RESEARCH ARTICLE

Alternative stable states and the role of fire–vegetation–soil feedbacks in the temperate wilderness of southwest Tasmania

Sam W. Wood · David M. J. S. Bowman

Abstract Two ecological models have been put forward to explain the dynamics of fire-promoting and fire-sensitive vegetation in southwest Tasmania: the alternative stable states model of Jackson (in Proc Ecol Soc Aust 3:9–16, 1968) and the sharpening switch model of Mount (in Search 10:180–186, 1979). Assessing the efficacy of these models requires high resolution spatio-temporal data on whether vegetation patterns are stable or dynamic across landscapes. We analysed ortho-rectified sequences of aerial photography and satellite imagery from 1948, 1988 and 2010 to detect decadal scale changes in forest and non-forest vegetation cover in southwest Tasmania. There was negligible change from forest to non-forest (<0.05%) and only a modest change from non-forest to forest over the study period. Forest cover increased by 4.1% between 1948 and 1988, apparently due to the recovery of forest vegetation following stand-replacing fire prior to 1948. Forest cover increased by 0.8% between 1988 and 2010, reflecting the limited ability of forest to invade treeless areas. The two models include interactions between vegetation, fire and soil, which we investigated by analysing the

chemical (phosphorus, nitrogen) and physical properties (clay, silt) of 128 soil samples collected across 34 forest–non-forest boundaries. Phosphorus in the upper horizon was typically lower in non-forest vegetation compared to forest vegetation, which is consistent with proposed fire–vegetation–soil feedbacks. Mineral horizons were dominated by sand, with low levels of clay under all vegetation types. Available field evidence lends support to the Jackson (1968) alternative stable states model as the most suitable model of vegetation dynamics on nutrient poor substrates in southwest Tasmania although modifications of the timeframes for transitions toward rainforest are required.

Keywords Alternative stable states · Fire · Forest · Positive feedbacks · Aerial photography · Phosphorus

Introduction

Mosaics of fire-resistant and fire-prone vegetation within the same environmental settings have long fascinated ecologists (Mutch 1970; Geldenhuys 1994; Bowman 2000; Bond et al. 2005). There has been a recent surge of interest in whether a range of coexisting terrestrial vegetation communities persist as alternative stables states that are maintained by fire (Hoffmann et al. 2009; Warman and Moles 2009; Odion et al. 2010; Lehmann et al. 2011; Staver et al. 2011). Across flammable landscapes, alternative stable state theory

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predicts that a complex suite of feedbacks between fire, vegetation and other environmental variables act to maintain coexisting vegetation communities through time (Wilson and Agnew 1992) and that the breakdown of these feedbacks may result in relatively rapid transitions between otherwise stable states (Petraitis and Latham 1999; Scheffer et al. 2001).

One of the earliest examples of an alternative stables states model for landscapes experiencing periodic fire was put forward by Jackson (1968; see also Bowman and Jackson 1981) to explain 'islands' of relatively fire resistant forest amongst frequently burnt moorland and heath communities in the southwest of Australia's island state, Tasmania (Wood et al. 2011a). In his 'ecological drift' model Jackson (1968) argued that each vegetation community in southwest Tasmania actively modifies the rate of fuel accumulation and fuel characteristics (and therefore fire frequency), soil nutrient capital and light environment in a direction that enhances its own growth and survival, and simultaneously hinders or constrains other vegetation types (Fig. 1). Jackson (1968) suggested that these positive feedbacks engender an inherent resilience to vegetation change, but also included the possibility that highly improbable deviations from average fire frequencies can push an otherwise stable vegetation community beyond its 'resilience threshold' and cause a transition to an alternative vegetation community (Fig. 1).

Mount (1979) proposed an alternative model for southwest Tasmania that underscores the importance of site characteristics and predicts geographically static vegetation patterns (Fig. 1). This so-called 'stable fire cycles' model is effectively a 'one-factor sharpening switch' (sensu Wilson and Agnew 1992) where fire merely reinforces environmentally determined vegetation patterns. Whilst Jackson's alternative stable states model allows for vegetation state transitions, Mount's model suggests that the positive feedbacks between fire and vegetation are strong enough to eliminate vegetation state transitions and that physical environmental factors exert significant control over vegetation patterns. Accordingly, fire alone does not determine vegetation; rather, the risk of fire is determined by vegetation, which in turn, is related to 'site factors' in the landscape (i.e. geology, drainage, topography).

Testing the efficacy of these competing models— and alternative stable states models in general—

requires multiple lines of ecological evidence collected at a range of appropriate temporal and spatial scales (Petraitis and Latham 1999; Thomas et al. 2010). In southwest Tasmania there has been a multitude of millennial scale palaeoecological studies (reviewed by Thomas et al. 2010) which have traditionally favoured scenarios of fluctuating vegetation patterns in response to quaternary climate change (Macphail 1979; Colhoun 1996). However, Fletcher and Thomas (2007, 2010) recently posited largely stable vegetation patterns throughout the Holocene, arguing that moorland and rainforest was held in place by regular aboriginal burning and underlying edaphic features in the landscape. These palynological studies are necessarily limited in their spatial resolution and cannot detect short-term shifts in vegetation boundaries; a problem that could not be overcome using stable carbon isotopes in the organic soils of the region (Wood et al. 2011b). Studies in the region focussing on shorter temporal scales are limited to a spatially restricted set of monitoring plots which showed negligible shifts in boundaries between structural types in southwest Tasmania over a 20 year period (Brown et al. 2002). Thus the historical context for understanding the dynamics of this region remains limited and ecologists have relied on modelling (Henderson and Wilkins 1975; King et al. 2006) and space-for-time chronosequences (Brown and Podger 1982; Bowman et al. 1986) to infer vegetation dynamics and engender a general acceptance of the Jackson (1968) alternative stable states model (Bowman and Wood 2009). The question remains: are forest boundaries stable or shifting over decadal to century scales? If so, what are the environmental drivers of these dynamics and are they related to feedback mechanisms that act to maintain alternative stable vegetation communities?

