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ORIGINAL ARTICLE

The origin and temporal development of an ancient cultural landscape

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ABSTRACT

Aim To reconstruct the Late Glacial and Holocene vegetation history of western Tasmania and to test the long-held notion of a replacement of forest by moorland during the mid to late Holocene in western Tasmania, Australia.

Location Western Tasmania, Australia.

Methods Fossil pollen data were screened with a modern pollen dataset using detrended correspondence analysis and charcoal data were analysed using significance tests.

Results At the landscape scale, the distribution of vegetation types in western Tasmania has remained remarkably stable through the post-glacial period. Open moorland has dominated the landscape since the Late Glacial, while rain forest expanded at that time in to areas which it occupies today. Vegetation development in the Holocene is markedly different and charcoal values are significantly higher when compared with those in previous interglacial periods.

Main conclusions The dominant paradigm of a replacement of rain forest by moorland across western Tasmania during the mid to late Holocene is not supported by this regional analysis. The arrival of humans in Tasmania during the Last Glacial Stage provided an ignition source that was independent of climate, and burning by humans through the Late Glacial period deflected vegetation development and facilitated the establishment of open moorland in regions occupied by rain forest during previous interglacial periods. It is concluded that the present dominance of the landscape of western Tasmania by open moorland is the direct result of human activity during the Late Glacial and that this region represents an ancient cultural landscape.

Keywords
Cultural landscape, fire, Holocene, Late Glacial, moorland, pollen analysis, quantitative reconstruction, rain forest, Tasmania.

INTRODUCTION

An appreciation of the long-term history and dynamics of vegetation is integral to our understanding of how plants and associations of plants respond to environmental change. The analysis of fossil pollen, the most abundant proxy for past vegetation dynamics, has revealed much about how, for example, climate change and the activities of humans have influenced vegetation, as well as adding a valuable long-term temporal perspective that enriches studies of vegetation change and landscape evolution. Here, we present an analysis of pollen data using a modern vegetation–pollen database that is aimed at ascertaining, at a broad spatiotemporal scale, the sequence of post-glacial vegetation changes that led to the modern phytogeographical landscape of western Tasmania, Australia, and at addressing a number of long-standing debates over the timing, direction and causes of post-glacial vegetation change in this region.

The post-glacial vegetation history of western Tasmania is complex. Arguments have been put forth for both temporally synchronous and asynchronous vegetation change in response to the latest in a repeated sequence of glacial–interglacial

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transitions, from the Last Glacial Maximum (LGM) to the Holocene (Macphail, 1979; Markgraf *et al.*, 1986; Colhoun, 1996). Both arguments are supported by a limited chronology, and to date this issue is unresolved. Another disputed facet of the post-glacial vegetation history of western Tasmania is the origin and maintenance of over a million hectares of fire-promoted treeless moorland in a landscape where rain forest is the predicted climax vegetation. The moorland system of western Tasmania, a broad classification for a series of treeless communities in which *Gymnoschoenus sphaerocephalus* (Cyerpaceae) is ubiquitous, dominates the landscape and represents one of the largest peatland systems in the Southern Hemisphere. The western Tasmanian blanket moors owe their existence to an anomalous combination of fire and high rainfall (Brown, 1999; Whinam & Hope, 2005) and, like the Lake District of Britain, this region has the curious distinction of being regarded as a wilderness despite recognition as a cultural landscape.

Various models of Late Glacial and Holocene climatic, edaphic and anthropogenic forcing have been derived from pollen sequences to account for the dominance of moorland in western Tasmania; these models invoke either a replacement of forest by moorland after the mid Holocene (Macphail, 1979; Colhoun, 1996) or a Late Glacial inheritance of treeless vegetation (Fletcher & Thomas, 2007a, 2010). Embedded in models of a region-wide replacement of rain forest by moorland during the late Holocene are notions of an earlier expansion of rain forest across the western Tasmanian lowlands driven by a uniform increase in rainfall from the Late Glacial period towards a mid Holocene maximum wetter than the present day (Macphail, 1979; Markgraf *et al.*, 1986; Harrison & Dodson, 1993; Donders *et al.*, 2007). Under these conditions, fire, rare in the modern landscape due to a combination of high rainfall and infrequent lightning strikes (Bowman & Brown, 1986; Kuleshov *et al.*, 2002), was considered ineffective in halting the post-glacial expansion of rain forest, the latest in a predictable sequence of rain forest expansion and contraction driven by glacial–interglacial transitions over the Quaternary period (Colhoun, 1996, 2000; Colhoun & van der Geer, 1998).

Models that depict dominance of the Late Glacial and early Holocene landscape by rain forest have recently been challenged, and instead fire has been implicated in a region-wide expansion of moorland during the Late Glacial (Fletcher & Thomas, 2007a, 2010). This latest model of post-glacial vegetation change is based on numerical analyses of selected fossil pollen spectra from moorland vegetation using a modern pollen database that reveals a remarkably close relationship between modern-pollen spectra and vegetation type in western Tasmania (Fletcher & Thomas, 2007b). In this paper, we use the western Tasmanian modern pollen database to review Late Glacial, Holocene and previous interglacial pollen sequences and analyse charcoal sequences from western Tasmania in an attempt to objectively reconstruct the post-glacial vegetation changes that led to the modern moorland-dominated landscape. We specifically ask: (1) was rain forest the dominant vegetation type during the early Holocene, (2) when did moorland expand in the region, (3) is the dominance of moorland during the present interglacial unique, and (4) what was the main factor responsible for the expansion of moorland in western Tasmania?

WESTERN TASMANIA

Present environment

Tasmania is a large island, approximately the size of Ireland or Sri Lanka, located to the south of mainland Australia between 41 and 44° S. Western Tasmania shares remarkable geographic, climatic and ecological affinities with the west coasts of Chile and New Zealand between 41 and 44° S: mountainous and perennially wet regions where the Southern Hemisphere westerlies impose a cool and wet maritime climate; a annual precipitation range of 1500–3500 mm; and average annual temperatures between 5 and 7 °C in winter (June, July, August) and 14–16 °C in summer (December, January, February) (Nuñez, 1979; Garreaud *et al.*, 2009). Precipitation exceeds evaporation for most of the year and the climate is classed as superhumid (Fig. 1; Gentilli, 1972). Fletcher & Thomas (2007b) provide a detailed description of the vegetation of western Tasmania in relation to pollen analysis and we will only briefly summarize that information here. The regional distribution of vegetation in western Tasmania reflects its variable topography and geology, and the widespread influence of fire. On mountain peaks (above *c.* 900 m a.s.l.) and on elevated areas of the Central Plateau (above *c.* 900–1100 m a.s.l.), alpine communities prevail (Kirkpatrick, 1982).

