C for 1 min

and 72 °C for 1 min with a final extension of 72 °C for 10 min. Total genomic samples were amplified in a 15- μ l PCR reaction containing 1 μ l genomic DNA, 1.5 μ l 10 $\times$ Gold buffer, 2.5 mM MgCl₂, 0.5 U Ampli Taq Gold, 10 μ M fluorescence-labelled forward primer and 10 μ M reverse primer (Applied Biosystems, Carlsbad, CA, USA) and 0.2 mM deoxynucleotide triphosphate (dNTPs). Fragments were analysed with ABI PRISM 3100 Genetic Analyser (Applied Biosystems) using LIZ 500 size standard with sizes determined with Genemapper software. Mean haplotype diversity (Schneider *et al.*, 1997) and expected variance (Gordon 1997) were determined for each species and the spatial autocorrelation of samples tested with GENALEX v.6 (Peakall and Smouse, 2001).

Analysis

Genealogies of the samples were inferred through coalescent analysis (Kingman, 1982) using the application BATWING v.1.03 (Wilson *et al.*, 2003). The method uses a Bayesian paradigm in which the posterior distribution of θ , being the conditional probability of the prior given the data (haplotypes), is obtained, where $\theta = 2N_e\mu$ (N_e being the effective population size and μ the mutation rate). The number of steps taken to reach coalescence depends on the variability in the data and is measured as T_{mrca} . The application uses linked multi-locus haploid data in a step-wise mutation model, which, in the absence of recombination or selection, can be used to derive a genealogical tree (Wilson *et al.*, 2003). Chloroplasts are not subject to recombination, being passed predominantly through the maternal line in angiosperms (Birky, 1995), and because microsatellites are deemed to be non-coding they are not subject to the same selective pressures as functional genes (Provan *et al.*, 2001). The assigned previous distribution for θ was uniform on the interval (0,100), giving equal probability between these values. Given an upper estimate of chloroplast μ at 3.2×10^{-5} (Provan *et al.*, 1999), N_e can range from 0 to over 1.5 million, increasing with lower estimates of μ , allowing a diffuse prior. Numerous trials were conducted to assess the influence of different values of θ and the number of chain runs in the MCMC resulting in the above distribution for θ and 10 000 runs with the first 200 discarded. Determination of satisfactory convergence of the chain and post-processing was undertaken with the package BOA (Smith, 2005) in TIBCO Spotfire S+ 8.1 (<http://spotfire.tibco.com/iful/>). Posterior distributions were derived for θ and T_{mrca} in coalescent units. A lower bound for T_{mrca} in generations $T_{(gen)}$ was derived using μ above and the mean of the posterior of θ , where $T_{(gen)} = T_{mrca} \times N_e$. Generation times for plants in fire-prone environments are correlated with the fire frequency (Bond and van Wilgen, 1996), in this case 5 years (Williams *et al.*, 2002; Felderhof and Gillieson, 2006), which was used to derive T_{mrca} in years by simply multiplying $T_{(gen)}$ by 5. The justification for this methodology was that a fire event either (a) results in a complete turnover of individuals in the population (that is, *Triodia* sp.) or (b) resprouting and regeneration by ramets also initiates a periodic somatic mutation event equivalent to that which occurs in meiosis. Consensus trees were produced in Phylip (Felsenstein, 1989) and drawn in FigTree v1.2 (Figure 2) to show

Figure 2 Consensus trees for *T. bitextura* (top), *T. epactia* (middle) and *Triodia* sp. (bottom) scaled to equivalent T_{mrca} . Branch lengths indicate the comparative diversity between adjacent branch tips, with longer branches requiring more mutation steps before they coalesce. Branch tips are the haplotypes of the sampled individuals. Scale bar = 0.1 mutation steps.

Table 1 The number of alleles per locus and size ranges in base pairs

Locus	No. of alleles	Size range, bp
atpI/atpH	5	74–80
atpB/rbcL	5	144–148
23S-5S ITS	4	196–199

the topology common to all trees produced in the analysis.

Results

The size of the microsatellite fragments (Table 1) closely matched those of other grass species reported in Provan *et al.* (2004) and McGrath *et al.* (2006) and all species had similar, low levels of mean haplotype diversity and similar expected variance (*Triodia* sp. $H = 0.443$, $V = 0.735$), *T. bitextura* ($H = 0.482$, $V = 0.641$) and *T. epactia* ($H = 0.438$, $V = 0.715$). No spatial autocorrelation was detected among the samples of any species.