We used sequences of remotely sensed images to investigate decadal scale dynamics of forest and non-forest vegetation communities in southwest Tasmania. Analysis of historical sequences of aerial photographs and satellite images have provided invaluable 'snapshots' of change in vegetative cover since the 1940s (reviewed by Fensham and Fairfax 2002) and have been particularly powerful in detecting often surprising savannah and rainforest dynamics in Northern Australia (reviewed by Bowman et al. 2010). When combined with spatially explicit data on disturbance regimes (i.e. fire, herbivory) and resource availability
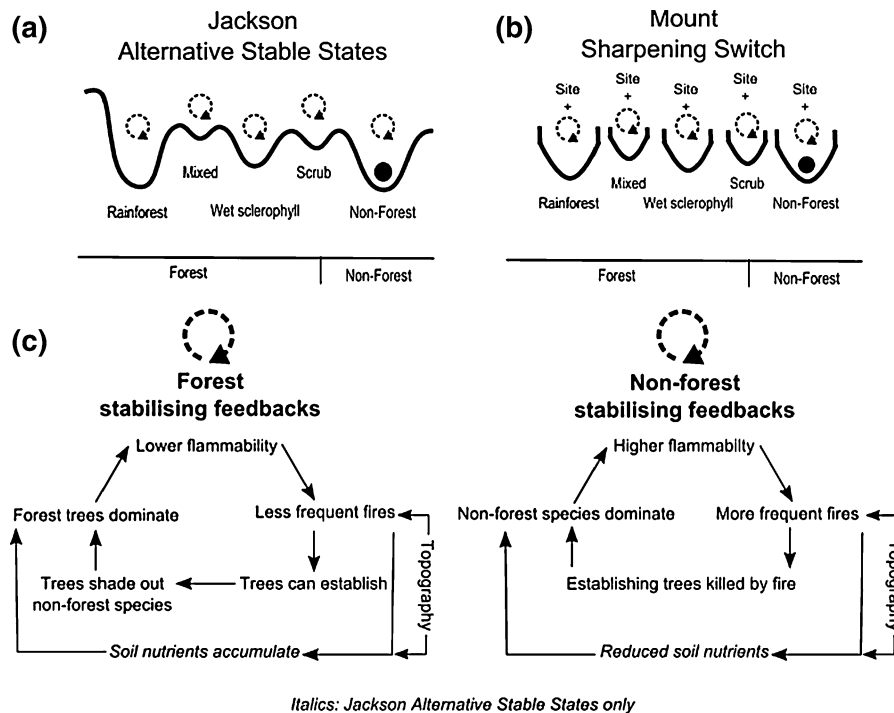
Fig. 1 Models of vegetation dynamics for southwest Tasmania illustrated with the 'ball and cup' (or 'stability landscape') heuristic model commonly used to describe alternative stable states (see Scheffer et al. 2001; Warman and Moles 2009). **a** In Jackson's (1968) 'alternative stable states' model each vegetation community can occupy any underlying physical environmental setting. Each potential vegetation state is determined by fire–vegetation–soil feedbacks (**c**) and the cumulative effect of these feedbacks is represented by resilient 'basins of attraction'. A vegetation community—represented by the ball—will resist disturbance by fire initially and return to the original state, but if pushed beyond the threshold by repeated stand replacing fire (or lack thereof), positive feedbacks from the neighbouring stable state will take over and the system will undergo a transition to another stable state. **b** In Mount's (1979) 'sharpening switch' model each vegetation community is initially determined by the underlying physical environment (or 'site', sensu Mount 1979). Feedback mechanisms between fire and vegetation (**c**) reinforce these patterns by creating deeper 'basins of attraction'. The resilience created by these feedbacks is strong enough to prevent vegetation state transitions creating stable vegetation patterns. **c** Conceptual model showing the stabilising feedbacks that maintain the forest and non-forest vegetation states investigated in this study. Adapted from Petraitis and Latham (1999)

(i.e. rainfall, soil type) these maps of vegetation change can unlock the mechanisms driving vegetation dynamics in the landscape (e.g. Brook and Bowman 2006; Banfai et al. 2007). In this study we used aerial photographs and high resolution satellite imagery from 1948, 1988 and 2010 to document the dynamics of forest and non-forest vegetation cover over 62 years for a ~60,000 ha region in remote southwest Tasmania. We then linked these observed dynamics with available spatial proxies for fire spread (Wood et al. 2011a) to investigate some of the key concepts proposed by Jackson (1968) and Mount (1979).

A second aim of our study was to investigate whether the chemical and physical properties of soils in forest and non-forest communities have the potential to influence vegetation dynamics. Jackson (1968, 2000) proposed feedbacks between vegetation, fire and the regions unique organic soils that act to further stabilise vegetation communities (Fig. 1). Frequent fires in flammable vegetation communities are hypothesised to deplete nutrient stocks to an extent that impedes the development of forest vegetation (see Bond 2010) and—in contrast—rarely burnt forest vegetation has the potential to accumulate nutrients in its biomass and underlying organic soils enabling rapid post-fire recovery of forest vegetation. Similar feedbacks invoking soil characteristics are discussed for other vegetation mosaics purported to function as fire-mediated alternative stable states (Perry and Enright 2002; Hoffmann et al. 2009; Murphy et al.

2010; Odion et al. 2010). Field studies have found disparities in nitrogen and phosphorus in organic soils between forest and non-forest vegetation across three boundaries in southwest Tasmania (Bowman et al. 1986; Wood et al. 2011b), but the generality of these results across the landscape is yet to be tested. Further, Pemberton (1989) and di Folco (2007) noted that forest and rainforest vegetation in southwest Tasmania may be associated with sites with relatively clay rich mineral soils, which, if true, would lend support to Mount's (1979) emphasis on physical environmental variables such geology and its constituent soils exerting significant controls on vegetation patterns. We collected soil samples from organic and mineral soil horizons to test whether soil characteristics (phosphorus, nitrogen, clay and silt) differ across forest–non-forest boundaries.

Methods

Study area

The study was focused on the remote Melaleuca region (Fig. 2) in southwest Tasmania—an area that is conserved as part of the Tasmanian Wilderness World Heritage Area. The regional climate is classified as perihumid cool (Gentilli 1972) with an average annual rainfall at Melaleuca of approximately 2,400 mm (Brown and Podger 1982). Approximate mean winter and summer minimum and maximum temperatures are 3 and 10°C, and 10 and 20°C, respectively. Infertile Precambrian metamorphic rocks dominate the region's geology (Pemberton 1989). Multiple glaciations during the quaternary have created a terrain characterised by rugged mountains emergent from broad terraced plains of glacial outwash (Macphail et al. 1999). Lowland vegetation throughout southwest Tasmania forms a mosaic of treeless heath-moorland, sclerophyllous scrub, eucalypt forest and rainforest vegetation with shallow to deep organic soils forming under all vegetation types (Wood et al. 2011b). Aboriginal occupation in the region stretched back to 35,000 years BP which provided an ignition source to the region that was independent of climate (Fletcher and Thomas 2010). European colonisation caused the expatriation of the Aboriginal tribes and the creation of a wilderness, except for localised small-scale tin mining operations at Melaleuca and Coxes Bight (Fig. 2).

Humans remain the predominant ignition source of wildfires, although lightning is known to start fires. Fire maps of the study area (Marsden-Smedley 1998) suggest that almost two thirds of the study area were affected by a wildfire in 1933/1934 which burned over 600,000 ha of southwest Tasmania (Marsden-Smedley and Kirkpatrick 2000).