Below the variable climatic tree line (hereafter termed lowland, *c.* < 900 m a.s.l.) the 'climatic climax' vegetation is *Nothofagus cunninghamii*-dominated rain forest (Jackson, 1968). Arboreal species diversity in western Tasmanian rain forests is generally low, with *N. cunninghamii* sharing dominance throughout its range with podocarps (*Phyllocladus aspleniifolius* and *Lagarostrobos franklinii*), as well as *Eucryphia lucida* and *Atherosperma moschatum* (Jarman & Brown, 1983). Despite an ideal climate for rain forest development (Jackson, 1965, 1968; Brown & Podger, 1982a; Busby, 1986), most (41%) of lowland western Tasmania is dominated by a treeless, fire-promoted plant community: buttongrass moorland (blanket moor) (Brown, 1990, 1999). Broadly speaking, moorland is an oligotrophic system that occupies perennially damp places in which the main plant taxa are sedges (Cyperaceae) and wire-sedges (Restionaceae). Much of the present-day range of moorland extends on to sloping terrain where seasonal drying of the organic substrate is common and where flammable sclerophyll shrub taxa, including Ericaceae and Myrtaceae, are important (Jarman *et al.*, 1988; Brown, 1999).

Some degree of regionalism is evident in the distribution of the lowland vegetation of western Tasmania. Persistent year-round humidity and rainfall in the south-western sector have conspired with fire and a predominance of nutrient-poor quartzitic bedrock to produce a landscape blanketed by moorland (56.2%) that grows on skeletal (± 30 cm) layers of

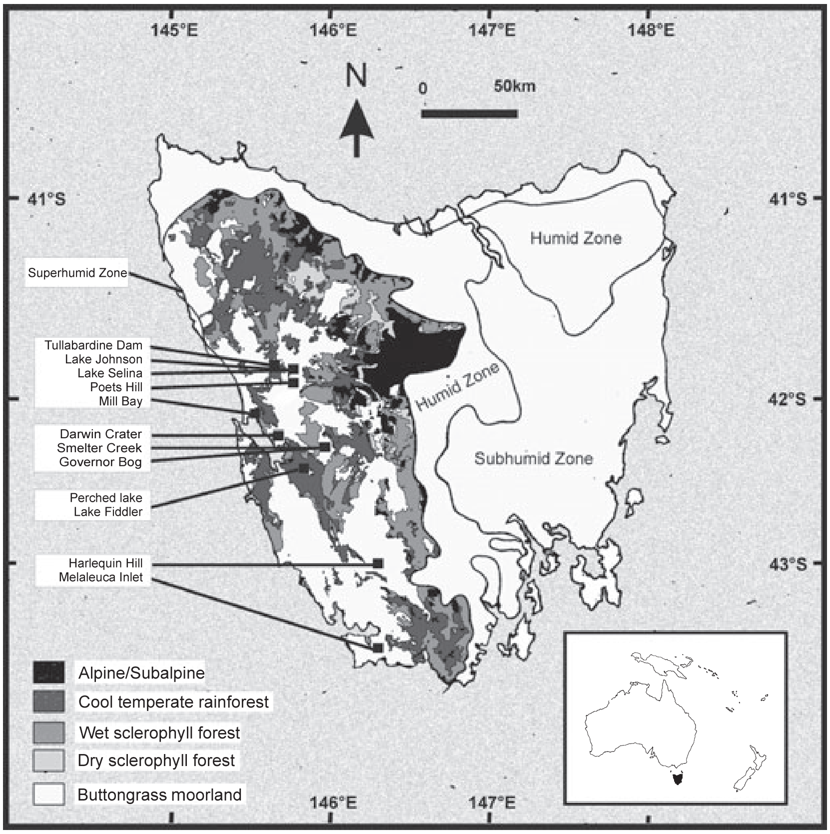


Figure 1 Map showing the distribution of vegetation types in the western Tasmanian superhumid zone and the location of sites analysed.

blanket peat. The rain forests that occupy 19.5% of the south-west are mostly represented by a low and tangled form growing in areas protected from frequent fire. Given adequate protection from fire, rain forest forms on even the most waterlogged and infertile substrates in the south-west (Jarman *et al.*, 1987; Wood & Bowman, 2009). A greater complexity of geological types is present in the mid- to north-west, where the seasonal migration of the Southern Hemisphere westerlies allows the incursion of dry continental air, resulting in a more variable rainfall regime, and the occurrence of more fertile geologies supports a greater proportion of (often) tall and open rain forest (26.5% of the landscape). While geology alone cannot account for the distribution of rain forest and moorland (27.4%) in the mid- to north-west, moorland is most commonly underlain by quartzitic material and rain forest on more fertile limestones and volcanics. Other vegetation types in western Tasmania include *Eucalyptus*-dominated forest and sclerophyllous scrub assemblages that are considered to be seral stages in the successional sequence from rainforest to moorland (Jackson, 1968).

Fire and succession

Fire is the main agent of vegetation disturbance (Gilbert, 1959; Jackson, 1968; Mount, 1979; Bowman & Jackson, 1981; Brown & Podger, 1982b; Bowman, 2000) and the distribution of (non-coastal) lowland vegetation types is inextricably linked to fire. The dominant model of temporal vegetation development is a Clements (1916) inspired mono-climax succession model, termed ecological drift, that is based on space for time observations and that has undergone little conceptual change since its inception (Jackson, 1965, 1968; Bowman & Jackson, 1981). In this model, the development of vegetation communities is deterministic, with all lowland vegetation communities existing along a continuum mitigated by fire frequency. The occurrence of fire is random in space and time, with an increase in the frequency of fire resulting in a drift from rain forest (the climatic climax) to moorland (the disclimax) through a number of seral stages increasingly dominated by flammable sclerophyll taxa (and vice versa). The chance of fire and the rate of succession towards rain forest in the absence of fire are modulated by the nutrient content, hydrology, topography and prevailing wind direction of a site, with more fertile, freely draining and protected sites displaying the most rapid forest development (Bowman & Jackson, 1981; Bowman *et al.*, 1986; Brown *et al.*, 2002). The implications of this model for palaeoecological research are that long-term changes in fire regimes will result in a drift between rain forest and moorland.

An alternative and generally less favoured model of vegetation–fire dynamics for western Tasmania differs from the ecological drift model by arguing for multiple stable vegetation units (poly-climax) that are governed and maintained by fuel accumulation (Mount, 1979, 1982). In this model, all vegetation types are intrinsically flammable and fire is a constant factor in the environment. The boundaries between vegetation communities are reinforced when sufficient fuel accumulates in one community but a lack of fuel in a neighbouring community prohibits the spread of fire beyond the vegetation boundary. Conceptually, this model is based on short-term processes, although the implications of this model for long-term vegetation change are that, given the current climate, vegetation will burn and boundaries are fixed in space and time.