The growth signatures of the coalescent trees (Figure 2) suggest that each of the three samples has had a stable population size since T_{mrca} (see Kuhner, 2009). However, their genealogies differ in the number of coalescent events, shown by the difference in tree lengths and values of θ and T_{mrca} (Figure 2, Table 2). *Triodia* sp., having the lowest values of θ and T_{mrca} , is both the comparatively smallest and youngest population (Figure 3). *T. bitextura*, with the largest value of θ and

Table 2 Posterior mean, median and 95% probability density interval for theta (θ) and T_{mrca} in coalescent units (T) and generations ($T_{\text{(gen)}}$), for *T. bitextura* (obligate resprouter), *Triodia* sp. (obligate seeder) and *T. epactia* (facultative resprouter) using a constant population size model with a uniform θ prior of (0,100) (see text for details)

Species	Mean	Median	95% Probability density interval
<i>T. bitextura</i>			
θ	4.20	3.76	(1.56, 9.4)
T	1.33	1.15	(0.45, 3.27)
$T_{\text{(gen)}}$	65 625		(10 969, 480 281)
<i>Triodia</i> sp.			
θ	2	1.76	(0.6, 4.76)
T	1.30	1.13	(0.42, 3.20)
$T_{\text{(gen)}}$	40 625		(3938, 238 000)
<i>T. epactia</i>			
θ	3.28	2.96	(1.22, 7.25)
T	2.17	1.94	(0.75, 4.82)
$T_{\text{(gen)}}$	111 212		(14 297, 546 016)

an equally small T_{mrca} indicates a larger population of equally closely related individuals, while *T. epactia* with an intermediate θ value and the longest T_{mrca} indicates a comparatively intermediate-sized population with the greatest diversity among individuals of the population. Despite *T. bitextura* and *Triodia* sp. having similar values for T_{mrca} , differences in θ between them result in $T_{\text{(gen)}}$ being twice as long for *T. bitextura*. Given a generation time of 5 years, based on the mean fire frequency in this landscape, mean T_{mrca} values in years for *Triodia* sp., *T. bitextura* and *T. epactia* are 203, 328 and 556k years, respectively.

Discussion

The study shows that each of the three species, regardless of functional group, have existed in this environment for millennia. The shortest possible T_{mrca} based on the minimum range of the 95% probability density interval (PDI), is approximately 19k years for *Triodia* sp. given a 5-year generation time. The presence of these fire-adapted species, which are totally (*Triodia* sp., *T. epactia*) or partially (*T. bitextura*) reliant on fire to initiate regeneration, reflects the fact that fire is the most common disturbance in this environment and has been a prominent evolutionary force since the Tertiary (Kershaw *et al.*, 2002). The fire history across northern Australia, derived from marine and terrestrial core samples (Moss and Kershaw, 2000; Kershaw *et al.*, 2003), shows an increase in fire activity and fire-tolerant species at approximately 300k years before present (bp) and a subsequent decrease in *Eucalyptus* and increase in *Poaceae* at 185k years bp (Kershaw *et al.*, 2003). While the mean T_{mrca} of *Triodia* sp., at 203k years, is similar to this date, *T. bitextura* and *T. epactia*, with a mean T_{mrca} of 328k and 556k years, respectively, may have been early colonisers into this environment. However, given the large 95% probability density intervals (Table 2), it is only possible to infer with any certainty that they have all been present, and therefore successful species in this environment, for a significant number of generations.

Figure 3 Estimated posterior density plots of Theta and time to most recent common ancestor (T_{mrca}) for *T. bitextura* (solid line), *Triodia* sp. (dotted line) and *T. epactia* (dashed line). *T. bitextura* and *Triodia* sp. are nearly superimposed over each other in T_{mrca} . See text for definitions of θ and T_{mrca} .

Stable population size during T_{mrca} inferred by the structure of the three genealogical trees (Figure 2), also suggests that *T. epactia*, and possibly *Triodia* sp., have been geographically stable during this time. If either population had expanded or reduced their range size during this time, the genealogical trees would infer population growth or decline, owing to serial founder or extinction events at the forward and trailing edge of the species range (Excoffier *et al.*, 2009; McNerny *et al.*, 2009). This was not detected despite *T. epactia* being sampled at the extreme northern limit of its range and *Triodia* sp. toward the southern edge of its, comparatively smaller, range. It is not possible to determine the geographical stability of *T. bitextura* during T_{mrca} because it was not sampled near the edge of its range. The apparent range stability and therefore potential coexistence of *T. epactia* and *Triodia* sp., over an area of approx. 2500 km², for thousands of years indicates that both species have been

Figure 4 (a) Typical hummock structure common to many *Triodia* spp. (plants are approximately 1 m in height and growing on a rock pavement) and (b) the labyrinthine stand structure, seen from the air, showing considerable bare ground between individual plants, in this case growing on sand.

equally resilient to the same fire regime. It is likely that these two species have been in sympatry with *T. bitextura* for some considerable time also because the expected colonisation rate of this facultative resprouter over such a large area would not be fast.