Landscape change analyses

Repeat image analysis of vegetation dynamics 1948–2010

Digitised aerial photographs from 1948 (black and white; 1:16,000) and 1988 (colour; 1:25,000), and an 0.5 m resolution panchromatic World-View 2 satellite image from 2010 were analysed to assess vegetation cover. Ortho-rectified mosaics of 1948, 1988 and 2010 imagery covering the study area were created using the ortho-photography software Landscape Mapper (Myriax Software Pty Ltd, Hobart: http://www.myriax.com). A comprehensive landscape wide analysis of these image-mosaics was not possible because of localised regions of blurred 1948 imagery or misaligned image sequences, particularly on photo-mosaic joins. Instead we focussed our analysis on a series of sixty-seven 600 m × 600 m sample areas distributed randomly across parts of the landscape that did not coincide with (a) overtly blurred 1948 imagery, (b) an image-mosaic join or (c) a $\sim$3 km buffer around the tin-mining areas at Melaleuca and Coxes Bight (Fig. 2). At each sample area, the 1948, 1988 and 2010 images were clipped to the 600 m × 600 m squares and overlaid within ArcGIS10, where obvious misalignments were corrected using the spline function in the ArcGIS10 Georeferencing Toolbox.

A 30 × 30 grid of 20 m² cells ($n = 900$) were overlaid onto each sample area and the vegetation of each cell was manually classified for 1948, 1988 and 2010 at a common scale of 1:2,500 (Fig. 2). We used a classification scheme of 'treeless moorland and low scrub' (herein, 'non-forest', NF) and 'tall scrub and forest with trees' (herein, 'forest', F) based on the presence of tree canopies occupying >50% of the cell. More detailed classification systems were prohibited by the quality of the 1948 aerial photographs and the resolution of the 1988 aerial photographs. These classifications were necessarily subjective and consequently only one of us (SW) conducted this task. The

Fig. 2 **a** Map of Melaleuca Study Area in southwest Tasmania showing the extent of forest cover (31.9%: Harris and Kitchener 2005), the location of 67 sample grids used in repeat image analysis and the locations of 34 soil sampling transects. **b** An example of repeat image analysis using aerial photography (1948 and 1988) and satellite imagery (2010). At this location the area of forest increased by 4.0% between 1948 and 1988 and then 0.9% from 1988 to 2010. Soil profile locations for this sample area are also shown
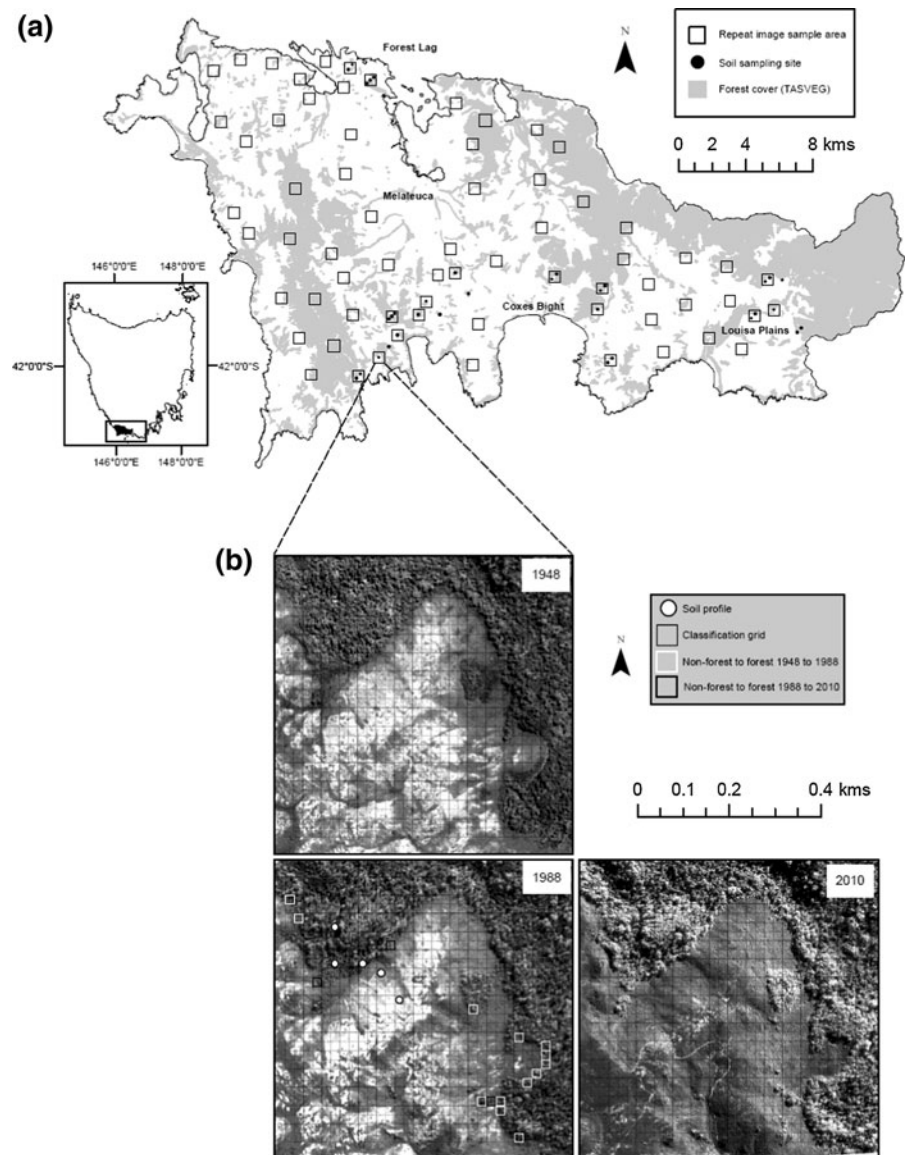
accuracy of our classification was assessed using the GPS location of assessments of vegetation type (i.e. forest or non-forest) made at 169 points collected during the field survey of soils described below. Our sampling design appeared to be representative of the wider landscape given that the proportional area classified as forest in our sampled areas in 1988 (Fig. 2; ~2,304 ha; 31.2%) compares well with the proportion of forest calculated from the TASVEG mapping product for the Melaleuca Study Area (Fig. 2; ~65,000 ha; 31.9%) and the nutrient poor substrates of southwest Tasmania (Wood et al. 2011a; ~540,000 ha; 34.3%).

To examine the dynamics of individual cells, we calculated the percentage of forested (F) and non-forested (NF) cells that changed (i.e. F–NF or NF–F) or remained stable (i.e. F–F, NF–NF) between the two time periods (1948–1988 and 1988–2010). For all cells that changed from non-forest to forest (NF–F), we calculated the distance to the nearest forest (F) cell in each grid using the Spatial Join tool in ArcGIS10. The total area—in hectares—of forest (F) and non-forest (NF) vegetation in our sampled area was calculated based on each cell being 0.4 ha. This information was used to calculate statistics for vegetation cover and vegetation cover change over time.