Post-glacial vegetation and climate

All LGM pollen assemblages from western Tasmania are dominated by Poaceae, Asteraceae and Cyperaceae, with the implication being that the lowlands of western Tasmania were occupied by alpine and sub-alpine communities and that the climatic tree line was near the modern coastline (Macphail, 1975; Colhoun & van der Geer, 1986; Colhoun *et al.*, 1999; Colhoun, 2000). During the Late Glacial, pollen from arboreal taxa increases in all pollen records from western Tasmania in a predictable *Eucalyptus–Phyllocladus–Nothofagus* sequence that is thought to reflect the establishment of climax rain forest in areas made equable by climatic change (Colhoun, 2000). Markgraf *et al.* (1986) reviewed pollen records from high-elevation lakes and concluded that the regional expansion of rain forest occurred synchronously across the region during the Late Glacial. Alternatively, Colhoun (1996) argues for asynchronous vegetation change in response to Late Glacial climate change governed by local site factors such as hydrology and nutrient status.

The dominant paradigm of Holocene vegetation change depicts an expansion of rain forest across western Tasmania in response to increasing temperature and precipitation, culminating in the region-wide dominance of rain forest during the early to mid Holocene (Macphail, 1979; Markgraf *et al.*, 1986; Colhoun, 1996). Colhoun (1996) argues for the development of rain forest during this time at sites now occupied by moorland, invoking an expansion of sclerophyllous taxa and moorland communities during the late Holocene that was driven by nutrient depletion and reinforced by more effective anthropogenic fires resulting from the increase in sclerophylly. Alternatively, Fletcher & Thomas (2007a, 2010) argue that while the regional distribution and composition of rain forest was driven by climatic cues, rain forest expansion was limited to areas protected from frequent fire and that burning in the landscape through the Late Glacial–Holocene climatic transition favoured the expansion of plants tolerant of increasing temperature, moisture and frequent fire (i.e. moorland taxa). Furthermore, Fletcher & Thomas (2007a, 2010) argue that the primary ignition source in the region during the Late Glacial was humans and that the region represents a cultural landscape of significant antiquity.

MATERIALS AND METHODS

The pollen data

In this analysis, we use the relationship between modern pollen representation and vegetation type identified by Fletcher & Thomas (2007b) to objectively assign fossil pollen spectra to a modern vegetation analogue. The modern pollen data are presented in a cumulative pollen diagram in the following categories: alpine taxa, trees, shrubs, graminoids and other taxa (Fig. 2). A clear phytosociological separation is evident in an ordination (detrended correspondence analysis, DCA) of the modern pollen dataset, with axis 1 of this ordination significantly correlated with average annual temperature (Fig. 2; Fletcher & Thomas, 2007b).

Twelve post-LGM and two pre-Holocene interglacial pollen records published from superhumid western Tasmania are analysed in this study (Fig. 1, Table 1). Relative pollen values were averaged within fossil pollen zones identified using CONISS (Grimm, 1987) based on a square-root transformation of the fossil pollen data as recommended by Grimm (1987). Arrows in Fig. 3 indicate the direction from the oldest fossil zone to the youngest. Chronological control of pollen records is poor in western Tasmania, with some records undated through the Holocene (Colhoun *et al.*, 1991, 1999) or with as little as one date constraining reconstructions, and we have elected to use the following nomenclature in discussions: Last Interglacial, Late Glacial and early, mid and late Holocene, etc.

Prior to analysis, all pollen data (modern and fossil) were reduced to 32 pollen types based on the following criteria.

1. *Leptospermum*/*Baeckea*-type and *Leptospermum*-type, and *Melaleuca squarrosa* and *Melaleuca squamea* were grouped into *Leptospermum* and *Melaleuca*.

2. Taxa were excluded that were not present in at least five sites at or above a percentage level of 1% (*sensu* McGlone & Moar, 1997).

3. Percentages were calculated after exclusions.

Screening of pollen data

Screening of the fossil data was accomplished by calculating supplementary ordination axis scores for fossil samples using the following procedure. All data analysis was performed using PC-ORD for Windows version 4.27 (McCune & Mefford, 1999).

1. The ordination axis scores for the modern pollen samples were used as weights to find the average position of each pollen taxon along each ordination axis (pollen taxa weights) (McCune *et al.*, 2002).

2. Pollen taxa weights were then used to calculate scores for fossil pollen samples based on a weighted average (*sensu* Whittaker, 1967; McCune *et al.*, 2002) of pollen taxa weights for pollen taxa present in the fossil pollen samples (*sensu* McGlone *et al.*, 2000).

3. The resulting supplementary axis scores allow fossil samples to be placed passively into the modern ordination space, thus permitting assignment of a modern vegetation type to the fossil pollen assemblage (*sensu* McGlone *et al.*, 2000).

Charcoal

A post-LGM western Tasmanian charcoal curve was constructed by standardizing all (10) post-LGM charcoal

