Vegetation Dynamics in Coastal Heathlands of the Sydney Basin

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Keith, D.A. and Tozer, M.G. (2012). Vegetation dynamics in coastal heathlands of the Sydney Basin. *Proceedings of the Linnean Society of New South Wales* **134**, B181-B197.

Heathlands are dynamic ecosystems that change in response to fire regimes and climate variations, as well as endogenous processes such as competition between component species. An understanding of how heathlands change through time is central to the development of management strategies that aim to conserve them and maintain coexistence of their plants and animals. We briefly review the development of this understanding for Sydney's coastal heathlands from the emergence of the first published work in the 1930s. In our previous work, we focussed on fire regimes and interspecific competition between plants as important processes that drive ecosystem dynamics (succession) and mediate species coexistence and diversity. Here, we synthesise our understanding of heathland dynamics into a state and transition framework. We first develop a simple classification of heathland states based on their composition of plant functional types and developmental stage with time since fire. We then propose a qualitative model that predicts transitions between states conditional upon intervals between fires,, fire-mediated life cycle processes of component plant species and interactions between species. We applied the model to predict qualitative changes in heathland state under contrasting fire regime scenarios, and tested example predictions using a long-term study of heathland dynamics in Royal National Park. Empirical observations of overstorey and understorey change were generally consistent with model predictions, subject to variability between sites. Importantly, the model helps to identify fire scenarios that promote dynamic coexistence of multiple heathland states that each support different components of heathland biota. We conclude that simple process models can be very useful for informing management decisions by describing expected responses to alternative management strategies. These predictions lend themselves to testing in adaptive management experiments that seek to spread risks and improve understanding of ecosystem dynamics for future management.

Manuscript received 26 March 2012, accepted for publication 29 May 2012.

Keywords: adaptive management, biodiversity monitoring, competition, fire management, fire regime, long term ecological study, plant functional types, state and transition model, succession, vegetation change.

INTRODUCTION

Heathlands are a spectacular feature of Sydney's coastline, familiar to residents who venture into the city's bushland, as well as visitors who approach the city by air or sea. These heathlands are greatest in extent and diversity within Royal National Park, although the peninsula between Sydney Harbour and Botany Bay may once have supported a similar area and diversity of heathland communities. The striking transformation of bushland into urban landscapes within a few human generations makes it easy to think of the remaining bushland as unchanged. Yet these ecosystems themselves undergo remarkable cyclical and directional changes over decadal time scales and there is evidence that this dynamism is partly responsible for maintenance of biological diversity within heathland landscapes (Keith et al. 2007a). Understanding cause - effect mechanisms of vegetation dynamics is therefore fundamental to the development of management strategies for conservation of biodiversity in the remaining natural areas.

By summarising a set of beliefs about how the world works, process models can help explain the

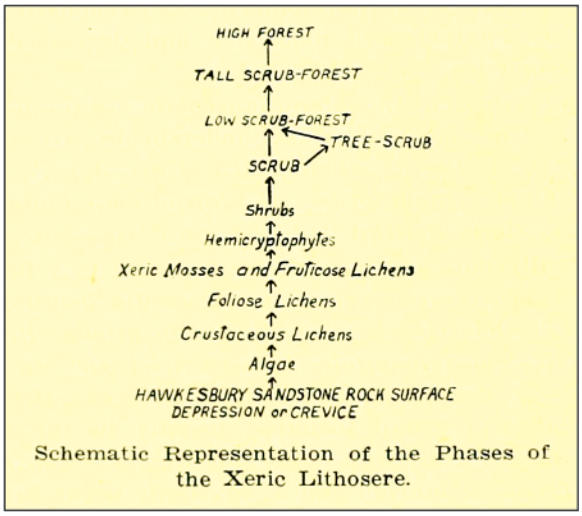


Figure 1. Pidgeon's (1938) model of plant succession on the Hawkesbury sandstone (Source: Proceedings of the Linnean Society of New South Wales Volume 63, p16). Heath is represented by the terms 'shrubs' and 'scrub'.

causes and effects of ecosystem behaviour. Models may be verbal, graphical, diagrammatic, physical or quantitative representations of ecosystem behaviour (Pickett and Cadenasso 2002). As well as serving explanatory roles, models may be used to make predictions about future ecosystem responses to particular scenarios or circumstances. The construction of a model can also have collateral benefits by enforcing logical consistency, promoting scrutiny of dependencies between ecosystem components and highlighting gaps in current knowledge that may be pivotal to predictive outcomes. Process models are therefore useful tools for translating concepts and generalisations into practical support for decision-making in ecosystem management (Hobbs and Suding 2009) and are central to adaptive management strategies where they can be used to inform setting of objectives, designing plausible alternative management strategies and measuring performance of management actions (Rumpff et al. 2011).

In this paper we present the first step in the development of a model of vegetation dynamics for coastal heathlands of the Sydney basin. We focus on heathlands in Royal National Park, but also draw from research in other Sydney coastal heathlands, so the model is generically applicable to those areas. We first describe the heathlands and briefly review the development of knowledge about salient processes that govern vegetation dynamics. We then construct a model framework to describe alternative heathland states, identify the variables that define them, and the salient processes that govern transitions between different states over time. We apply the model to different scenarios of environmental change and compare predictions to observed outcomes by use of retrospective comparisons. Finally, we summarise some implications of model predictions for future management and research in the heathlands and comment on the potential of the model to contribute to adaptive management.

Sydney coastal heathlands

The scope of our model is defined by the Sydney Coastal Heaths vegetation class described by Keith (2004). These heaths are fire-prone plant communities restricted to very infertile soils derived from Triassic and Permian quartzose sandstones on elevated plateaus within a few kilometres of the coast between Gosford and Jervis Bay. They are characterised by a high diversity of sclerophyllous plants from families Proteaeceae, Myrtaceae, Ericaceae, Fabaceae, Lomandraceae, Xanthorrhoeaceae, Cyperaceae and Restionaceae, including many taxa that are endemic to the Sydney basin. Tozer *et al*. (2010) provide a detailed floristic description and distribution map (see their map units p117 'Coastal sandstone plateau heath', p126 'Coastal rock plate heath' and p127 'Sandstone headland scrub'). Related vegetation classes include Coastal heath swamps, found within drainage-impeded sites on the coastal sandstone plateaus; Wallum sand heaths, found on coastal sand plains; and Sydney montane heaths of the Blue Mountains and Morton plateaus (Keith 2004).

