CONCEPTS, CHARACTERISTICS, COMPETITION: TOOLS IN THE SEARCH FOR SUSTAINABLE FIRE REGIMES

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Abstract
Fire ecology researchers risk bombarding managers with a 'blizzard of detail'. Over the past decade, efforts to synthesize information from ecological research into management guidelines have been made; in particular, ecologists have sought to provide guidance as to fire frequencies compatible with retention of species complements in different vegetation types. This paper takes a step back, and uses some of the ecological concepts and models which underpin understanding of the role of fire in fire-prone ecosystems to explore issues around appropriate fire regimes for biodiversity conservation. Concepts include disturbance, succession, plant species vital characteristics, interspecific competition, landscape productivity and patch dynamics. Ideas are illustrated through discussion of the dynamics of a subcoastal grassy woodland, a shrub/grass wet sclerophyll forest, and coastal heath.

Introduction
The by-line for this conference is "translating science into practice." However the science of fire ecology advances not through Noble-prize-winning leaps, but incrementally through many painstaking studies that range across a multitude of species, ecosystems, and aspects of fire. How can this wealth of information be transmuted from a confusing 'blizzard of detail' into a form which managers can use?

I believe there is value in explicitly presenting and discussing ecological concepts and models which underpin scientific understanding of the dynamics of fire-prone ecosystems across the world. This exercise can assist scientists to produce sound management recommendations; help scientists, managers and advocates to understand the considerable differences between vegetation types and regions; and assist stakeholders to find common ground where conflict currently exists. Of course, concepts and models are "abstractions of reality, caricatures" (Gill and Bradstock 1995:311), and their ability to describe what happens in the real world is necessarily limited. Still, they provide frameworks for understanding, and thus have the potential to contribute considerably to the search for sustainable fire regimes.

In this paper I use a series of ecological concepts to explore issues around the question of appropriate fire regimes for biodiversity conservation. These thoughts represent my understanding after eight years of reading, discussing, researching and writing about fire frequency in shrubby and grassy ecosystems in south-east Queensland and NSW (Watson 2001, 2005, Watson and Wardell-Johnson 2004). They are presented as a stimulus to discussion and research and of course are amenable to change and development. One aim of the paper is to suggest ways to build on recent work in the NSW Department of Environment and Conservation (DEC) on the development of fire regime guidelines (Bradstock and Kenny 2003, Kenny *et al.* 2004).

Ecological concepts and principles which underlie current understanding of fire regimes include disturbance, succession, plant species vital attributes, interspecific competition, landscape productivity and patch dynamics.

Disturbance, succession and a paradigm shift
Fire is a **disturbance**. A disturbance can be defined as "any relatively discrete event in time that removes organisms and opens up space which can be colonised by individuals of the same or different species" (Begon *et al.* 1990). The concept encompasses recurring discrete events such as storms, floods and fires, as well as on-going processes like grazing. Disturbance may stem from natural phenomena or human activities (Hobbs and Huenneke 1992), and is ubiquitous throughout the world's ecosystems (Sousa 1984).

Succession follows disturbance. This concept has been of interest to ecologists since Clements outlined what is now called 'classical succession' in 1916. In classical succession "following a disturbance, several assemblages of species progressively occupy a site, each giving way to its successor until a community finally develops which is able to reproduce itself indefinitely" (Noble and Slatyer 1980:5). Implicit in this model is the idea that only the final, 'climax' community is in equilibrium with the prevailing environment.

A popular metaphor for this **equilibrium paradigm** is ‘the balance of nature’. Conservation practice aligned with this model focuses on objects rather than processes, concentrates on removing the natural world from human influence, and believes that desirable features will be maintained if nature is left to take its course (Pickett *et al.* 1992). Fire does not sit easily in the ‘balance of nature’ approach, which influenced attitudes to burning, both in Australia and elsewhere, for many years. For example, forester C.E. Lane-Poole argued to the Royal Commission following the 1939 fires in Victoria for total fire exclusion on the grounds that this would enable natural succession to proceed resulting in a less flammable forest (Griffiths, 2002).

Over recent decades, however, a paradigm shift has been underway. Drivers include the realisation that multiple states are possible within the one community (Westoby *et al.* 1989), as are multiple successional pathways (Connell and Slatyer 1977). Most importantly from a conservation perspective, it has increasingly been recognised that periodic disturbance is often essential to maintain diversity, allowing species which might otherwise have been displaced to continue to occur in a community (Connell 1978).