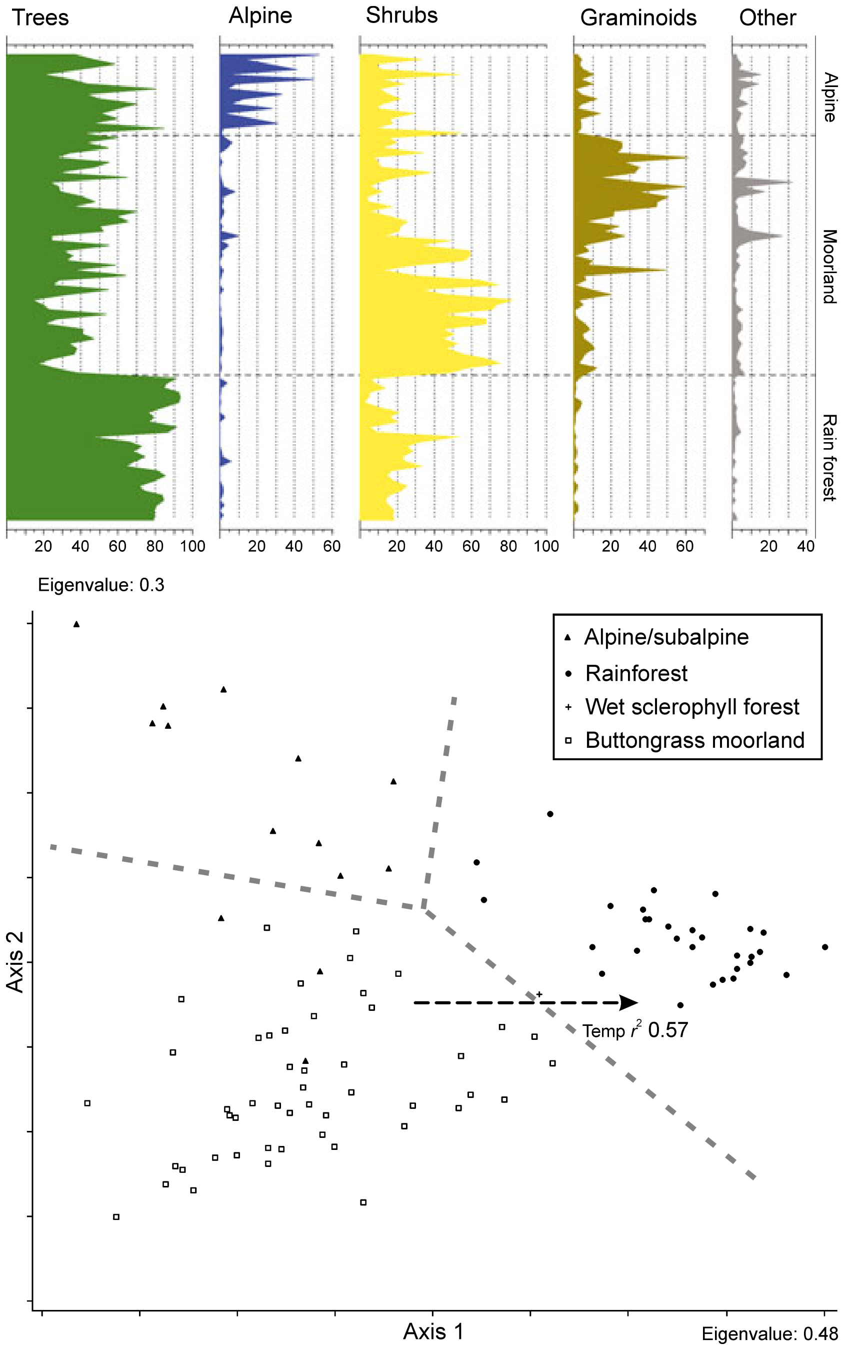


Figure 2 Summary percentage pollen diagram and detrended correspondence analysis (DCA) ordination biplot of the modern pollen dataset of Fletcher & Thomas (2007b). Samples in the pollen diagram are ordered by vegetation type and by decreasing elevation within each vegetation type.

sequences (Table 1). Various methods of charcoal quantification (area estimates, absolute counts, relative counts) have been employed in western Tasmania, precluding a direct inter-site comparison of charcoal data, and we have adopted the method of Power *et al.* (2008) to account for this fact: *z*-scores for each record were calculated, based on a whole post-glacial mean (restricted to 14 ka in this analysis) for each site or, when a record was younger than 14 ka, the entire record. The data were smoothed to 1 kyr time slices by averaging within-site *z*-scores and a regional curve was produced by averaging across-site *z*-scores for each 1 kyr time slice. The chronology is based on linear extrapolations between ^{14}C dates calibrated using Calib 5.0 (Stuiver & Reimer, 1993). An intra-site comparison between glacial and interglacial charcoal values was made for the Lake Selina and Darwin Crater Late Quaternary records. Charcoal values were averaged for glacial and interglacial periods and two-tailed *t*-tests were performed to assess the degree of similarity/difference between glacial and interglacial charcoal quantities.

RESULTS

No change in vegetation type is recorded at any moorland or lowland rain forest site through the post-LGM period

Table 1 List of sites used in this analysis and their geographic position, elevation, modern vegetation, site type, age range, presence of a charcoal record, method of data acquisition (raw or digitized) and data source. The Lake Selina and Darwin Crater sites provide records of pre-Holocene interglacial and glacial stage vegetation.

Site	Latitude (S)	Longitude (E)	Elevation (m)	Modern vegetation	Site type	Age range	Charcoal	Data	Source
Tullabardine Dam	41.67	145.65	230	Wet sclerophyll forest	Swamp	Late Glacial–present	Yes	Digitized	Colhoun & van der Geer (1986)
Lake Johnson	41.90	145.55	900	Rainforest	Lake	Early Holocene–present	Yes	Digitized	Anker *et al.* (2001)
Lake Selina	41.90	145.63	540	Buttongrass moorland	Lake	OIS* 5e–present	Yes	Digitized	Colhoun *et al.* (1999)
Poets Hill Lake	41.90	145.58	620	Buttongrass moorland	Lake	Late Glacial–present	Yes	Digitized	Colhoun (1992)
Mill Bay	42.14	145.30	5	Buttongrass moorland	Peat section	Early Holocene–present	Yes	Raw	Fletcher & Thomas (2010)
Smelter Creek	42.20	145.63	200	Buttongrass moorland	Peat section	Late Glacial–present	Yes	Digitized	Colhoun *et al.* (1992)
Governor Bog	42.20	145.65	180	Buttongrass moorland	Peat section	Late Glacial–present	Yes	Digitized	Colhoun *et al.* (1991)
Darwin Crater†	42.30	145.67	180	Buttongrass moorland	Peat section and lake	OIS 9–OIS 5e, Holocene	Yes	Digitized	Colhoun & van der Geer (1998)
Lake Fiddler	42.50	145.68	5	Rainforest	Lake	Early Holocene–present	Yes	Digitized	Harle *et al.* (1999)
Perched Lake	42.56	145.68	35	Rainforest	Lake	Mid-Holocene–present	No	Raw	Fletcher (2009)
Harlequin Hill	42.95	146.31	320	Buttongrass moorland	Lagoon	Late Glacial–present	Yes	Raw	Fletcher & Thomas (2007a)
Melaleuca Inlet 1	43.30	146.08	10	Buttongrass moorland	Peat section	Late Glacial–present	Yes	Raw	Thomas (1995)
Melaleuca Inlet 2	43.30	146.08	5	Buttongrass moorland	Peat section	Late Glacial–present	No	Raw	Macphail *et al.* (1999)

*OIS, oxygen isotope stage, where OIS 9 and OIS 5e represent interglacial stages and OIS 8 and 6 represent glacial stages.

†The Darwin Crater site is discontinuous between OIS 5e and the Holocene and is composed of lake sediments between OIS 9 and OIS 5e that are overtopped by peat.

(Fig. 3). It is clear that by the early Holocene, moorland and rain forest were established in regions that these vegetation types occupy today. The high-elevation rain forest site, Lake Johnson, records a change from moorland vegetation with moderate levels of charcoal in the early Holocene to high-elevation rain forest/alpine vegetation with little charcoal until European contact (Anker *et al.*, 2001). The swamp forest site, Tullabardine Dam, records a transition from moorland vegetation in the Late Glacial–early/mid Holocene to wet sclerophyll/rain forest vegetation in the mid/late Holocene (Fig. 3). A comparison of interglacial assemblages indicates that rain forest similar to modern rain forest assemblages was established at Lake Selina and Darwin Crater during the Last Interglacial [oxygen isotope stage (OIS) 5e] and an earlier interglacial period, OIS 9, whilst both were occupied by moorland through the Holocene to present (Fig. 4).