Testing the effect of fire on vegetation dynamics

We used two proxies for fire to investigate the effect of fire on observed boundary dynamics from the repeat image analysis. Firstly, we used digitised maps of fires (Marsden-Smedley 1998) to provide a broad-scale understanding of fire activity in our study area. Using these maps, each cell in our sampled area was attributed with the presence/absence of fire for the 20–22 year periods 1928–1948, 1948–1968, 1968–1988 and 1988–2010. The coarse spatial resolution of these fire maps precluded detailed spatial analysis.

Secondly, we adopted the modelling framework of Wood et al. (2011a) to test whether parts of the landscape that changed from non-forest (NF) to forest (F) were the result of regeneration of forest after a stand-replacing fire. In an analysis of patterns of fire spread, Wood et al. (2011a) showed that fire in southwest Tasmania preferentially burns particular parts of the landscape terrain—namely, ridges and flats but not valleys; and steep northern slopes but not steep southern slopes. We hypothesised that if parts of the landscape that changed from non-forest to forest show the same relationships with topography as those observed between fire and topography, then it is likely that this change is associated with the regrowth of forest canopies following stand-replacing fire.

We randomly selected 4,000 cells that were classified as forest in 1988 and attributed each cell with a presence/absence of non-forest to forest change (NF–F) between 1948 and 1988. Each cell was also assigned three topographic attributes derived from a digital elevation model (topographic position, northness index, elevation; see Supplementary material). The same cell attribution process was repeated for cells that changed from non-forest to forest (NF–F) between 1988 and 2010. All combinations, without interactions, of the three topographic variables considered important correlates of non-forest to forest conversion were constructed in generalised autoregressive error (GAR$_{err}$) models (Murphy et al. 2010; Wood et al. 2011a). This type of model has been recently developed by Murphy et al. (2010) to analyse spatially autocorrelated non-normal data. It is analogous to the simultaneous autoregressive error model for normal data (Cressie 1993), but can cope with non normal data types in the same way as a generalised linear model. All statistical analysis was done with R (v.2.12; R Foundation for Statistical Computing, Vienna, Austria).

Change from non-forest to forest represented presence/absence data and was modelled using binomial errors. Models were evaluated using a robust form of Akaike's Information Criterion, AIC$_c$, a model selection index favouring both model fit and model simplicity (Burnham and Anderson 2002). Lower values of AIC$_c$ indicate greater support for a model, relative to other models in the same candidate set. From AIC$_c$, Akaike weights (w_i) were calculated for each model, and these are equivalent to the probability of a given model being the best in the candidate set. The importance of each variable was evaluated by calculating $w+$, the sum of w_i for all models in which that variable occurred. For each variable, $w+$ is equivalent to the probability of the best model containing that variable, and is a useful expression of the weight of evidence for the importance of the variable. We considered that $w+$ values of <0.73 were indicative of substantial model selection uncertainty. A $w+$ value of 0.73 is equivalent to an AIC$_c$ difference of two units between models containing the variable under examination and those not containing it. An AIC$_c$ difference of two units is a common 'rule of thumb' used by ecologists to assess clear evidence of an effect (Richards 2005).

Soil characteristics of forest and non-forest vegetation

Soil sampling

We established 34 transects across forest boundaries prior to our repeat image analysis, with locations and boundary delineation based on existing vegetation mapping from 1:25,000 aerial photography (TAS-VEG: Harris and Kitchener 2005). Vegetation change trajectories and the distance to the forest boundary for each soil profile were subsequently determined using data from the repeat image analysis described above. On each transect we dug five soil profiles—three in forest and two in non-forest—and recorded the location in a GPS (Fig. 2). The 'forest' soil profiles were situated in rainforest, mixed eucalypt-rainforest or sclerophyll forest >5 m tall. The 'non-forest' profiles were situated in treeless moorlands dominated by buttongrass (*Gymnoschoenus sphaerocephalus*) with or without a low (<2 m) heathy scrub component. Topographic position was classified into valley, ridge, valley flat, upper, mid and lower slope. Soil pits were

dug down to the regolith, rocky substrate or an impenetrable gravel layer. The depth of the organic and mineral layers were measured and the organic layer classified to a simplified von Post scale (i.e. sapric, hemic or fibric; Isbell 2002). We collected samples from the upper 10 cm (usually organic, but sometimes mineral) and from the lowest distinguishable soil horizon (usually mineral but sometimes organic).

Lab methods

The organic content of all soil samples from the upper and lower horizons was derived by loss on ignition, where 5–10 g samples were combusted at 550°C for 6 h. Given our statistical design (see below) we conducted our analyses only on soil profiles that included a distinct mineral horizon (i.e. lower profile organic content <20%; Isbell 2002). Soil samples from the upper 10 cm were ground to powder in a Retsch MM200 ball mill (MEP Instruments Australia, North Ryde, Australia) and analysed for total phosphorus and total nitrogen. For phosphorus analysis, ground soil samples were dried at 70°C for 24 h, finely ground, and digested in concentrated sulphuric acid on an open block digester. Total phosphorus concentrations were determined colorimetrically using a modified ascorbic acid method (Kuo 1996). Soil samples were analysed for nitrogen concentration on a Perkin Elmer 2400 Series II elemental analyser (Analytical Development Company, Adelaide, Australia). We conducted a particle size analysis on all soil samples from the lower profile using a hydrometer to determine the percent sand (0.2 mm), silt (0.02 mm) and clay (0.002 mm) (Australian Standard AS1289.3.6.30). All samples were pre-treated with hydrogen peroxide to remove organic matter.

Statistical analysis

We evaluated the importance of four soil variables in explaining differences in vegetation across forest–non-forest boundaries: (1) total phosphorus and (2) total nitrogen in the upper horizon; and (3) percent clay and (4) percent silt in the lower horizon. Drawing on the fire–vegetation–soil interactions outlined in Fig. 1, we hypothesised that phosphorus and nitrogen would be higher in forest vegetation compared to non-forested vegetation (Jackson 1968; Bowman et al.

1986; di Folco 2007; Wood et al. 2011b) and that forest vegetation would preferentially occupy sites with finer textured soils (Mount 1979; Pemberton 1989; di Folco 2007).

Topography is a key driver of soil processes in southwest Tasmania (Wood et al. 2011b), with topographic position (i.e. basin, slope, shelf) influencing the effects of fire and drainage on soil accumulation and carbon dynamics in the region (di Folco and Kirkpatrick 2011). We followed the logic of di Folco and Kirkpatrick (2011) and divided our dataset into two topographic classes: (1) soil profiles from 'run-off' topographic positions such as ridges, mid slopes and upper slopes; and (2) soil profiles from 'run-on' topographic positions such as valleys, valley flats and footslopes. For each of these two datasets, models representing all combinations of the four soil response variables, without interactions, were constructed as linear mixed effects models and analysed using the lme4 package (Bates et al. 2008) in R (v.2.12; R Foundation for Statistical Computing, Vienna, Austria). Mixed effects models allowed us to account for the correlation between soil variables located on the same transect. The vegetation type (forest or non-forest) explanatory variable was considered on the basis of the presence/absence of forest and was modelled using binomial errors. Models and response variables were evaluated using the same approach outlined above (i.e. AIC_c and $w+$). Finally, we examined the relationship between total phosphorus and distance from the forest boundary.