This **non-equilibrium paradigm** can be encapsulated by the phrase ‘the flux of nature’. **Scale** is important in this paradigm: equilibrium at a landscape scale may be the product of a distribution of **states** or **patches** in flux (Wu and Loucks 1995). Implications include a legitimate – or even vital – role for people in ecosystem management, and a focus on the conservation of processes rather than objects. This does *not*, of course, imply that all human-generated change is okay; it does mean human beings must take responsibility for maintaining the integrity of ecosystem processes (Pickett *et al.* 1992, Partridge 2005). Fire fits much more comfortably into the non-equilibrium paradigm, where it takes its place as a process integral to many of the world’s ecosystems.

The concepts of disturbance and succession are basic to the science of ecology; they could even be considered too basic to rate a mention. However shifts in thinking over recent decades have not always made their way into the public arena. Adherence to the idea that fire is an undesirable impediment to the natural process of succession may underlie the attitudes of some people, including some sincere conservationists, to fire.

Theory into thresholds

The non-equilibrium paradigm forms the basis for a number of theories and models which have been used to inform an understanding of fire regimes in Australia. These include the **vital attributes model** of Noble and Slatyer (1980). This scheme employs a small number of life history characteristics of plant species to predict successional pathways. It can also be used to define disturbance frequency domains compatible with maintenance of particular suites of species. This model has recently been used to develop fire management guidelines for broad vegetation types in NSW (Kenny *et al.* 2004), and is also used in Victoria (Friend *et al.* 2003). Here is one way to present at least some of the ‘blizzard of detail’ in a manager-friendly form.

The basic idea is that, to keep all species in a community, fire intervals should vary within an upper and a lower threshold. Lower thresholds are set to allow all species vulnerable to frequent fire to reach reproductive maturity, while upper thresholds are determined by the longevity of species vulnerable to lack of burning. ‘Vital attributes’ are used to group species into functional types whose populations have similar methods of persistence and re-establishment after fire (Noble and Slatyer 1980, Keith *et al.* 2002b). The vulnerability of each group, and of species within sensitive groups, can be assessed through consideration of species life history characteristics.

Functional types most sensitive to **short interfire intervals** (high fire frequency) contain obligate seeder species whose seed reserves are exhausted by disturbance (obligate seeder species are killed by fire and rely on regeneration from seed). Populations of these species are liable to local extinction if the interval between fires is shorter than their primary juvenile period (Noble and Slatyer 1980), the time from seed germination to reproductively mature adult. The minimum interfire interval to retain all species in a particular vegetation type (lower threshold) therefore needs to accommodate the taxon in this category with the longest juvenile period (DEC 2002).

Species whose establishment is keyed to fire (Noble and Slatyer call these ‘I species’) are highly sensitive to **long interfire intervals** (infrequent fire): they are liable to local extinction if fire does not occur within the lifespan of established plants and/or seedbanks (Noble and Slatyer 1980). The maximum interval (upper threshold) therefore

needs to accommodate the taxon in this category with the shortest lifespan, seedbank included (DEC 2002, Bradstock and Kenny 2003).

Data on plant life history attributes relevant to setting **lower thresholds** – regeneration modes and juvenile periods – are reasonably easy to obtain. Predictions of shrub abundance based on these vital attributes have recently been tested through a field study of woodland vegetation in areas with known fire histories, and were supported (Watson 2005). It should be noted that when thresholds are determined for a very broad geographic area, as is the case in the DEC guidelines for the state of NSW (Kenny *et al.* 2004), lower thresholds may be set by species which are not found in particular local areas, and thus may be higher than if local species only were considered.

Data relevant to setting **upper thresholds** – longevity of adults and seeds – are much less readily available. Kenny *et al.* (2004) note the lack of quantitative data on these attributes, and point out that as a result, upper thresholds in the NSW guidelines are "largely based on assumptions and generalisations" and are therefore surrounded by "considerable uncertainty" (Kenny *et al.* 2004:31). Work on these variables is an important task for the future. Additionally, in determining upper thresholds for NSW vegetation types, "any data considered dubious was excluded from guideline calculations" (Kenny *et al.* 2004:25). This included estimates in forms such as "life span possibly 20-30 years." Where a range of figures for lifespan was available, the *highest* figure was used (Kenny *et al.* 2004:26). Decision rules have therefore tended to set upper thresholds higher, rather than lower. It could be argued that application of the precautionary principle in relation to species liable to local extinction through lack of fire would imply that decision rules should lower, rather than raise, thresholds at this end of the interval domain.