The post-LGM charcoal curve (Fig. 5) reveals increasing charcoal values across western Tasmania from the Late Glacial towards an early Holocene maximum. The post-LGM charcoal curve is plotted against a reconstruction of Tasmanian lake level data, an indicator of relative moisture (Harrison & Dodson, 1993), revealing increasing charcoal despite the supposed region-wide increase in moisture. There is no statistical difference between charcoal values during the LGM and the Holocene at Lake Selina, while Holocene charcoal values in that record are significantly higher than during the Last Interglacial (OIS 5e) (Fig. 6). In the Darwin Crater record, all glacial or interglacial charcoal values are statistically different (Fig 6), yet the Holocene values display the greater similarity (highest *P*-values) with glacial periods than previous interglacial periods.

DISCUSSION

The results presented enable discussion of a number of issues pertaining to the development of the post-glacial phytogeographical landscape of western Tasmania, as well as raising interesting questions over the drivers and mechanisms of vegetation change in this region. In the following discussion we: (1) place our findings within the framework of post-glacial vegetation change in western Tasmania, conciliating the disparity between existing models of vegetation change and our results; (2) discuss the relevance of our results for the debate over the timing of post-glacial vegetation change; (3) examine the disparity between vegetation development and fire history during the present interglacial (the Holocene) and previous interglacial periods; (4) discuss the role of humans as an ignition agent and driver of vegetation change in this region, posing the hypothesis that western Tasmania represents an ancient cultural landscape; (5) address the apparent disparity between our results and the dominant model of vegetation succession for the region; and (6) discuss the implication of our results for the debate over the relative importance of climate, fire and people in the global distribution of vegetation.

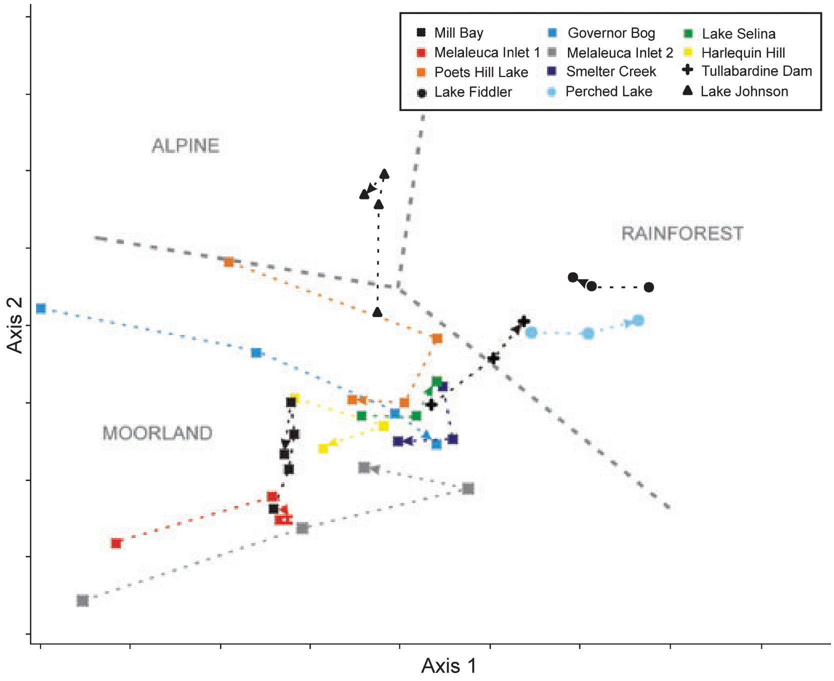


Figure 3 Ordination analysis (DCA) of western Tasmanian post-Last Glacial Maximum (LGM) pollen records using the western Tasmanian modern pollen database (Fletcher & Thomas, 2007b) to screen fossil pollen zones for modern vegetation analogues. Points represent pollen zones for each pollen record identified by CONISS (Grimm, 1987) and arrows indicate the direction of decreasing age.

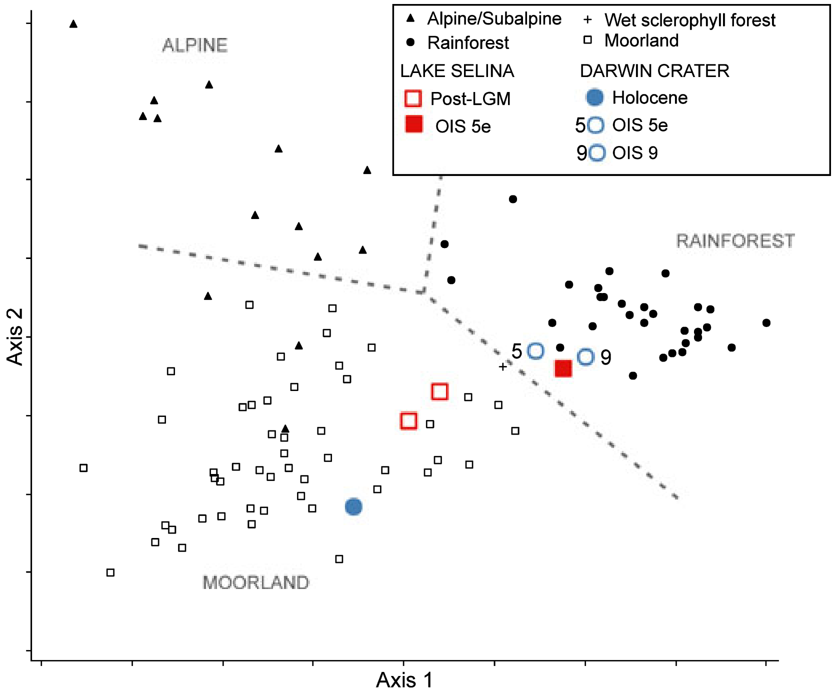


Figure 4 Ordination analysis (DCA) of western Tasmanian interglacial [post-Last Glacial Maximum (LGM), oxygen isotope stage (OIS) 5e, OIS 9] pollen assemblages using the western Tasmanian modern pollen database (Fletcher & Thomas, 2007b) to screen interglacial fossil pollen assemblages for modern vegetation analogues.