Results

Repeat image analysis of vegetation dynamics

There was a strong concordance between our image classification and field classified vegetation types, with the correct image classification of 163 of 169 (97%) field surveyed points. The vast majority of cells classified as non-forest (NF) or forest (F) remained the same through time (NF–NF, F–F), with negligible change from forest to non-forest (F–NF) but a modest amount of change from non-forest into forest (NF–F; Fig. 3). The total area of forest in our sampled area (2,304 ha) increased from 700 ha (29.9%) in 1948 to 729 ha (31.2%) in 1988 to 735 ha (31.4%) in 2010. The proportional change in forest area (relative to the

initial forest coverage on the earliest image) differed for the two time periods with a 4.1% increase in forest area from 1948 to 1988 and a 0.8% increase in forest area from 1988 to 2010. Most areas transitioning from non-forest to forest were situated within 20 m of the forest boundary (Fig. 4).

Assessment of broad scale fire maps (Marsden-Smedley 1998) revealed a decline in fire activity in our sampled area. The proportion of repeat image analysis sample cells burnt for each time period examined was 61% (1928–1948, all in summer 1933/1934), 3% (1948–1968), 3% (1968–1988) and 12% (1988–2010). There were no topographic variables that were strongly correlated with cells that changed from non-forest to forest from 1988 to 2010 (Table 1). However, modelling showed that cells that changed from non-forest to forest between 1948 and 1988 were clearly correlated with topographic position and northness index (Table 1; see Supplementary material). According to the selected model, the increase in forest area from 1948 to 1988 was more likely to occur on flats, gentle slopes and ridges, but not valleys; and steep northern slopes compared with steep southern slopes (Fig. 5a).

Fig. 4 Proportion of all classified cells that transitioned from non-forest (NF) to forest (F) that occurred at different distances from the forest boundary for the periods 1948–1988 and 1988–2010

Table 1 Importance values (Akaike weights, $w+$) for fire-related topographic variables thought to explain the transition from non-forest to forest between 1948–1988 and 1988–2010 respectively

Topographic variable	Non-forest to forest ($w+$)	
	1948–1988	1988–2010
Topographic position	0.99	0.25
Northness index	0.96	0.34
Elevation	0.31	0.30

Model summaries are provided in Supplementary material

Soil characteristics of forest and non-forest vegetation

Of the 169 soil profiles, 41 lacked a mineral horizon and were excluded giving us a final dataset of 128 soil profiles (Table 2). Examination of the 1948, 1988 and 2010 photo sequences revealed that vegetation at all 128 soil profiles has remained stable for the past 62 years. In general, the forested profiles were dominated by shallow to deep fibric upper horizons whereas the non-forest profiles were dominated by shallow to deep sapric and hemic upper horizons (Table 2). The lower horizons of both forest and non-forest soils were dominated by sand, with clays present in only small amounts (Table 2). Model selection ($w+$) suggested that the contrast between forest and non-forest vegetation was strongly correlated with total phosphorus on all topographies and percent clay on slopes, but less strongly correlated with total nitrogen or percent silt (Fig. 6; see Supplementary material). Accordingly, both phosphorus and clay were higher in soils under forest compared to
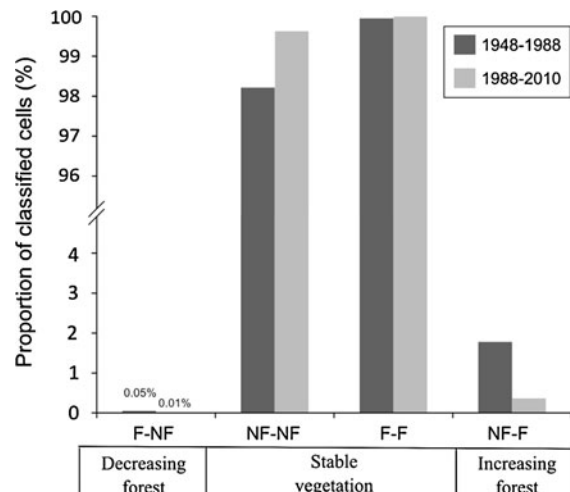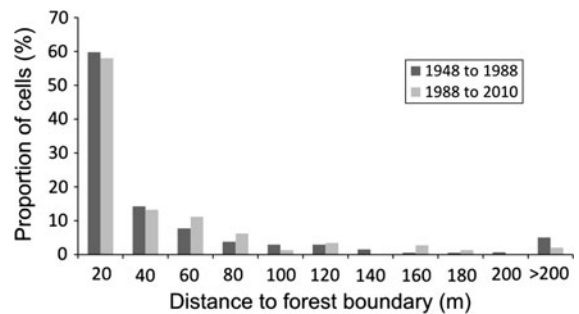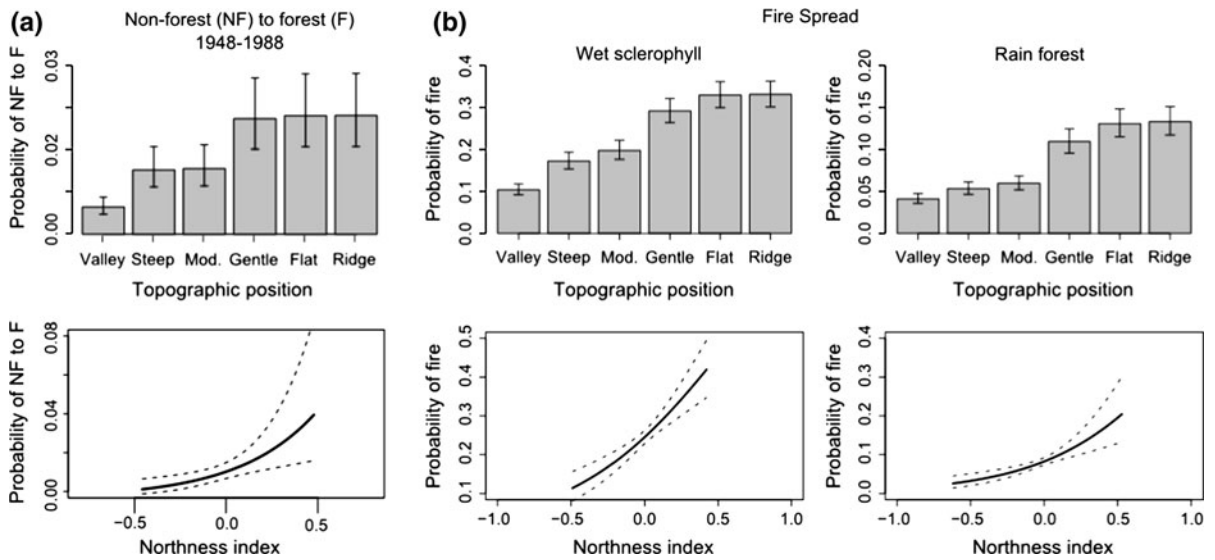