HEATHLAND VEGETATION DYNAMICS

The purpose of our review is to highlight some key developments in understanding processes that drive heathland vegetation change, rather than a comprehensive evaluation of published literature. One of the earliest interpretations of vegetation dynamics in the region was Pidgeon's (1938) study of plant succession on the Hawkesbury sandstone. Her model of landscape evolution proposed that vegetation developed on bare rock through a sequence of stages culminating in 'high forest' (Fig. 1). The mosaic of plant communities observable on sandstone plateaus were interpreted as patches in varying stages of development, in some cases arrested by local conditions. Moisture availability was a key process driving change in Pidgeon's (1938) model, with deeper soil profiles and shelter from desiccating winds promoting greater moisture retention and thus supporting development of 'more advanced' vegetation (i.e. with greater biomass). Heathlands, described by Pidgeon (1938) as 'scrub', were an intermediate stage in this succession, with high levels of sclerophylly and low stature indicating their ability to tolerate periods of moisture deprivation without wilting. While Beadle (1966) and subsequent workers established the association between sclerophylly and soil nutrition, Pidgeon (1938) postulated that progression from scrub to forest was allogenic, and controlled by development of both soil and topographic shelter from severe wind, through their effects on moisture retention.

Pidgeon (1938) also identified fire as having an influence on the distribution of sandstone vegetation. She suggested that, as the flora was particularly rich in species capable of vegetative regeneration, there was a tendency for similar floristic composition before and after pyric denudation. Seedlings apparently were at a disadvantage to renascent individuals, even though many species regenerated from resistant seeds or fruits that were either attached to plants or lying in soil at the time of fire (Pidgeon 1938). Hence, post-pyric seedlings only matured in dense stands where competition from resprouters was less severe.

The dynamism and potential vulnerability of plant species that lack vegetative recovery organs and rely only on seed for population persistence were first reported by Siddiqi *et al*. (1976). They observed that stands of these obligate-seeder species were eliminated from an area exposed to a short interval (<5 years) between successive fires because there had been insufficient time for post-fire seedlings from the first fire to mature and re-establish a seedbank before the next fire. Seeder species with canopy seedbanks (serotinous) appear to be the species most vulnerable to elimination. Bradstock and O'Connell (1988) quantified the relationship between fire intervals and population persistence for *Banksia ericifolia* and *Petrophile pulchella*, showing that optimal population growth occurred when fire return intervals were longer than 15 years and that populations may be eliminated when intervals were less than 6 years.

Morrison *et al*. (1995) and Cary and Morrison (1995) demonstrated strong fire frequency effects at the community level within Sydney coastal heathlands. They showed that diversity of obligate seeders was reduced in heathlands exposed to short fire intervals and that these trends were essentially independent of changes that occurred in composition with time since fire.

Obligate seeding plants may be buffered from elimination by adverse fire regimes, at least in the short term, if they have a persistent soil seedbank that may be released from dormancy by fire-related cues such as heath shock or smoke (Auld and O'Connell 1991; Morris 2000; Thomas *et al*. 2003). A majority of heathland plant species have persistent soil seedbanks (Auld and Ooi 2008), which may remain dormant and viable for several years to several decades (Auld *et al*. 2000). In some of these species, a residual fraction of the soil seedbank may remain dormant and viable after a fire, providing some capacity for regeneration after a second fire even if the intervening period was too short to permit seedbank replenishment (Auld and Denham 2006; Ayre *et al*. 2009).

Resprouters are often considered to be resilient to a wide range of fire regimes (Morrison *et al*. 1995; Pausas *et al*. 2004), but mortality of standing plants occurs through several fire-related mechanisms (Zammit 1988; Bradstock and Myerscough 1988; Keith *et al*. 2007a). Depending on fire regimes, replenishment of these individuals may be insufficient to maintain population stability due to low rates of fecundity and growth (Keith *et al*. 2007b). Sequences of short fire intervals or severe fires may cause gradual attrition or episodic declines, respectively, of established woody resprouters (Regan *et al*. 2011) if losses are not compensated by equivalent levels of recruitment. The factors promoting establishment of resprouters and increases in their populations are still not well understood.

Competition is another potential mechanism of change in plant diversity. As well as strong self-regulatory effects within populations of some heathland species (Morris and Myerscough 1988), there is evidence of strong competitive hierarchies related to plant stature within Sydney coastal heathlands (Keith and Bradstock 1994; Tozer and Bradstock 2003; Keith *et al*. 2007a). Resprouters may have a competitive advantage over seedlings in the initial post-fire period (Pidgeon 1938), however recruits of woody obligate seeders with large canopies eventually overtop the resprouters, casting deep shade that substantially reduces rates of growth, fecundity and survival of plants beneath their canopies. The role of below-ground competition is uncertain, but could also be significant. Nevertheless, above-ground competition is mediated by periodic fires that interrupt the elimination of inferior competitors and promote co-existence. Furthermore, there is evidence that thickets of competitive dominants move around the landscape in response to spatial and temporal variations in fire regimes (Keith 1995; Keith *et al*. 2007a).

Functional classification of species based on plant life-history traits has proved to be valuable for interpretation of vegetation change in Sydney heathlands. This approach provides an adaptable conceptual framework for predicting responses to contrasting scenarios, as species with shared traits tend to have similar mechanisms of response (Keith and Bradstock 1994; Morrison *et al*. 1995; Keith *et al*. 2007a; Keith 2012).

In summary, there have been substantial advances in understanding of vegetation dynamics in Sydney coastal heathlands since Pidgeon's (1938) early studies. While soil development and topography tend to structure major vegetation patterns on the sandstone plateaus and control long-term transitions between heathlands and other communities, both fire regimes and soil moisture variation have key roles in dynamics of the heathland mosaic over decadal time scales, and potentially generate long-lasting legacies. A synthesis of these processes is needed to support management for conservation of the diverse heathland biota. Below, we contribute to such a synthesis by constructing a model that incorporates the salient processes reviewed above.

MODEL STRUCTURE

We adopted a state and transition framework for our model of heathland vegetation dynamics. This structure involves classification of heathland vegetation into a number of alternative states, each of which is defined by a set of state variables. The values of these state variables may change through time or in response to particular environmental cues or events. Consequently, transitions may occur between certain states under particular conditions. State and transition models are used widely as explanatory and predictive tools in ecology, management and restoration (Westoby *et al*. 1989; Bestelmeyer *et al*. 2009; Rumpff *et al*. 2011). They involve a significant abstraction by representing vegetation as discrete classes, rather than as a continuum, but this is offset by many advantages. State and transition models are easy to grasp in their simplest diagrammatic form and therefore powerful communication tools between scientists and managers. They also have capacity for extension to mathematically explicit quantitative predictions and may be implemented in ways that accommodate uncertainties and permit updating as new knowledge emerges (Rumpff *et al*. 2011).

State variables

A set of state variables describes the floristic, structural and environmental features of alternative heathland states. We used the classification of species functional types proposed by Keith *et al*. (2007a) to define floristic state variables. This approach allows a substantial simplification of the flora by classifying more than 200 vascular plant taxa found in heathland into six broad functional types based on life history attributes. Selection of life history attributes was based on salient processes that mediate heathland vegetation dynamics (reviewed above): fire response of standing plants; propagule characteristics; timing of life life-history processes; and competitive relationships. Initial species groupings were based on factorial combinations of traits and were simplified by deleting trait combinations that did not exist in nature (due to correlations between traits), and grouping those considered likely to have similar responses to the mediating processes (Keith *et al*. 2007a; Table 1).