It can also be argued that upper thresholds might be better set somewhat lower than lifespan + seedbank longevity (y) of species liable to be lost from a community if fire is insufficiently frequent. West Australians Burrows and Abbott (2003:446) suggest $0.75y$ may be more appropriate. Population decline, both above and below ground, may occur over a long period prior to the point of local extinction (Auld 1987). Flowering may peak in the years following the juvenile period: McFarland (1990) found flowering and seeding in south-east Queensland's wallum heath peaked at four to eight years after a burn, and dropped markedly by 11 years post-fire. A species may therefore still occur in the landscape, but its fecundity might be greatly reduced in later post-fire years (Auld and Myerscough 1986).

Finally, the potential for one or a small number of species to dominate under extended interfire intervals, and related competitive interactions, may mean that upper thresholds need to be lower than an assessment based solely on life history characteristics would suggest. This issue is explored in the next section.

Competition and productivity

The effect of dominant heathland shrubs, such as *Banksia ericifolia* and *Allocasuarina distyla*, on other species has been recognised in Sydney's sandstone country (Keith and Bradstock 1994, Tozer and Bradstock 2002). When life history characteristics alone are considered, a feasible fire frequency for the conservation of both these dominant obligate seeders and understorey species appears to be 15-30 years. However at this fire frequency, the dominant species form high-density thickets which reduce the survival and fecundity of species in the understorey, an effect which carries through to the next post-fire generation. Similar dynamics have been observed in other Australian heath communities (Specht and Specht 1989, Bond and Ladd 2001) and in South Africa's heathy fynbos (Bond 1980, Cowling and Gxaba 1990, Vlok and Yeaton 2000). An understanding of this dynamic has highlighted the need to include in heathland fire regimes some intervals only slightly above the juvenile period of the dominant species, thus reducing overstorey density for a period sufficient to allow understorey species to build up population numbers before again being overshadowed. This need is reflected in fire frequency recommendations in Bradstock *et al.* (1995).

The effect on understorey vegetation may be particularly profound where dominant shrubs resprout (Bond and Ladd 2001). Unlike the Sydney obligate seeder heath dominants, dominant resprouters will continue to exert competitive pressure immediately after a fire by drawing on soil resources, and once their cover is re-established, on light resources too. For example in the grassy woodlands of Western Sydney's Cumberland Plain, the prickly shrub *Bursaria spinosa* forms dense thickets which can dominate the landscape where fire has been excluded for several decades (Watson 2005). After a burn, this shrub resprouts and grows rapidly. Other shrub species in this vegetation type, particularly obligate seeders, are less abundant in Bursaria-dominated landscapes than in sites which have burnt once or twice a decade, an outcome which probably reflects competitive pressure from Bursaria. Ground layer species are also affected. Thus the strategy recommended to provide relief for competitively inferior species in heaths – inserting one

short interval amongst longer ones (Keith *et al.* 2002b) – is unlikely to work in this community. Upper thresholds need to be sufficiently low to allow for the moderately frequent fires that will let Bursaria thickets, obligate seeder shrubs and a diverse ground layer of native grasses and herbs co-exist long-term.

In Cumberland Plain Woodland, Bursaria – and some introduced shrubs such as African Olive (von Richter *et al.* 2005) – have the advantage of being able to recruit between fires. This characteristic differentiates them from almost all other shrubs in this community, which like most sclerophyllous shrub species, recruit almost exclusively after a fire (Purdie and Slatyer 1976, Cowling *et al.* 1990, Keith *et al.* 2002a). The vital attributes model explicitly identifies species able to recruit between fires – Noble and Slatyer call them 'T species'– and their propensity to dominate in the absence of disturbance is also explicitly noted (Noble and Slatyer 1980). However to date little emphasis has been placed on the role of T species when determining fire frequency guidelines.