Fig. 3 The proportion of cells ($n = 58,493$) from repeat aerial image analysis classified as forest (F) or non-forest (NF) that stayed the same (i.e. F–F or NF–NF) or changed (i.e. F–NF or NF–F) between 1948–1988 and 1988–2010, respectively. Indicative forest dynamics are indicated below the X axis. Note the break in the Y axis

Fig. 5 a The modelled relationship between parts of the landscape that changed from non-forest (NF) to forest (F) between 1948 and 1988 and the variables topographic position and northness index (this study; see Table 1). **b** The modelled relationship between fire occurrence and the variables

topographic position and northness index in wet sclerophyll and rainforest vegetation (reproduced from Wood et al. 2011a). The northness index represents a gradient from steep southern slopes (strongly negative values) to steep northern slopes (strongly positive values). The 95% confidence intervals are shown

	Forest		Non-forest	
	Slope–ridge	Valley–flat	Slope–ridge	Valley–flat
Number of profiles	52	27	29	20
Organic horizon depth (cm)				
Mean	14.4	15.4	18.0	27.5
Range	2.0–44.0	2.0–50.0	2.0–63.0	0.0–50.0
Mineral horizon depth (cm)				
Mean	24.6	34.0	21.5	15.9
Range	5.0–60.0	5.0–100.0	5.0–70.0	5.0–35.0
Organic horizon texture (%)				
Fibric	**77**	**81**	0	0
Hemic	8	4	8	25
Sapric	2	4	**52**	**60**
Inorganic	13	11	10	15
Mineral horizon texture (%)				
Sand	**79.8**	**79.8**	**87.8**	**90.9**
Silt	15.8	17.3	11.9	9.0
Clay	4.4	2.9	0.3	0.1

Table 2 Soil characteristics for 128 soil profiles collected from two topographic settings ('run-off' slopes and ridges; 'run-on' valleys and flats) in forest and non-forest vegetation

The mode for organic horizon texture and mineral horizon texture are indicated in bold. Mineral horizon depth is indicative only as the maximum depth of 18 profiles was not reached

non-forest vegetation (Fig. 6). However, there was considerable overlap of the ranges and quartiles of measured soil properties across vegetation types

(Fig. 6). Total phosphorus showed a systematic decrease across the forest–non-forest vegetation boundary (Fig. 7).

Discussion

Vegetation dynamics from repeat image analysis

Our analysis of time-series aerial photography revealed remarkably stable vegetation patterns in the study area with the vast majority of classified vegetation remaining stable between 1948 and 2010 (62 years). Nevertheless, we identified some modest increases in forest cover. Between 1948 and 1988, forest cover in the study area increased by 4.1% and this increase was more likely to occur on forest edges associated with flats, ridges and steep northern slopes and less likely to occur in valleys and on steep southern slopes. These relationships between topographic positions and probability of forest cover change mirror the findings of Wood et al. (2011a) who showed that forest fires in southwest Tasmania most commonly burn on ridges, flats and north facing slopes, and rarely burn in valleys and steep southern slopes (compare Fig. 5a and Fig. 5b). Collectively, this suggests that the increase in forest area prior to 1988 is linked to the regrowth and regeneration of trees following stand-replacing fire prior to 1948. Examination of available fire maps point to the 1933/1934 fire that is estimated to have burnt approximately 22–24% of forest vegetation in southwest Tasmania (Marsden-Smedley 1998; Marsden-Smedley and Kirkpatrick 2000), however field studies within these areas of forest regeneration are required to rule out the possibility of currently unmapped pre-1948 fire events.

Between 1988 and 2010 forest cover increased by only 0.8% and this increase was not associated with topographic setting. There were few fires in the landscape in the two decades pre- or post-1988 and this would explain why we found no support for a relationship between topographic settings conducive to fire and the increase in forest area. In the absence of post-fire recovery, we suggest that the forest increase during this period is due to the establishment of trees (largely by seed) in long unburnt moorland and low scrub communities. It appears that this forest expansion was strongly associated with distance to forest edge and was extremely slow. Indeed, field evidence from long-term monitoring plots at Forest Lag within our study area (Fig. 2) support our findings, with Brown et al. (2002) reporting only minor shifts in the boundaries between moorland and scrub communities

and no apparent shifts in the boundaries between scrub and forest over 20 years from 1980 to 2000.

The relatively low rate of forest expansion in our study area becomes apparent when compared with other studies that have analysed forest boundary dynamics using sequences of aerial photography in Australia. Discounting the 1948–1988 forest increase that we assume to be related to forest recovery following fire (see above), we estimate an increase of total forest cover of <1% over 62 years. In contrast, repeat aerial photography studies have revealed a 13–97% increase in monsoon rainforest cover in tropical savannas over 40–53 years in Northern Australia (reviewed by Bowman et al. 2010), a 2–8% increase in rainforest cover in a savanna matrix over 53 years in Far North Queensland (Tng et al. 2010) and a 8–12% increase in eucalypt and rainforest cover over 55 years in Northern Tasmania (Sanders 2010). Given these emerging patterns of markedly different forest boundary dynamics observed across the Australian continent, it is likely that local factors (e.g. changed fire regimes, edaphic factors, land use history; Bowman 2000) may be just as important as proposed continental factors (e.g. increased rainfall and/or CO_2 fertiliser effect; Bowman et al. 2010) in driving landscape-scale vegetation dynamics.

The role of soil on vegetation stability

Our findings of higher phosphorus in forest compared to non-forest vegetation provide landscape scale confirmation of similar trends in phosphorus found across other boundaries in southwest Tasmania (Bowman et al. 1986; Wood et al. 2011b). This is consistent with Jackson's (1968, 2000) hypothesis that repeat fires deplete nutrient stocks in the organic soils of frequently burnt non-forest vegetation and that the absence of fire in forested vegetation allows net nutrient accumulation. Jackson (1968, 2000) and other studies proposing fire-mediated alternative stable states in vegetation (Wilson and Agnew 1992; Perry and Enright 2002; Hoffmann et al. 2009; Murphy et al. 2010; Odion et al. 2010) argue that such gradients in soil nutrients engender an increased degree of resilience by contributing an additional barrier to tree growth (along with fire) in non-forest vegetation (i.e. Bond 2010) and facilitating rapid post-fire tree growth in forested vegetation (i.e. Hoffmann et al. 2009).