Structural state variables included the height and combined projective cover (foliage and branches) of tall shrub, mid shrub, ground layer and litter strata. These variables were assessed by assigning individual plants to a stratum based on their potential height at maturity. Thus, it would be possible for the tall shrub stratum to be shorter than the ground layer if the former was at an immature stage.

The environmental state variables include soil depth, drainage, topography and post-fire age. Although more realistic and elaborate characterisations would be possible, we characterised variation in these attributes using broad categories.

Heathland states

In this study we only used qualitative descriptors of the attribute states to illustrate our modelling approach, although it is possible to characterise them with quantitative estimates (Table 2). For example, each heathland state was characterised floristically as having high, medium or low relative abundance and diversity of each of the six plant functional types, rather than using metrics of diversity and abundance. Similarly, we used qualitative descriptors to characterise structural variables (e.g. cover of tall shrub stratum was described as absent, sparse or dense) and a categorical descriptor for the environmental state variable. We limited our current analysis to treeless vegetation on shallow, moderately drained soils of exposed sandstone plateaus, although we recognise that these coexist with other vegetation states including heathlands on rock plates, woodlands and upland swamps, which differ notably in environmental state variables soil depth and drainage. Consequently, several structural and environmental state variables are essentially invariant amongst the subset of states considered (Table 2).

Table 1. Summary of six major plant functional types (PFTs) in Sydney coastal heathlands and their life history traits (adapted from Table 1 in Keith et al. 2007a). For authorities, see Pellow et al. (2009).

Functional Type	Fire persistence	Propagule type	Vertical stratum	Standing plant longevity	Example
1 Serotinous obligate seeder shrubs	killed	serotinous seedbanks	upper	30-50 years	*Banksia ericifolia*
2 Non-serotinous obligate seeder shrubs	killed	persistent soil seedbanks	middle	10-30 years	*Epacris microphylla*
3 Resprouter shrubs	survives	serotinous, persistent and transient soil seedbanks	middle	>50 years	*Banksia oblongifolia*
4 Fire ephemeral herbs	killed	Persistent soil seedbanks	ground	<5 years	*Mitrasacme polymorpha*
5 Non-rhizomatous herbs and graminoids	survives	Persistent and transient soil seedbanks	ground	>10-50 years	*Burchardia umbellata*
6 Rhizomatous herbs and graminoids	survives	Persistent and transient soil seedbanks, vegetative propagation	lower	>50 years	*Leptocarpus tenax*

Transitions

The heathland states (Table 2) were organised into four main lineages according to their developmental relationships (Fig. 2): diverse thicket (DT); depauperate thicket (PT); diverse heath (DH); and depauperate heath (PH). Thus, a given stand of heathland may undergo autogenic transitions between states of increasing time since fire within the same lineage. Transitions between lineages are triggered allogenically in response to particular fire events, or may also occur autogenically late in the fire cycle (Fig. 2). The states and transitions represented diagrammatically in Fig. 2 were incorporated into a conditional matrix model, which defines the possible transitions from each state and conditions under which they may occur (Table 3). With a matrix model framework, it is possible to specify the rates and probabilities of transitions. In this paper, however, we focus on the structure of the model and only show qualitative information on the transitions. Below, we use example scenarios to demonstrate the application of the model.

MODELLING ALTERNATIVE FIRE REGIME SCENARIOS

Methods

We used the model to predict qualitative vegetation responses to example fire regime scenarios and compared the predictions with observed responses. The example scenarios were developed by examining the fire history and historical vegetation states in an area of heathland on the sandstone plateau between Jibbon Hill and the Marley track, Royal National Park (Fig. 3). Studies of heathland vegetation dynamics have been ongoing since a fire burnt the entire site in October 1988 (Keith 1991; Keith and Bradstock 1994; Keith 1995). In this paper, we use observations gathered at Transects 2 and 7 to evaluate specific model predictions. Prior to 1988, fires occurred in 1976 (both transects) and 1980 (Transect 7 only). A subsequent fire burnt the entire area in January 1994.

We determined the fire history and structural states of vegetation at the transect sites by interpreting a chronosequence of aerial photographs (Keith 1995). At Transect 2, Diverse Thicket developed after the

	Floristic						Structural					Environmental
State variable State	1 Serotinous obligate seeder shrubs	2 Non-serotinous obligate seeder shrubs	3 Resprouter shrubs	4 Fire ephemeral herbs	5 Non-rhizomatous herbs and graminoids	6 Rhizomatous herbs and graminoids	Tall shrub height	Tall shrub cover	Mid shrub cover	Ground cover	Litter cover	Time since fire (years)
DTb Post-fire diverse thicket	high	high	high	high	high	high	low	absent	dense	dense	sparse	tsf<5
DTj Juvenile diverse thicket	high	high	high	low	medium	high	medium	sparse	medium	dense	medium	5<tsf<10
DTy Young-mature diverse thicket	high	low	high	low	medium	medium	tall	dense	sparse	medium	dense	10<tsf<20
PTb Post-fire depauperate thicket	high	high	low	high	low	low	low	absent	sparse	medium	sparse	tsf<5
PTj Juvenile depauperate thicket	high	high	low	low	low	low	medium	sparse	sparse	medium	medium	5<tsf<10
PTy Young-mature depauperate thicket	high	low	low	low	low	low	tall	dense	sparse	sparse	dense	10<tsf<20
PTo Old-mature depauperate thicket	high	low	low	low	low	low	tall	dense	sparse	sparse	dense	20<tsf<30
PTs Senescent depauperate thicket	medium	low	low	low	low	low	tall	sparse	sparse	medium	dense	tsf>30
DHb Post-fire diverse heath	low	high	high	high	high	high	low	absent	dense	dense	sparse	tsf<5
DHj Juvenile diverse heath	low	high	high	low	high	high	medium	sparse	dense	dense	sparse	5<tsf<10
DHy Young-mature diverse heath	low	high	high	low	high	high	tall	sparse	dense	dense	medium	10<tsf<20
DHo Old-mature diverse heath	low	low	high	low	high	high	tall	sparse	dense	dense	medium	20<tsf<30
DHs Senescent diverse heath	low	low	high	low	high	high	tall	sparse	medium	dense	medium	tsf>30
PHb Post-fire depauperate heath	low	medium	low	high	low	low	low	absent	medium	dense	sparse	tsf<5
PHj Juvenile depauperate heath	low	medium	low	low	medium	medium	medium	sparse	medium	dense	sparse	5<tsf<10
PHy Young-mature depauperate heath	low	medium	low	low	medium	medium	tall	sparse	sparse	dense	sparse	10<tsf<20
PHo Old-mature depauperate heath	low	low	low	low	medium	medium	tall	sparse	sparse	dense	medium	20<tsf<30
PHs Senescent depauperate heath	low	low	low	low	medium	medium	tall	sparse	sparse	dense	medium	tsf>30

Figure 2. Aerial photograph of Jibbon study area taken in 2001, seven years after previous fire, showing open heath (grey-green) in vicinity of Transect 2 and development of thicket shrub canopy (dark green) in vicinity of Transect 7. Canopies of individual serotinous obligate seeder shrubs are visible within the open heath.