Currently, the vital attributes model is concerned with species presence or absence, not with issues of abundance or dominance. Noble and Slatyer (1980:19) recognise this limitation, and suggest that "to account for relative density… and other interactions, a more quantitative description of one or more vital attributes may be required." For example species could theoretically be ranked, Noble and Slatyer (1980) point out, in terms of their ability to recruit in the presence of established adults. A fourth vital attribute related to growth rate and size at maturity could be added.

The importance of competition between plant species, and thus the importance of disturbance to disrupt competitive exclusion, is likely to vary with **landscape productivity**. A second non-equilibrium paradigm offshoot, the **dynamic equilibrium model** (Huston 1979, 2003, 2004), considers the interaction of productivity and disturbance in mediating species diversity. In harsh environments where productivity is low, interspecific competition is unlikely to be great. Here, a-biotic factors such as low rainfall, heavy frosts and infertile soils limit the number of plant species able to grow, and also limit their growth rates. The need for disturbance to reduce competitive superiority is therefore minimal. In fact, a high disturbance frequency is predicted to reduce diversity in these ecosystems, as organisms will be unable to grow fast enough to recover between disturbances. In highly productive, resource-rich environments, however, competition is likely to be much more intense, as many species can grow in these areas, and they grow quickly. Here, diversity is predicted to decline where disturbance frequency is low, as some species will outcompete others, excluding them from the community.

Landscape productivity, as defined by plant biomass as an example, is likely to increase with rainfall, temperature, season of rainfall – where rainfall and warm temperatures coincide, there is a greater potential for plant growth – and soil fertility (clay soils are often more fertile than sandy soils, however they also tend to support more herbaceous, and fewer shrub, species; Specht 1970, Prober 1996, Clarke 2003). Relatively frequent fire may thus be more appropriate in wet, warm, productive fire-prone systems than in those whose productivity is limited by poor soils, low rainfall or a short growing season.

A second reason why shorter interfire intervals may be appropriate in more productive systems is because shrubs may reach life history milestones more rapidly. Juvenile periods of obligate seeder shrubs may be shorter where resources are more readily available. On the New England Tablelands, where the growing season is constrained by severe frosts, shrub juvenile periods can be several years longer than those of the same species in coastal areas (Knox and Clarke 2004). Senescence, and/or overtopping of low growing shrub species, may also occur more rapidly in more productive areas (Specht and Specht 1989). Productive areas may potentially host a larger pool of woody 'T species', adapted to recruitment in gaps rather than being cued to fire, particularly where landscapes contain a mosaic of fire-prone and rainforest vegetation (Campbell and Clarke 2006).

This discussion brings us back to the concept of succession. South African fire ecologists Bond *et al.* (2003, 2005) divide global vegetation types into three categories:

- **Climate-limited systems**. These communities are not prone to either major structural change, nor to succeeding to another vegetation type in the absence of fire, although fire frequency may mediate species composition to some extent. In South Africa, these communities occur in arid environments, and also in areas nearer the coast where rainfall is moderate but occurs in winter.
- **Climate-limited but fire modified systems**. These vegetation types do not succeed to another vegetation type in the absence of fire, but their structure may alter from grassy to shrubby. The Cumberland Plain Woodland described above fits into this category.

- **Fire-limited**. These vegetation types will succeed to a different community in the absence of fire. In South Africa, these communities occur in higher rainfall areas, and include both savannas and heath.

Climate-limited but fire-modified systems can occur in at least two 'states', for example grassy woodland and Bursaria-dominated shrub thicket woodland on the Cumberland Plain (Watson 2005). Fire-limited vegetation types could also be said to be able to exist in different states, although the differences between them are so great that they are rarely thought about in this way. For example, in north Queensland, *Eucalyptus grandis* grassy wet sclerophyll forest is succeeding to rainforest, probably due to a reduction in fire frequency and/or intensity (Unwin 1989, Harrington and Sanderson 1994). However rainforest and grassy wet forest are not generally considered as different states of a single vegetation type, but rather as two different types of vegetation.

Patch dynamics

These examples illustrate how dynamic vegetation can be in relation to fire. In some productive landscapes, variation in interfire intervals within broad thresholds, that is variation in *time*, may not be sufficient to maintain all ecosystem elements. Variation in *space* may also be needed to ensure all possible states, and the plants and animals they support, are able to persist in the landscape. Fire can mediate a landscape of different patches, whose location may change over time.