Fig. 6 Box plots (median, quartiles, range) and importance values (Akaike weights, *w*+; *inset*) for four soil variables (phosphorus, nitrogen, clay, silt) thought to be correlated with the contrast between forest and non-forest vegetation in two topographic settings. Importance values were calculated separately for the two topographic settings. Model summaries are provided in the Supplementary material
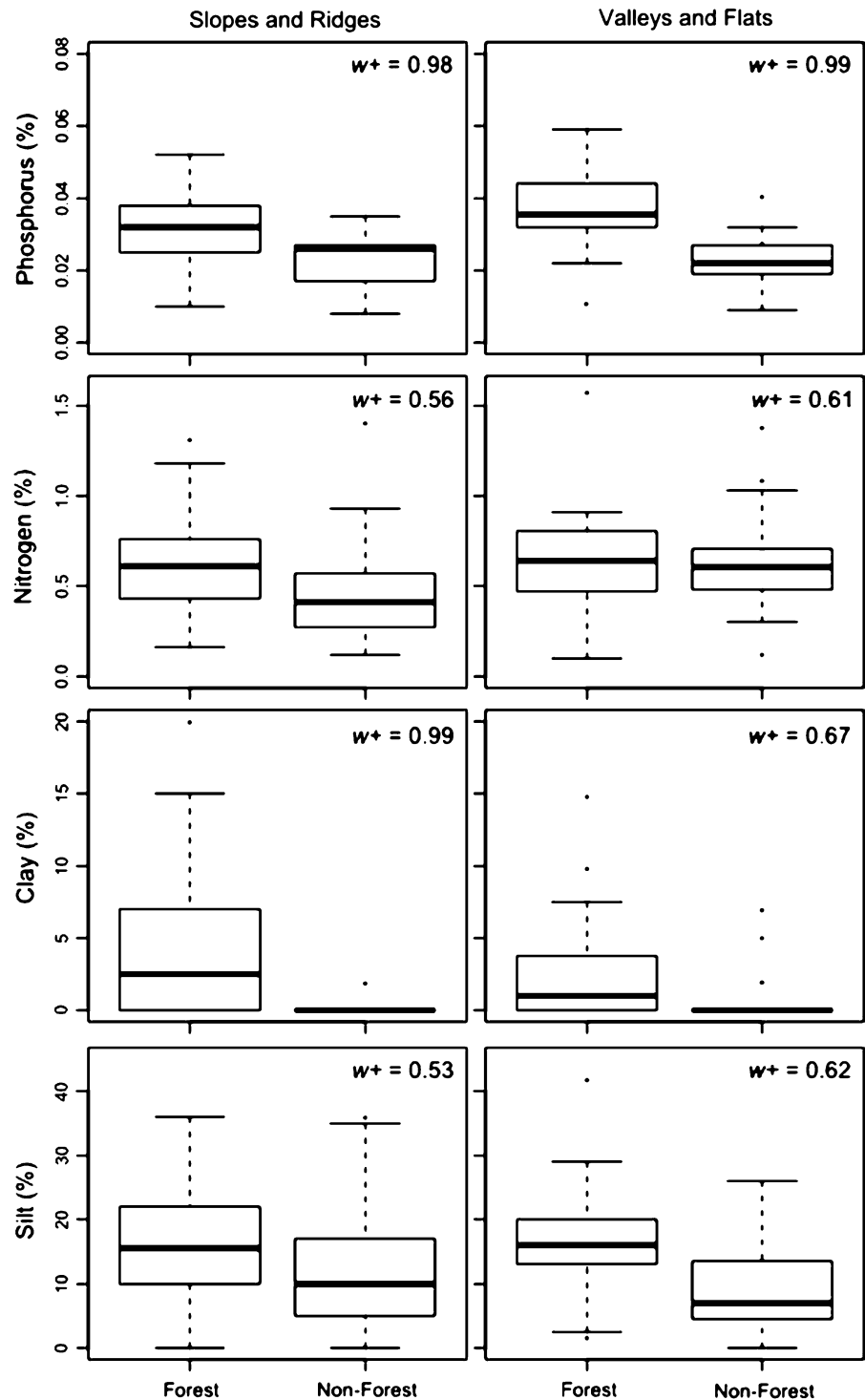
Whether observed differences in phosphorus are the cause or the effect of vegetation and fire is difficult to untangle without manipulative experiments, although the trend of phosphorus decreasing (into non-forest) and increasing (into forest) systematically with distance from the forest boundary lends tentative support to the concept of fire–vegetation–soil feedbacks (Fig. 7). Regardless of cause and effect, we posit that
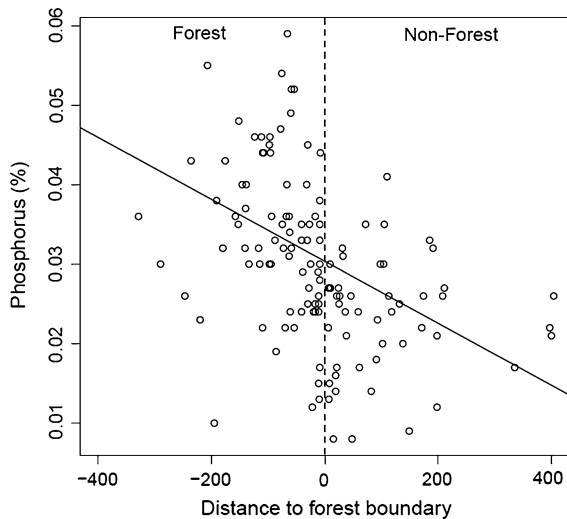
Fig. 7 The trend in total phosphorus with distance from the forest–non-forest boundary. The *dotted line* indicates the position of the boundary. Negative distances refer to soil profiles within the forest and positive distances refer to soil profiles within non-forest. A linear regression model was fitted to the data ($r^2 = 0.17$, $n = 128$)

the observed phosphorus gradient would contribute to the extremely slow rate of forest expansion in our study area. Importantly, however, we do not suggest that phosphorus entirely precludes tree growth in non-forest areas given that forest vegetation was found to grow on soils with low levels of phosphorus (Figs. 6, 7; see also Read 2001; Wood et al. 2011b). Reciprocal transplant experiments (i.e. Maranon and Bartolome 1993; Peltzer 2001), where forest species are planted in non-forest soil and vice versa, are an obvious pathway for future investigations into the influence of fire–vegetation–soil feedbacks in southwest Tasmania. The effects of added nutrients and different burning regimes could be incorporated into these experiments.