1976 fire and was in a young mature state (DTy, Table 2) when it was burnt in 1988. Diverse Thicket reached a juvenile state (DTj) when it was burnt again in 1994. At Transect 7, the 1980 fire interrupted development of Diverse Thicket and the vegetation underwent a putative transition to burnt Diverse Heath (NBB fire history in Fig. 5 of Keith 1995). Transect 7 was positioned 5 m from the 1980 fire boundary, beyond which Diverse Thicket continued to develop until the 1988 fire. Following the 1988 fire, Transect 7 underwent a transition from Diverse Heath to Diverse Thicket due to dispersal of seed from an adjacent thicket (<5 m away). Since 1994, both Transects have remained unburnt except for a small fire in 2005 that partially scorched small areas of Transect 7. For purposes of prediction, we assumed that this last fire had no effect on the transect.

Table 2 (Opposite). Attribute states of alternative heathland states for six floristic state variables (relative abundance and diversity of plant functional types, Table 1), five structural state variables and one environmental state variable. Two structural variables and three environmental state variables not shown as they are essentially invariant across listed heathland states (Mid shrub height - medium, Ground layer height - low, Soil depth - 0.2 - 0.6 m, Soil moisture - periodically damp and dry with limited humus accumulation, Topographic shelter - exposed plateau surface).

The model predictions were evaluated using data on population densities of selected plant species collected from Transects 2 and 7 in repeated surveys between 1990 and 2011 (see Keith and Bradstock 1994 for field methods).

Predictions

Based on the above history, we identified several scenarios with contrasting initial states and fire events at the two transects and used the model to predict measurable outcomes (Fig. 4). We first focussed on transitions at each transect as a consequence of the 1988 and 1994 fires (Scenarios 0 - 2, Table 4). At the

	DTb	DTj	DTy	PTb	PTj	PTy	PTo	PTs	DHb	DHj	Dhy	DHo	DHs	PHb	PHj	PHy	PHo	PHs
DTb	FD	F	F					FD		FD	FD	FD			FD	FD		
DTj	NF																	
DTy		NF																
PTb				FD	F	F	F								FD	FD	FD	FD
PTj				NF														
PTy					NF													
PTo			NF			NF												
PTs							NF											
DHb	FN	FN						FD	F	F	F	F	F		FD	FD		
DHj									NF									
Dhy										NF								
DHo											NF							
DHs												NF	NF					
PHb				FN	FN		FN	FN	FN					F	F	F	F	F
PHj														NF				
PHy															NF			
PHo																NF		
PHs								NF									NF	NF

NF	No fire
FN	Fire with no dispersal
FD	Fire with dispersal
F	Fire with or without dispersal

Table 3. A stand-based conditional state and transition matrix model for Sydney coastal heaths. Heathland states are arranged in four lineages: DT - diverse thicket; PT - depauperate thicket; DH - diverse heath; and PH - depauperate heath. Within each lineage are a time series of states that vary in post-fire age: b - burnt recently (0-5 years ago); j - juvenile (5-10 years since fire); young mature (10-20 years since fire); old mature (20-30 years since fire); s - senescent (>30 years since fire). Entries in cells indicate the fire and dispersal conditions required for a transition from an initial state (top row of matrix) to a new state (left column of matrix). We assume that fires consume or scorch the canopies of shrubs in the modelled stand. Dispersal denotes an influx of propagules for all plant functional types from adjacent stands of heathland.

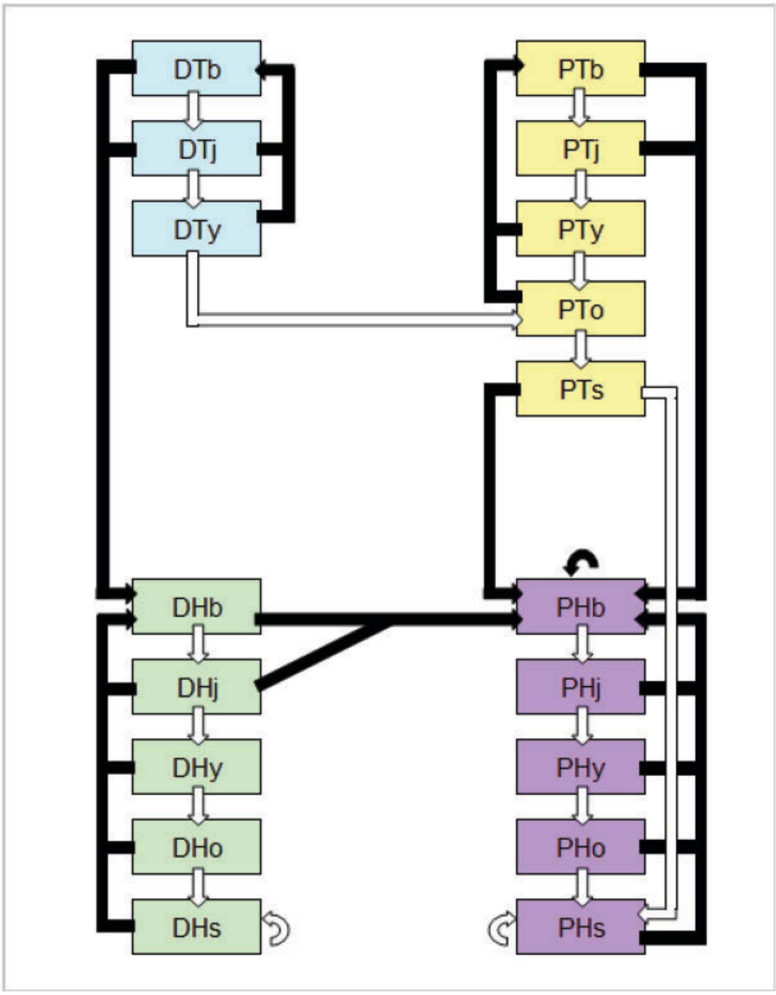


Figure 3. Simplified diagrammatic state and transition model for a stand of Sydney coastal heath. Heathland states represented in boxes are defined in Table 2. States within the same lineage are shown in the same colour. White arrows show autogenic transitions that occur with time in the absence of fire. Black arrows show allogenic transitions initiated by crown fires, assuming no dispersal of plant propagules from outside the patch. The matrix model in Table 3 incorporates additional transitions with propagule dispersal.

time of the 1988 fire, Diverse Thicket was present at Transect 2 and Diverse Heath was present at Transect 7. Transect 2 was a post-fire age of 12 years and at the young-mature diverse thicket stage (DTy) while Transect 7 was a post-fire age of 8 years and at the juvenile diverse heath stage (DHj), (Table 2). At Transect 2, the model predicts transition from DTy to DTb (Table 4 Scenario 0), and at Transect 7, the model predicts transition from DHj to DHb or DTb, depending on whether seeds of thicket dominants were dispersed from the adjacent area that was unburnt in 1980. We show only the latter transition in Fig. 4b (Table 4 Scenario 2). At the time of the 1994 fire both sites were a post-fire age of 5.3 years, on the interface between burnt and juvenile states (Table 2). At both transects the model predicts transition from DTj to either DTb or DHb (Scenario 1), depending on whether serotinous obligate seeders were at maturity (Table 3). For brevity, we show only the latter prediction in Fig. 4a.