Post-glacial vegetation of western Tasmania

Late Glacial

All sites analysed here that are currently occupied by moorland vegetation display a change from a moorland-like assemblage indicative of cooler temperatures during the Late Glacial to a modern moorland assemblage in the Holocene, excluding Governor Bog, in which lower charcoal values and fire-intolerant alpine taxa are dominant during the early part of the Late Glacial, prior to an increase in charcoal and the establishment of moorland at that site by the Late Glacial–early Holocene transition (Fig. 3; Colhoun *et al.*, 1991). Despite the likelihood of limitations imposed on the modern dataset by a lack of modern vegetation analogues for Late Glacial flora (*sensu* Williams & Jackson, 2007), we interpret the results as indicating that a treeless moorland assemblage prevailed across much of the western Tasmanian landscape

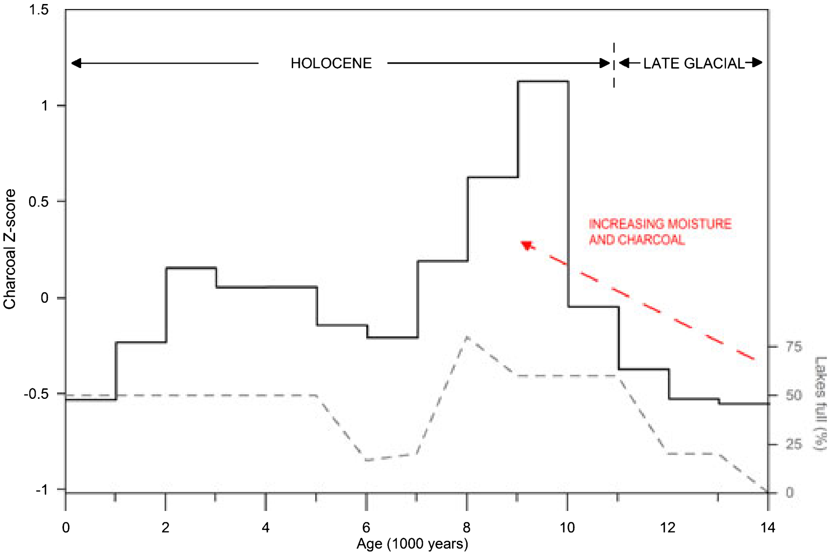
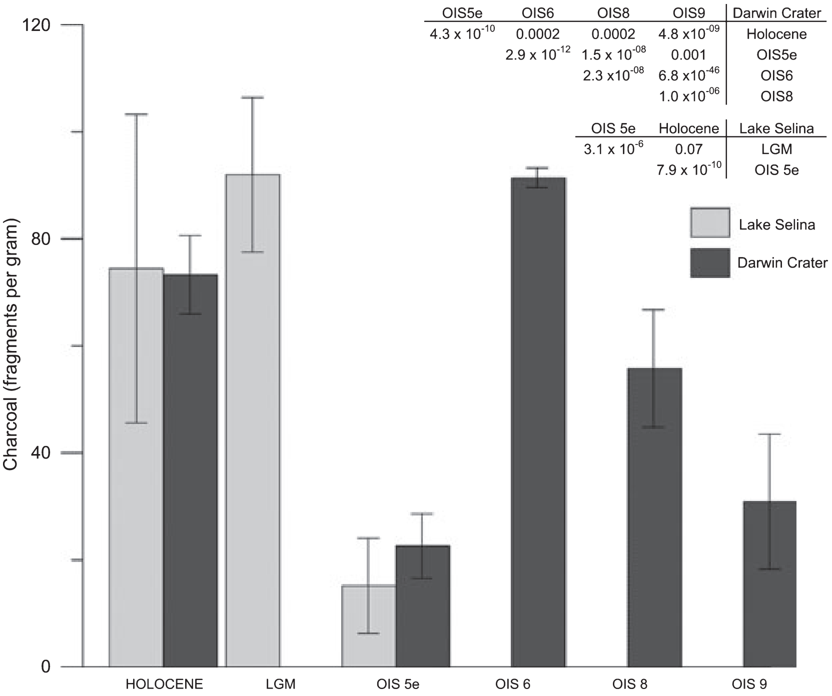


Figure 5 Western Tasmanian regional charcoal curve (solid line) and percentage of full Tasmanian lakes (dashed line) (Harrison & Dodson, 1993).



OIS5e	OIS6	OIS8	OIS9	Darwin Crater
4.3×10^{-10}	0.0002	0.0002	4.8×10^{-09}	Holocene
	2.9×10^{-12}	1.5×10^{-08}	0.001	OIS5e
		2.3×10^{-08}	6.8×10^{-46}	OIS6
			1.0×10^{-06}	OIS8

OIS 5e	Holocene	Lake Selina
3.1×10^{-6}	0.07	LGM
	7.9×10^{-10}	OIS 5e

Figure 6 Plot of average charcoal values and associated *P*-values (top right) for interglacial [oxygen isotope stage (OIS) 5e, OIS 9] and glacial [Last Glacial Maximum (LGM), OIS 6, OIS 8] periods in the Lake Selina and Darwin Crater pollen records. *P*-values were calculated using a Student's *t*-test and *P*-values > 0.05 indicate no statistical difference. Error bars indicate one standard deviation.

during the Late Glacial. Regional charcoal values increase across western Tasmania during the Late Glacial into the early Holocene, in spite of the proposed island-wide increase in effective precipitation at this time (Fig. 4), and furthermore, Holocene charcoal values are significantly higher than during any previous interglacial period (Fig. 5). Thus, it is evident that burning through the Late Glacial and early Holocene facilitated the expansion of moorland taxa across the region at that time.

Unfortunately, no rain forest site analysed here extends to the Late Glacial period. Three pollen records from within western Tasmanian rain forest do span the Late Glacial–Holocene period, Lake Vera, Adamson's Peak (Macphail, 1979) and Ooze Lake (Macphail & Colhoun, 1985), but the use of multiple pollen sums, grouping of pollen types and truncated profiles in publications precluded accurate digitization and inclusion in this synthesis. The Lake Vera site records the replacement of an assemblage dominated by graminoids (Poaceae, Restionaceae and Cyperaceae) to a rain forest-dominated assemblage during the Late Glacial and a dominance of rain forest until the present (Macphail, 1979). Likewise, the Adamson's Peak record, located within high-elevation rain forest, records the invasion of a graminoid-dominated assemblage by rain forest elements during the Late Glacial until the present (Macphail, 1979). Ooze Lake, the only one of these sites in which charcoal was counted, documents a transition from moorland vegetation with high charcoal content and in which *G. sphaerocephalus* was a constituent early in the Late Glacial to rain forest and low charcoal values by the end of the Late Glacial and into the Holocene. The Late Glacial and early Holocene section of the Tullabardine Dam record contains pollen from shrub taxa with poor pollen taxonomic control that are common to both moorland and rain forest (namely *Leptospermum*/*Baeckea* type) (Colhoun & van der Geer, 1986), potentially resulting in an erroneous association with open moorland surface samples (see Fletcher & Thomas, 2007b) and a therefore artificial transition from moorland to forest vegetation (Fig. 3).