For example, recent studies in north-eastern NSW indicate that some forests in high rainfall areas on moderately fertile soils can exist in more than one 'state'. Relatively frequent fire – at intervals between 1 and 5 years – is associated with open landscapes in which a diverse flora of tussock grasses, forbs and some shrubs thrives (Stewart 1999, Tasker 2002). This regime provides habitat for many invertebrate species (York 1999, York 2000, Andrew *et al.* 2000, Bickel and Tasker 2004), and for a number of rare small mammals (Tasker and Dickman 2004). Nearby areas which have remained unburnt for periods over 15 or 20 years support higher densities of some shrub and non-eucalypt tree species, particularly those able to recruit between fires (Birk and Bridges 1989, York 1999, Henderson and Keith 2002). Litter levels are higher in these multi-layered areas (Birk and Bridges 1989), which provide habitat for an equally diverse, but substantially different, array of invertebrates and small mammals to that found in frequently burnt areas (Catling *et al.* 2000, York 2000, Tasker and Dickman 2004).

Grassy wet sclerophyll forests in the Northern Rivers region can thus exist in at least two 'states.' The dynamic nature of these forests suggests they would fall into either Bond's 'climate limited but fire modified' or his 'fire limited' category (Bond *et al.* 2003, 2005). Burning at short intervals limits the extent to which vegetation progresses down the path towards shrubbiness and high litter levels; whether successional change in the absence of fire would result in a transition to rainforest remains to be determined, and could well vary with rainfall, slope, aspect, geology and proximity to existing rainforest patches.

The existence of two understorey 'states' supporting diverse but distinct suites of species in the grassy wet forests of Northern NSW suggests the need for a fire regime which supports the existence of each state somewhere in the landscape. In some places, fire needs to happen often enough to maintain open forest environments rich in grasses and herbs, where early-successional animal species can thrive. Other places need to support good-sized patches of thicker vegetation where mesophyll shrubs and late-successional fauna can flourish. For some fauna species, the juxtaposition of grassy and shrubby patches may be vital (Christensen 1998). The vulnerable Palma Wallaby (*Macropus parma*) is an example (Maynes 1977).

Conclusion

The concept of 'states' provides options for the creation and maintenance of habitat across space as well as time. It can reduce conflict between those who see the value in particular states (such as grassy or shrubby vegetation in sub-tropical wet sclerophyll forests), by pointing out the value of each and the need for both. Of course, it also raises questions as to the proportion of each state that may be desirable in the landscape, the scale of mosaics, the relationship between the 'visible mosaic' of times-since-fire and the 'invisible mosaic' of fire frequency, the links between topography, landscape features and states, and the impact of fragmentation and climate change on these factors. These questions are beyond the scope of this paper, and some are probably beyond the scope of our current understanding; they represent fertile ground for research and discussion in the future.

Acceptance of the need for different fire frequency-mediated states in some vegetation types may also require a somewhat different approach to the determination and presentation of fire frequency thresholds. Two or even three sets of thresholds may be needed to define regimes predicted to characterise different states. It may be appropriate to consider the vital attribute-related requirements of some species and/or species groups, but not others, when proposing guidelines for particular states. The role of competition may deserve more explicit consideration in these labile, productive vegetation types than is necessary in 'climate limited' ecosystems.

The 'blizzard of detail' generated by the large number of studies addressing aspects of the relationship between fire, vegetation and fauna can be ordered to some extent when one recognises that fire regimes vary considerably between different vegetation formations (Bond 1997, Watson 2001, Kenny *et al.* 2004). Concepts such as disturbance, succession, competition and productivity can help clarify *why* this is the case; they can assist both ecologists and on-ground managers to identify similarities and differences in the fire-related dynamics of different vegetation types, and to relate these differences to a-biotic factors. Ecological concepts can also inform the development and refinement of models linking characteristics of individual species to characteristics of ecosystems and disturbance regimes. Of course, models draw on empirical studies, and predictions *from* models, where possible, should be verified in the field (Cary *et al.* 2003). Concepts, models, empirical research, historical and indigenous perspectives should all be grist for the mill in the important work of developing fire management guidelines.

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