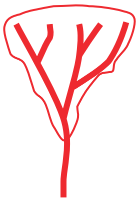
We next focussed on transitions at each transect over the 13 years after the 1994 fire (Scenarios 3 and 4, Table 4). In the absence of subsequent fire, the model predicted transition from DHb through DHj to DHy at Transect 2 (Scenario 3, Fig. 4c), with the community maintaining an open structure and an abundance of rhizomatous sedges (PFT 6). At Transect 7, the model predicted an autogenic progression from DTb through DTj to DTy (Scenario 4, Fig. 4d), with the development of a tall dense shrub canopy, and a coincident decline in resprouters (PFTs 3, 5 and 6).

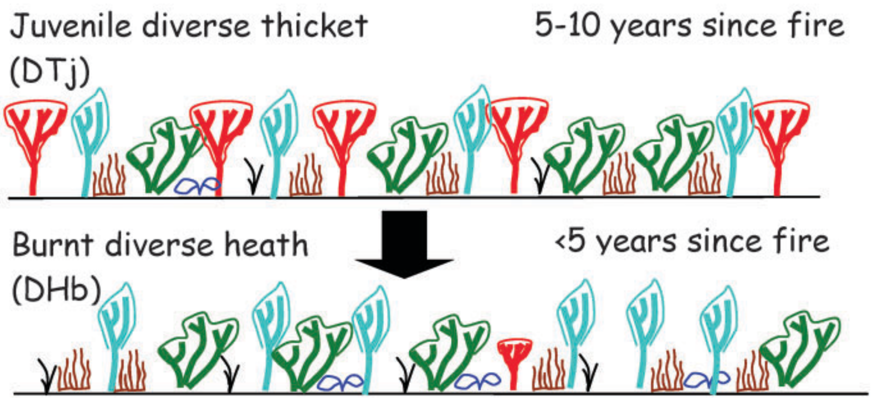
Finally, we applied the model to the interval between the 1988 and 1994 fires (Scenarios 5 and 6). Prior to 1988, Transect 7 was occupied by Diverse Heath and, there had been no suppression of rhizomatous sedges (PFT 6) by a dense shrub overstorey. Consequently, in Scenario 5 (Fig. 4e) the model predicted consistently high abundance of PFT 6 during the post-1988 transition from DTb to DTj (Table 4). In contrast, Transect 2 had been occupied by Diverse Thicket which had reached a post fire age of 12 years (DTy) by 1988, potentially reducing population densities of rhizomatous sedges (PFT6). In Scenario 6 (Fig. 4f), the 1988 fire was predicted to release these species from competitive suppression, allowing their density to increase by vegetative spread during the transition from DTb to DTj.

Observations

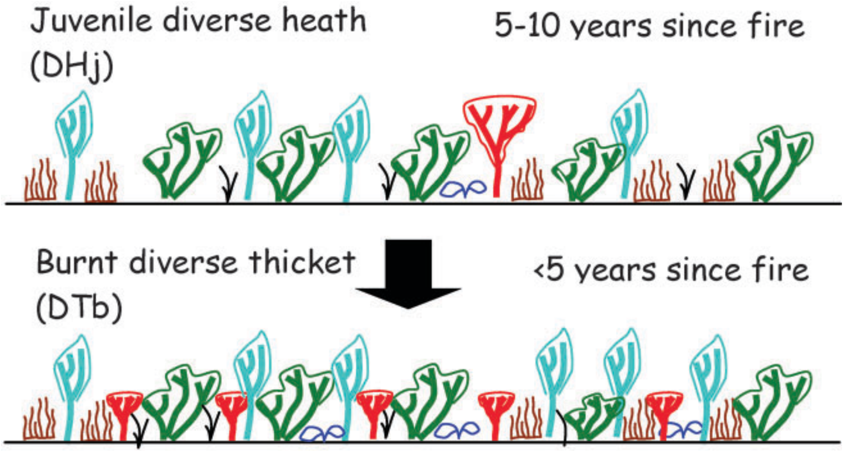
Transect 2 underwent transition from thicket (DTj) before the 1988 fire to heath (DHb) after the 1994 fire, and the density of serotinous obligate seeder shrubs was reduced by three orders of magnitude

Figure 4. Diagrammatic representation of predicted transitions between heathland states. Black arrows represent allogenic transitions initiated by crown fires, white arrows represent autogenic transitions in the absence of fire. See Table 1 for description of plant functional types and Table 2 for description of heathland states. Plant functional Types:

1 Serotinous obligate seeder shrubs  ; 2 Non-serotinous obligate seeder shrubs  ; 3 Resprouter shrubs  ; 4 Fire ephemeral herbs  ; 5 Non-rhizomatous herbs and graminoids ; and 6 Rhizomatous herbs and graminoids .

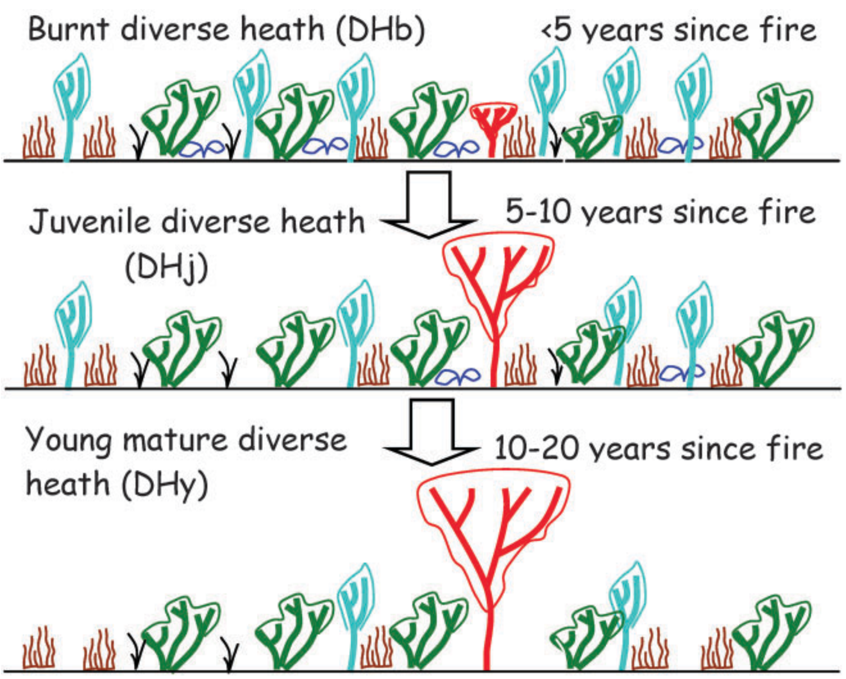


(a) Scenario 1: transition from juvenile diverse thicket (post-fire age 5.3 years) to burnt diverse heath in response to crown fire.