The Holocene

It appears that, at the spatiotemporal scale afforded by this analysis, the distribution of regional vegetation types remained remarkably stable through the Holocene. By the early Holocene, moorland was established at all sites where this vegetation type dominates today and, likewise, rain forest vegetation was established at sites in which that vegetation type dominates today (Fig. 3; Macphail, 1979; Macphail & Colhoun, 1985). Holocene charcoal levels significantly exceed previous interglacial phases at Lake Selina and Darwin Crater (Fig. 6) and it appears that during the Holocene the maintenance of moorland across the landscape beyond the 'mire niche', permanently waterlogged areas in which moorland assemblages are believed to occur irrespective of fire regime (Jackson, 1968), is a result of the continued influence of fire. Lake Johnson, Tullabardine Dam and Ooze Lake (Macphail & Colhoun, 1985), all forested sites, show a change in vegetation type from moorland to forest during the early Holocene, counter to the trend from rain forest to moorland proposed for lowland western Tasmania (Macphail, 1979; Colhoun, 1996).

Summary

The spatial spread of sites used here encompasses virtually the entire superhumid zone of western Tasmania and includes a range of site types: lakes, swamps and peat sections (Table 1). It is clear that the influence of fire during the re-assortment of western Tasmanian vegetation in response to the large-scale climate shift during the Last Glacial Transition facilitated the expansion of taxa tolerant of frequent fire, cool temperatures and high relative moisture (i.e. moorland taxa) across many parts of the landscape, resulting in the dominance of moorland and the restriction of rain forest vegetation to areas protected from fire, such as at Lake Fiddler (Harle *et al.*, 1999), Lake Vera (Macphail, 1979), Ooze Lake (Macphail & Colhoun, 1985) and other areas that are in topographic settings providing protection from wind-driven fires, growing on more fertile substrates and/or are proximal to large watercourses that, presumably, have buffered the effects of fire on vegetation development (Bowman, 2000).

During the more subtle climatic vicissitudes of the Holocene (see Mayewski *et al.*, 2004), no change in vegetation type has occurred at any of the lowland moorland or rain forest sites reviewed here. An inspection of individual pollen records reveals clear compositional changes that suggest a dynamic response by the vegetation to Holocene environmental changes; yet, at the scale of the present study, the resilience displayed by both moorland and rain forest vegetation through the Holocene implies metastabilty of these two vegetation types in the landscape of western Tasmania through the Holocene. Thus, we reject models of vegetation change invoking a replacement of rain forest by moorland during the Holocene (*sensu* Macphail, 1979; Colhoun, 1996).

Synchronous or asynchronous vegetation change?

Central to the notion of asynchronous post-glacial vegetation change in western Tasmania is the temporal offset between changes in pollen records from two proximal (< 1 km) and poorly dated lowland peat sections located within the same moorland system (Governor Bog, Smelter Creek; Table 1) (Colhoun, 1996). It is revealing that only the peat sections analysed by Colhoun (1996) show temporal asynchronicity with upland lakes. Poets Hill Lake, on the other hand, displays temporally synchronous changes with upland sites (Colhoun, 1992, 1996), as does the Harlequin Hill site, a more intensively dated western Tasmanian peat section (Fletcher & Thomas, 2007a). Loss of peat through fire is a frequent occurrence in western Tasmania, often resulting in complete erosion of peat layers (Brown & Podger, 1982a; Pemberton, 1989; Brown *et al.*, 2002; Bridle *et al.*, 2003) and hiatuses have been identified in all moorland peat sections subject to intensive dating (Macphail *et al.*, 1999; Fletcher & Thomas, 2007a, 2010). Charcoal peaks in the early Holocene in western Tasmania (Fig. 5), and it is likely that the temporal offset of vegetation development at Governor Bog and Smelter Creek reflects the removal of peat by fire in one or both records.

Is the Holocene unique?

In comparison to previous interglacial periods, the high charcoal and the dominance by moorland vegetation during the Holocene appears to be unique (Figs 4 & 6). There is a clear phytosociological separation between the OIS 5e and OIS 9 interglacial pollen assemblages, periods with a comparable climate to the Holocene (Harle *et al.*, 2004; Kershaw *et al.*, 2007; Dutton *et al.*, 2009), and Holocene pollen assemblages in both the Lake Selina and Darwin Crater records (Fig. 4). The critical difference in vegetation development between the Holocene and previous interglacial periods is fire (Fig. 6). High charcoal content and open vegetation is recorded in virtually all full glacial assemblages in western Tasmania and, prior to the Holocene, interglacial periods were characterized by markedly lower charcoal values and rain forest vegetation, with the transition from glacial to interglacial punctuated by a sequence of increases in arboreal taxa (Colhoun & van der Geer, 1998; Colhoun, 2000; and references therein). Post-LGM charcoal levels during the Holocene at Lake Selina and Darwin

Crater are at levels usually associated with glacial periods (Fig. 6) and these records show an increase in pollen from shrub taxa common in fire-promoted moorland vegetation. It is clear, then, that persistence of fire through the latest glacial–interglacial transition, a period of significant floral re-assortment, inhibited the development of rain forest and resulted in the expansion of moorland taxa.

An ancient cultural landscape?

Western Tasmania shares remarkable ecological, climatic and geographic affinities with other west coast regions in the Southern Hemisphere located between 41 and 44° S, Región de los Lagos in Chile and west coast South Island New Zealand, yet these regions share markedly different human occupation histories, providing a unique opportunity to assess the impact of humans on the vegetation of the southern cool temperate zones. Aboriginal Australians arrived in Tasmania during the Last Glacial Stage, *c.* 35 ka (Cosgrove, 1999), the earliest evidence for humans in Región de los Lagos is in the Late Glacial period (Meltzer *et al.*, 1997), while humans did not arrive in New Zealand until the most recent millennium (Wilmshurst *et al.*, 2008). Fires resulting from lighting strike are uncommon in the cool temperate and superhumid regions of the Southern Hemisphere (Bowman & Brown, 1986; Butler, 2008). Charcoal is found in significant amounts in the Late Glacial and Holocene sections of pollen records from western Tasmania and the Región de los Lagos (independent of volcanic activity in the latter), yet is virtually absent in records from the west coast of South Island New Zealand until after human arrival (Moreno, 2004; Newnham *et al.*, 2007; Whitlock *et al.*, 2007; Abarzua & Moreno, 2008; Butler, 2008; Power *et al.*, 2008; McWethy *et al.*, 2009), and it appears that while climate is likely to modulate the frequency and magnitude of fires (Whitlock *et al.*, 2007; Power *et al.*, 2008), humans are the primary source of fires (outside of volcanic sources) in these cool and superhumid temperate regions.