Coexistence of species with different regeneration responses to fire is hypothesised to be possible because each species utilises different temporal and spatial niche opportunities created by the stochastic nature of the fire regime. The empirical (Thuiller *et al.*, 2007) and theoretical (Miller and Chesson, 2009) evidence to support this is corroborated by modelling that shows species are able to utilise a range of overlapping fire return intervals and scales (Groeneveld *et al.*, 2002). Competition between species limits the potential niche of each, resulting in a single, narrow, realised niche in which all species coexist. Although this has been observed over decadal time scales, this study provides the first evidence that long-term coexistence of these species, from different functional groups, has occurred at least as far back as the late Pleistocene. This negates assumptions that obligate seeding *Triodia* spp. may be less resilient in northern Australia than resprouting species. While previous research on slow-growing, obligate-seeding *Triodia* spp. suggested that they would be unlikely to reach a sustainable reproductive output within the short fire return intervals experienced in northern Australia (Craig 1992), this study indicates that obligate seeders can persist in this environment. The obligate seeder *Triodia* sp. has persisted in this landscape for millennia, possibly owing to its relatively rapid life history and potentially because of stochasticity in the fire regime. *Triodia* sp. germinates quickly during the first post fire rains and

can set seed within a few months of germination (Armstrong, 2011). Reproductive output increases over subsequent seasons, ensuring that a viable seed bank is produced before the mean fire return interval. Such rapid regeneration has been unknown in *Triodia* spp. until recently (Armstrong, 2008). Variation in the mean fire frequency and stochasticity of fire behaviour could ensure suitable patches are always present within the landscape for the meta-population to survive. Owing to the labyrinthine structure of *Triodia* spp. stands (Figure 4), in which individual hummocks are separated by bare ground, fires will not spread through the stand unless wind speeds of over 12 km per h are attained (Burrows *et al.*, 1991). Fire behaviour is therefore strongly correlated with weather patterns at all scales.

Given the stochasticity in the spatial arrangement of fires in the landscape (see Felderhof, 2007: the fire patchiness paradigm and fire scar maps, Supplementary Appendix), resilience of an obligate seeder, such as *Triodia* sp., also requires the ability to disperse between suitable patches (Tilman, 2004). This is not required by *T. epactia* or *T. bitextura*, which can recolonise a burnt patch through resprouting. Despite evidence that shows that the majority of seed produced by *Triodia basedowii* falls close to the mother plant (Westoby *et al.*, 1988), the vast quantity of tiny seeds produced by *Triodia* sp. must ensure that at least some are dispersed away from the source, most probably by wind and water during rain events in the monsoon.

While it is true that no single fire frequency will favour all species in a community (Pausas and Lloret 2007), it must equally be true that there is a mean frequency, about which there is variation, which enables coexistence. Indeed, even where species from different structural groups coexist, such as *Acacia* trees and *Triodia* grasses, the minor perturbations observed at population boundaries, induced by fire, over decadal time scales (Nicholas *et al.*, 2007; Bowman *et al.*, 2008) probably have no long-lasting effect at the community level over much longer time scales. Single or multiple fire events that favour one species may, given enough time, become irrelevant at the community scale as other events favour different species. This study has shown that it is important to consider a wide range of temporal scales when considering the relative resilience of plants from different functional groups to fire. Although there are documented cases of localised extinctions of individual plant species to radically altered fire regimes (Russell-Smith *et al.*, 2002), these may represent extreme events and should not be used to generalise about the resilience of particular functional groups. This has not been possible at a global scale (Pausas *et al.*, 2004) and, as this study shows, regional effects, for example, a stable climate, may strongly influence community structure over very long time scales. However, it is important to determine the resilience of regional plant communities to fire, given regimes are changing globally across a range of scales owing to changes in land-use practices (Krawchuk *et al.*, 2009) and altered precipitation patterns both globally (Girardin *et al.*, 2009) and regionally (Hoffmann *et al.*, 2002).

Conflict of interest

The author declares no conflict of interest.

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