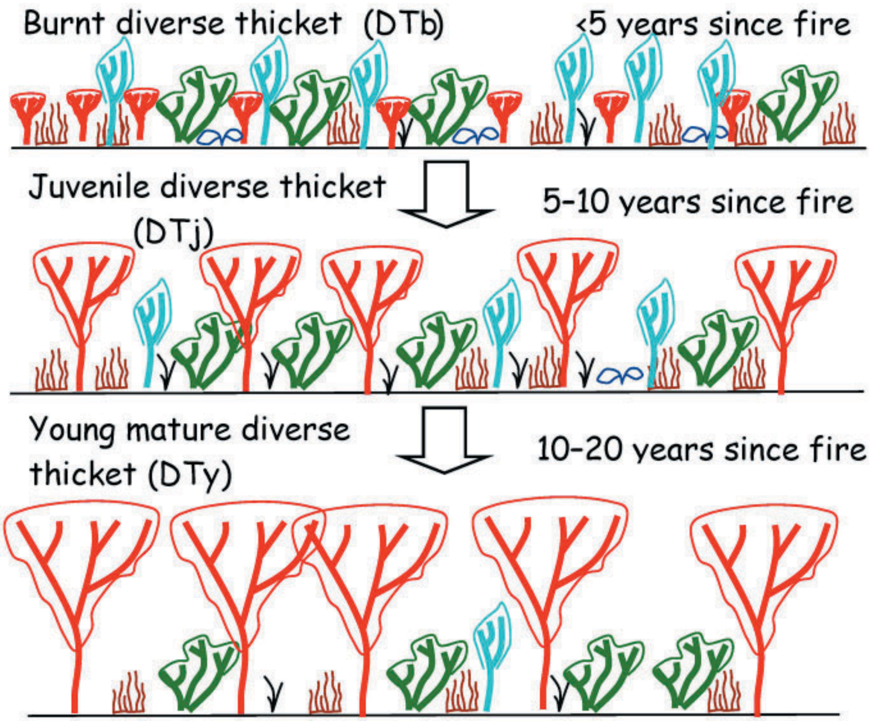


(b) Scenario 2: transition from juvenile diverse heath to burnt diverse thicket in response to crown fire.

Figure 4 Continued

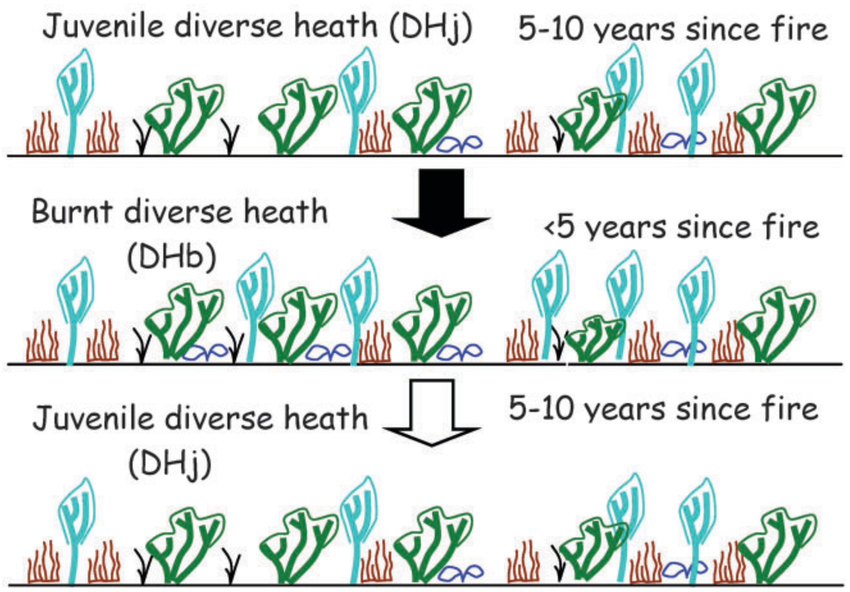


(c) Scenario 4: transition from burnt diverse heath to young mature diverse heath with time since fire.

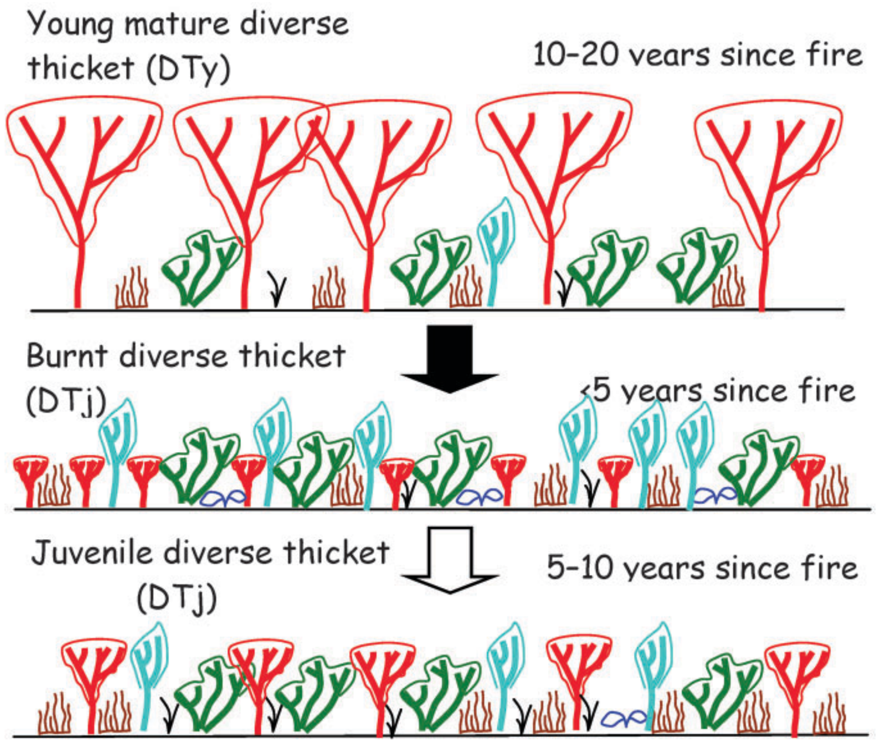


(d) Scenario 4: transition from burnt diverse thicket to young mature diverse thicket with increasing time since fire.