It is our opinion that the arrival of people on Tasmania during the Last Glacial Stage, between the Last Interglacial and the Holocene, introduced an ignition source to the region that was independent of climate. We have displayed that burning through the transition from the LGM to the Holocene inhibited rain forest expansion and resulted in the expansion and dominance of moorland during the Holocene. Western Tasmania, then, represents a cultural landscape resulting from the activities of humans prior to the onset of the Holocene and is of great antiquity. Today, natural ignitions, while rare, do result in the burning of significant areas of vegetation; yet, given the overwhelming dominance of human-lit fires in the region (Bowman & Brown, 1986) and the fact that humans have been present for at least 35 kyr (Cosgrove, 1999), it is not possible to postulate whether natural ignitions alone would be sufficient to maintain the present distribution of moorland under the modern climate regime or whether rain forest would expand into areas free from fire for a prolonged period.

Temporal vegetation dynamics in western Tasmania

Recent approaches to temporal vegetation dynamics highlight the importance of resilience to disturbance when considering notions of stability, or metastability, and of the propensity of disturbance events to result in bifurcation of vegetation development and/or phase shifts, particularly during long-term periods of increased system instability, termed macro-fluctuations (Naveh, 1998; Naveh & Carmel, 2003; Ingegnoli & Pignatti, 2007; Gillson, 2009; Virah-Sawmy *et al.*, 2009). Within this framework, transitions from glacial to interglacial climate regimes represent a significant driver of vegetation re-assortment and system instability, and the continued influence of fire through the latest transition in western Tasmania appears to have resulted in a bifurcation that has led to the development of two metastable vegetation states during the comparatively stable Holocene period: moorland (the fire-dependent state) and rain forest (the climate-dependent state) (*sensu* Bond *et al.*, 2005).

At present, the moorland-dominated landscape of western Tasmania is considered a fire disclimax (Brown *et al.*, 2002), implying that fire acts as an external negative factor in vegetation development. O'Neill (2001) has argued that the 'spatiotemporal spectrum of environmental variability determines ecosystem stability as surely as internal feedback mechanisms' (p. 3279) and that recurrent disturbances, such as fire, are an ecological process, not an external interference. The maintenance of moorland through the Holocene, despite a climate hostile to fire, suggests that the intrinsic flammability of this vegetation type and the presence of humans as an ignition source have been sufficient to maintain moorland distribution, and the failure of ecological studies to detect drift from moorland to forest (*sensu* Jackson, 1968), while possibly reflecting an insufficient time window of observation to detect 'ecological drift' (Brown *et al.*, 2002), may reflect the fact that moorland vegetation is a metastable vegetation phase maintained by self-regulating ecological processes that include fire.

Walker (1982) refers to the temporal perspective granted by pollen analysis as 'vegetation's fourth dimension' and the present analysis sheds considerable light on the dynamics of western Tasmanian vegetation over long time-scales. Furthermore, it has been argued that the problem of pattern and scale is the central problem in ecology (Levin, 1992) and, despite the almost universal acceptance of Jackson's (1968) space-for-time mono-climax vegetation succession sequence, at the broad spatiotemporal scale represented in this analysis fire does not appear to have occurred randomly in space and time and the distribution of the lowland vegetation of western Tasmania appears to have remained stable through the Holocene, providing empirical support for the generally neglected hypothesis of Mount (1979): that the boundaries of vegetation types are stable and reinforced by different fuel accumulation rates and fire return intervals intrinsic to each vegetation type. High-resolution studies targeted at detecting vegetation boundary dynamics through time are required to resolve whether phase shifts between moorland and rain forest have occurred through the Holocene at smaller spatiotemporal scales, viz. Jackson (1968).

Climate, fire, people and vegetation

Climate, fire, people and vegetation, rather than being independent of one another, interact in a complex manner (Bowman *et al.*, 2009). The clear role that fire has played in determining the modern phytogeographic landscape of western Tasmania is consistent with the conclusions of Bowman (2000), who found that fire was the only factor capable of explaining the island-like spatial distribution of Australian rain forests in a 'sea' of fire-dependent plant communities. The impact of fire on a global scale was demonstrated by Bond *et al.* (2005) who, using vegetation models, reported a replacement of substantial areas of fire-dependent grass- and shrub-land by trees in a simulated world without fire, concluding that biomes over much of the Earth have not reached their climate potential and that fire is the only disturbance agent capable of reducing biomass at a global scale. While it is clear from these and other studies that fire plays a key role in determining spatial vegetation patterns at local, regional and global scales, fires also operate within a temporal framework.

Fires are dependent on vegetation for fuel and changes in the quantity and type of combustible biomass govern the magnitude and frequency of fires. Re-assortment of global vegetation patterns during glacial–interglacial transitions (e.g. Pickett *et al.*, 2004) clearly alters the global pattern and availability of combustible biomass and fire occurrence (e.g. Singh *et al.*, 1981; Colhoun & van der Geer, 1998; Wang *et al.*, 1999; Power *et al.*, 2008). Furthermore, a global synthesis of charcoal records since the LGM by Power *et al.* (2008) reveals that, over multi-millennial time-scales, climate modulates the occurrence of fire on all vegetated continents. Available evidence suggests that under a glacial climate regime, the landscape of western Tasmania is characterized by increased fires and decreased vegetation biomass, while interglacial climate regimes (prior to the Holocene) discourage fire and allow the development of high-biomass rain forest. Continued burning by humans through the latest glacial–interglacial transition has resulted in the 'anomalous' situation in which a low-biomass fire-dependent vegetation state is metastable in the landscape of western Tasmania during an interglacial period. This anomaly needs to be understood, especially in the Southern Hemisphere where present-day open vegetation in New Zealand, South Africa and South America may all bear the deep imprint of anthropogenic fire.

CONCLUSIONS

Objective numerical analysis of Late Glacial and Holocene pollen spectra from western Tasmania reveals a remarkable degree of stability in the distribution of vegetation types through the Holocene at the broad spatiotemporal scale afforded by this analysis. We reject models of Holocene vegetation change that invoke a replacement of rain forest by moorland during the Holocene and propose that moorland became established across the region during the Late Glacial and that, while shifts between moorland and rain forest may have occurred at smaller spatiotemporal scales, moorland has dominated the landscape since that time. An analysis of pollen data from previous interglacial periods reveals that sites occupied by moorland today hosted rain forest assemblages during previous interglacial periods and that charcoal levels during the Holocene are significantly higher than during previous interglacial periods. Thus, fire is revealed as the primary agent responsible for the present-day moorland-dominated landscape of western Tasmania. We conclude that burning by humans through the Late Glacial has deflected interglacial vegetation development, facilitating the expansion of moorland, and that the region represents an ancient cultural landscape.

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