Whilst there has been considerable attention focussed on the unique organic upper horizons of southwest Tasmanian soils (e.g. Bowman et al. 1986; di Folco 2007; Wood et al. 2011b), the nature and characteristics of the underlying mineral horizons have been largely ignored (but see Balmer 1990). We showed that the mineral soil horizons underlying all vegetation types in southwest Tasmania are dominated by sand—a result that is not surprising given the predominance of quartzitic substrates across the landscape. Our modelling showed that the clay content of mineral horizons constitute an important point of difference between soils associated with forest and

non-forest vegetation on ridges and slopes, with percentage clay being higher in forest vegetation. However, despite the statistically significant trend we detected, the clay content of forested soils is still very low (Fig. 6) and may not be functionally important to plant growth and therefore rates of forest expansion in southwest Tasmania. Therefore, we consider it unlikely that the underlying geological substrate and its mineral soils are controlling forest–non-forest boundaries associated with the Precambrian quartzites that dominate the Melaleuca Study Area and greater southwest Tasmania.

Alternative stable states in southwest Tasmania?

Whilst well documented theoretically, demonstrating alternative stable states in terrestrial landscapes with long lived species is inherently difficult, with few studies able to meet the criteria required to unambiguously demonstrate vegetation stability or persistence (Petraitis and Latham 1999; Beisner et al. 2003; Schroder et al. 2005). Southwest Tasmania is no exception, however, the evidentiary basis upon which assessments of the proposed ecological models can be based (Table 3; see also reviews by Bowman 2000; Bowman and Wood 2009; Thomas et al. 2010) is equivalent to most other studies that speculate fire-mediated alternative stables states in similar terrestrial landscapes (e.g. Perry and Enright 2002; Latham 2003; Hoffmann et al. 2009; Warman and Moles 2009; Odion et al. 2010; Nicholas et al. 2011).

The lowlands of southwest Tasmania have been the subject of a range of historical ecology studies that have revealed predominantly stable vegetation patterns at decadal to millennial time-scales (Table 3). This supports the concept of long term resilience of vegetation communities inferred by both Jackson (1968) and Mount (1979) (Fig. 1). However, observations of localised vegetation transitions close to forest boundaries (Table 3) appear to be more congruent with the state-transition dynamics inherent in Jacksons (1968) alternative stable states model rather than the fixed vegetation boundaries postulated by Mount (1979). Nevertheless, our analyses of sequences of aerial photographs indicate that the expansion of forest into non-forest vegetation is far slower than Jackson (1968) implied.

The ubiquity of sand dominated mineral soil profiles with very low levels of clay across vegetation

Table 3 Field evidence from southwest Tasmania relating to key processes in the alternative stable states model of Jackson (1968) and the sharpening switch model of Mount (1979)

Hypothesis	Model	Evidence
Vegetation patterns largely resilient to change	Jackson and Mount	Overall stability of core vegetation communities over 20 years based on permanent plots (Brown et al. 2002)
		Overall stability of core vegetation communities over 62 years based on aerial photography (this study)
		Overall stability of vegetation communities throughout the Holocene inferred from pollen studies (Fletcher and Thomas 2007, 2010)
Transitions between vegetation types can occur	Jackson	Vegetation transitions near forest boundaries over 20 years based on permanent plots (Brown et al. 2002) and vegetation structure and floristics (Brown and Podger 1982)
		Vegetation transitions near forest boundaries over 62 years based on aerial photography (this study)
		Rainforest converted to moorland by recurrent fires over ~100 years (Podger et al. 1988)
Each vegetation community has a characteristic fire frequency (fire–vegetation feedback)	Jackson and Mount	Time since fire varies systematically amongst vegetation communities (Jackson 1968; Mount 1979; Brown and Podger 1982)
		Flammability varies systematically amongst vegetation communities (Marsden-Smedley and Kirkpatrick 2000; Wood et al. 2011a)
		Rainforest communities limited to infrequently burnt topographic fire refugia (Wood et al. 2011a) and fire-protected islands (Wood et al. 2011b)
Each vegetation community has a characteristic soil nutrient status (fire–vegetation–soil feedback)	Jackson	Nutrient status of organic soils varies systematically according to vegetation and putative fire frequency (Bowman et al. 1986; Jackson 2000; Wood et al. 2011b, this study)
Vegetation distribution dictated by physical environmental variables (i.e. site factors)	Mount	No functionally relevant gradient in mineral soil across vegetation boundaries in landscapes dominated by Precambrian quartzites (Balmer 1990, this study)
		Not tested for drainage patterns and geologically complex landscapes

Refer to Fig. 1 for conceptual diagrams of the two models

types in the Melaleuca Study Area indicate that the distribution and resilience of vegetation is not controlled by the geological substrate and its constituent mineral soils (i.e. Mount 1979). Instead, it seems that a long history of human lit fires burning within a topographically complex landscape dictates the pattern of vegetation (Fletcher and Thomas 2010; Wood et al. 2011a) and that the observed resilience of these vegetation patterns is related to a complex suite of stabilising feedbacks between fire and vegetation, and between fire, vegetation and soil (Table 3). Therefore, the available field evidence lends tentative support to the Jackson (1968) alternative stable states model as the most suitable model of vegetation dynamics in the lowlands of southwest Tasmania although significant modifications of the timeframes for transitions toward rainforest are required.

We caution that our conclusions are context specific and necessarily speculative for a number of reasons.

Firstly, whilst we have shown that Jackson's (1968) model appears work well on Precambrian quartzites that dominate both the Melaleuca Study area and greater southwest Tasmania, the relationship between vegetation and geology in localised regions of southwest Tasmania with more complex geologies (i.e. where limestone, dolerite and quartzite intersect) remains untested. Secondly, the relationship between poorly drained, seasonally waterlogged valley flats and moorland vegetation (Pemberton 1989) has not been investigated. These relationships underpin the Mount (1979) model and could be investigated using the spatial modelling framework of Wood et al. (2011a) but significant improvements in spatial datasets are required before such modelling exercises can be undertaken.

That the vegetation communities of southwest Tasmania may represent a range of alternative stable states has important implications for the management

of the regions high conservation value rainforest vegetation under projected climate and fire scenarios. It is clear from this study that transitions from non-forest to forest in southwest Tasmania are exceedingly slow and forest expansion may be further impeded by the drier, warmer summers and increased fire activity predicted for the region (Lucas et al. 2007; Grose et al. 2010). Under such conditions, rainforest vegetation relying on strong internal feedbacks for their maintenance become vulnerable to a so-called 'fire trap' (Hoffmann et al. 2009; Odion et al. 2010; Lindenmayer et al. 2011). Feedbacks that maintain rainforest vegetation may be weakened by the drying out of currently wet and humid vegetation. Consequently, rapid transitions from rainforest to one of the more flammable communities become increasingly likely. These transitions are quickly reinforced by fire–vegetation–soil feedbacks, thus forcing a hysteresis in the system and creating a largely irreversible 'fire trap'. Detecting the onset of such transitions and subsequently restoring these landscapes presents a considerable research and management challenge (Hobbs and Suding 2008).

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