Figure 4 Continued



(e) Scenario 5: transition from burnt diverse heath to juvenile diverse heath with time since fire after prior occupancy by juvenile diverse heath.



(f) Scenario 6: transition from burnt diverse thicket to juvenile diverse thicket with time since fire after prior occupancy by young mature diverse heath.

(Fig. 5). Conversely, the density of these shrubs increased from zero before the 1988 fire to more than 10 per square metre after the 1994 fire at Transect 7, signalling a transition from juvenile thicket (DTj) to burnt thicket (DTb). These observations were consistent with predicted transitions if Scenario 1 occurred at Transect 2 without dispersal and at Transect 7 with some serotinous obligate seeders at maturity (Table 3). Thus, the difference between sites was due to slightly faster maturation and development of a seedbank in the vicinity of Transect 7 after the 1994 fire (pers. obs.).

The development of a tall dense shrub canopy at Transect 7 after 1994 (Scenario 4) can be tracked on

Table 4. Qualitative predictions of the process model for six scenarios at Transects 2 and 7.

Scenario	Initial state	Predicted transition	Time frame	Response variable	Predicted change	Observed change	Site
0) Fire	DTy	DTb	before/after 1988 fire	PFT1 density	stable	stable	Transect 2
1) Fire without dispersal	DTj	DHb	before/after 1994 fire	PFT1 density	elimination	near elimination	Transect 2
2) Fire with dispersal	DHj	DTb	before/after 1988 fire	PFT1 density	increase	increase, Fig. 5	Transect 7
3) No fire	DHb	DHy	13-yr interval after 1994 fire	tall shrub cover	remains low	patchy development (aerial photos)	Transect 2
			13-yr interval after 1994 fire	PFT6 density	stable or slight decline	stable for 8 years, then gradual decline	Transect 2
4) No fire	DTb	DTy	13-yr interval after 1994 fire	tall shrub cover	marked increase	marked increase (aerial photos)	Transect 7
			13-yr interval after 1994 fire	PFT6 density	decline	strong decline	Transect 7
5) No fire, no prior thicket	DHb	DHj	5-yr interval after 1988 fire	PFT6 density	stable	stable	Transect 7
6) No fire, prior occupancy by dense thicket	DTb	DTj	5-yr interval after 1988 fire	PFT6 density	increase	increase, Fig. 6	Transect 2

a chronosequence of aerial photographs (e.g Fig. 3). Canopy development was similar to that tracked after earlier fires in the same area (Keith 1995). By 2001, the developing shrub canopy at this site had exceeded the height of mid-stratum shrubs (PFTs 2 and 3) and ground layer plants (PFTs 4, 5 and 6). These PFTs underwent a prolonged decline after the 1994 fire. For example, *Leptocarpus tenax*, a rhizomatous graminoid (PFT 6, Table 1), declined in density by two orders of magnitude over the 13 years since the 1994 fire (Fig. 6). In contrast, a continuous canopy of serotinous obligate seeders did not develop under Scenario 3 at Transect 2 due to the low densities of serotinous obligate seeding shrubs (Fig. 5). Instead, only a patchy cover of tall shrubs can be seen on aerial photographs after 2001. In the absence of a dense canopy, the density of *L. tenax* was essentially stable at Transect 2 after the 1994 fire, contrasting markedly with its decline at Transect 7 during the same time (Fig. 6). These observations are consistent with predictions of the model for transitions from DTb to DTy and DHb to DHy, respectively (Tables 2 and 3).

Transect 7 had consistently dense populations of *L. tenax* (PFT 6) during 1990-1994 (filled triangles, Fig. 6). Under Scenario 5, this site had been free of a tall shrub canopy for some years due to elimination of serotinous obligate seeder shrubs (PFT 1) by a short fire interval during 1976-1980 (reported in Keith 1995). In contrast, under Scenario 6, Transect 2 had

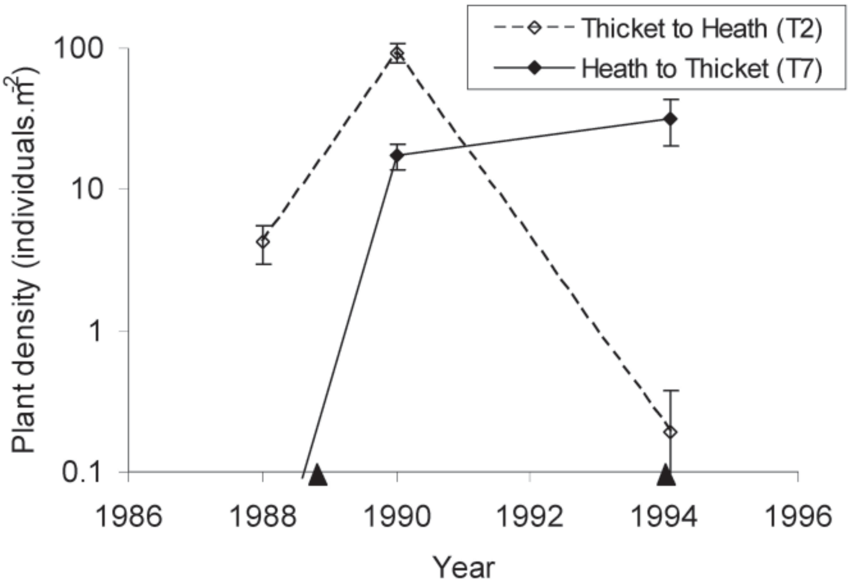


Figure 5. Change in population density of serotinous obligate seeder shrubs (PFT 1), primarily Banksia ericifolia, before and after the 1994 fire. Triangles on x-axis indicate timing of fires. Data for heath to thicket transition from Transect 7 and data for thicket to heath transition from Transect 2. Density estimates for 1988 were for mature stands (zero individuals recorded for T7), those for 1990 and 1994 were for post-fire seedlings, indicative of the capacity for future thicket development.

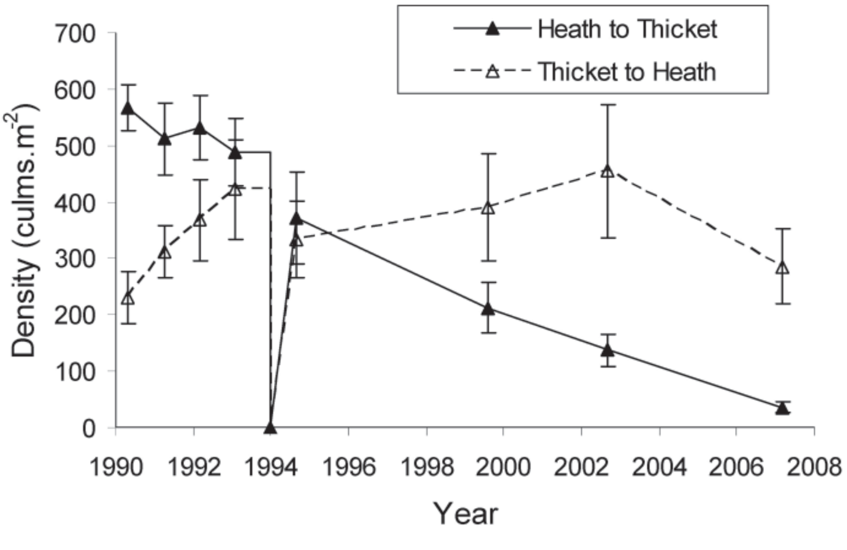


Figure 6. Trends in population density of Leptocarpus tenax (PFT 6) in relation to the 1994 fire. Data for heath to thicket transition from Transect 7 and data for thicket to heath transition from Transect 2. Note: preceding fire occurred in 1988, 5.3 years before the 1994 fire.

been occupied by young-mature thicket (DTy) prior to the 1988 fire. Just prior to 1988, serotinous obligate seeder shrubs (PFT 1) were present at a mean (±se) density of 7.0 ± 1.2 plants. m^{-2} (data from Keith 1991), forming a dense canopy 2 - 3 m tall. After removal of this canopy by the 1988 fire, *L. tenax* showed a steady increase in density until the site was burnt again in 1994 (Fig. 6). This change is consistent with model prediction for a transition from DTy to DHb in response to fire with no dispersal (Tables 2 and 3).

DISCUSSION

State and transition model

Model predictions were consistent with observed changes in heath vegetation at our Jibbon study site over recent decades. The predictions examined included species from two functional types and a range of fire scenarios. These findings agree with those of earlier studies that examined a broader range of functional types at different times and places within Sydney coastal heathlands and heath-swamps (Keith and Bradstock 1994; Keith 1995; Tozer and Bradstock 2003; Keith *et al*. 2007a). Collectively, these studies demonstrate the sensitivity of serotinous obligate seeder shrubs to short fire intervals (≤5 years), the sensitivity of woody and non-woody resprouters to competition from dense thickets of seeder shrubs, and the mobility of these thickets around sandstone landscapes over a series of fire intervals.

The most equivocal performance of the model was in Scenarios 1 and 2, which produced different observed outcomes at different sites, despite similar contemporary fire intervals. Two factors potentially explain these differences. First, the model predicted different outcomes depending on whether the sites were assigned to burnt or juvenile initial states, and the assignment of sites to one of these states was uncertain. The sites had a post-fire age of 5.3 years when burnt in 1994, which was very close to the nominal 5-year threshold age delimiting burnt and juvenile states in the model (Table 2). The observed response for Transect 2 was consistent with predictions for a burnt initial state, whereas the response for Transect 7 was consistent with predictions for a juvenile initial state. Although the age threshold delimiting states was specified precisely, and the age of the sites was accurately known, assignment of sites to states was vague (Regan *et al*. 2002) partly because the distinction between states is only indirectly related to age (as a proxy for reproductive capacity of serotinous obligate seeder shrubs). More broadly, vagueness is a pervasive form of uncertainty whenever two categories are delimited by thresholds or boundaries (Regan *et al*. 2002). A second source of uncertainty is attributable to natural variation. It seems likely that there were subtle differences in maturation and seedbank accumulation rates between the sites, which may have been responsible for establishment of serotinous obligate seeder shrubs at one site and not the other. This variability is likely to be most influential on transitions when the fire interval is close to the maturation period of obligate seeders, as it was in Scenarios 1 and 2. In summary, the model was able to accommodate these uncertainties to some degree by predicting alternative transitions from each initial state, conditional upon spatial variation in maturation times (Table 3).

State and transition models have been applied successfully in a range of ecosystems for a variety of explanatory and predictive purposes (Henderson and Wilkins 1975; Moore and Noble 1990; Hobbs and Suding 2009; Rumpff *et al*. 2011). Our model enables a synthesis of complex dynamics in which outcomes depend on the initial state of vegetation, its recent historical states, fire regimes, competitive interactions between species, propagule dispersal and functional traits of the species under consideration. Diagrammatic representation of the model enables effective communication with managers who need a logical framework to explore alternative future scenarios to support their management decisions for biodiversity conservation. Matrix representation of the model enables more complex scenarios to be explored by simulation over longer time frames that encompass multiple fires. In this paper we presented a qualitative matrix model. In future we will develop a numerically and spatially explicit matrix model capable of analysing uncertainties and conservation risks by simulation of alternative management options.

Management

Our model of vegetation dynamics provides a lucid framework for conservation of biodiversity in Sydney Coastal Heaths. Conservation of biodiversity requires persistence of the species within all six plant functional types. According to our model, this is only possible if management aims to: i) maintain both heath and thicket states within the landscape; and ii) promote diverse states and avoid depauperate states. In other words, a landscape configuration that includes a balanced and sustainable (albeit dynamic) representation of diverse heath and diverse thicket is more likely to meet the overall goal of biodiversity persistence than other landscape configurations. These aims can be achieved with a management strategy that is responsive to the current state of the landscape and cognisant of alternative pathways of change that may result from alternative management strategies and unplanned events. This approach should be combined with experimentation aimed at learning more about responses to alternative scenarios (Keith *et al*. 2011). For example, if a large proportion of the landscape is occupied by thicket (or soon will be), consideration should be given to alternative means of promoting transition from thicket to heath. Options include implementing fire intervals of less than 5 years in parts of the landscape or allowing parts of the landscape to go more than 30 years without fire (Table 3). This approach is the antithesis of management strategies based on fixed burning schedules and suppression plans that seek to avoid extremes in fire regimes. These strategies generally fail to account for the ecological state of the system, even though the schedules may be based on careful monitoring of fire history, and lack the flexibility to influence variability in fire regimes and their spatial patterns to promote specific transitions within targeted areas.

Finally, in focussing on management of plant functional types and vegetation states, our model currently risks ignoring other components of biodiversity that are important targets of conservation. Management strategies structured around the persistence of diversity of plant functional types are implicitly relevant to other biota. For example, serotinous obligate seeder shrubs (PFT 1) provide an important winter food source and nesting substrate for a range of avian and mammalian fauna (Keith *et al*. 2002). The much greater diversity of plant genera among the non-serotinous obligate seeder shrubs (PFT 2) is likely to support the greatest diversity of dependent invertebrate fauna, including insects with narrow host plant ranges (Moir *et al*. 2011). Thus, management trade-offs in the persistence of these two plant functional types also affect persistence of biota in other trophic levels. To address the persistence of all biota more explicitly in management strategies, however, these elements and their dependencies need to be integrated into the structure of future process models.

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