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ORIGINAL ARTICLE

Effects of European colonization on indigenous ecosystems: post-settlement changes in tree stand structures in *Eucalyptus–Callitris* woodlands in central New South Wales, Australia

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ABSTRACT

Aim There has been considerable debate about pre-settlement stand structures in temperate woodlands in south-eastern Australia. Traditional histories assumed massive tree losses across the region, whereas a number of recent histories propose that woodlands were originally open and trees regenerated densely after settlement. To reconcile these conflicting models, we gathered quantitative data on pre-settlement stand structures in *Eucalyptus–Callitris* woodlands in central New South Wales Australia, including: (1) tree density, composition, basal area and canopy cover at the time of European settlement; and (2) post-settlement changes in these attributes.

Location Woodlands dominated by *Eucalyptus* species and *Callitris glaucophylla*, which originally occupied approximately 100,000 km^2 in central New South Wales, Australia.

Methods We recorded all evidence of pre-settlement trees, including stumps, stags and veteran trees, from 39 relatively undisturbed 1-ha stands within 16 State Forests evenly distributed across the region. Current trees were recorded in a nested 900 m^2 quadrat at each site. Allometric relationships were used to estimate girth over bark at breast height, tree basal area, and crown diameter from the girth of cut stumps. A post-settlement disturbance index was developed to assess correlations between post-settlement disturbance and attributes of pre-settlement stands.

Results The densities of all large trees (> 60 cm girth over bark at breast height) were significantly greater in current stands than at the time of European settlement (198 vs. 39 trees ha^{-1}). Pre-settlement and current stands did not differ in basal area. However, the proportional representation of *Eucalyptus* and *Callitris* changed completely. At the time of settlement, stands were dominated by *Eucalyptus* (78% of basal area), whereas current stands are dominated by *Callitris* (74%). On average, *Eucalyptus* afforded 83% of crown cover at the time of settlement. Moreover, the estimated density, basal area and crown cover of *Eucalyptus* at the time of settlement were significantly negatively correlated with post-settlement disturbance, which suggests that these results underestimate pre-settlement *Eucalyptus* representation in the most disturbed stands.

Main conclusions These results incorporate elements of traditional and recent vegetation histories. Since European settlement, State Forests have been transformed from *Eucalyptus* to *Callitris* dominance as a result of the widespread clearance of pre-settlement *Eucalyptus* and dense post-settlement recruitment of *Callitris*. Tree densities did increase greatly after European

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settlement, but most stands were much denser at the time of settlement than recent histories suggest. The original degree of dominance by *Eucalyptus* was unexpected, and has been consistently underestimated in the past. This study has greatly refined our understanding of post-settlement changes in woodland stand structures, and will strengthen the foundation for management policies that incorporate historical benchmarks of landscape vegetation changes.

Keywords

Australia, cultural landscape, historical ecology, historical variation, land-use history, long-term vegetation dynamics, Murray–Darling Basin.

INTRODUCTION

In Australia and other continents that were colonized by Europeans in recent centuries, ecological conditions at the time of European settlement are often used as a reference benchmark against which current ecological conditions can be appraised. Pre-settlement benchmarks have been used to: (1) assess changes in the distributions of species and ecosystems (Smith, 1996; Radeloff *et al.*, 1999), (2) document changes in ecosystem structure and composition (Motzkin *et al.*, 1999; Huber & Markgraf, 2003), (3) assess the degree of ecosystem destruction, degradation or reservation (Kirkpatrick & Brown, 1994; Aagesen, 2000), and (4) set benchmarks for conservation planning decisions and ecosystem management and restoration activities (Egan & Howell, 2000; Allen *et al.*, 2002). Not surprisingly, uncertainty about the range of variation in pre-settlement conditions has promoted vigorous discussions about appropriate ecosystem management activities in many regions (Mendelson *et al.*, 1992; Benson & Redpath, 1997; Allen *et al.*, 2002).

Recently, there has been considerable debate concerning the pre-settlement vegetation structure of temperate woodlands in southern Australia (Mitchell, 1991; Norris *et al.*, 1991; Ryan *et al.*, 1995; Benson & Redpath, 1997; Flannery, 1998; Rolls, 1999, 2000). This debate has centred on two important questions: how dense were trees at the time of European settlement, and how have vegetation remnants changed since settlement? These questions are difficult to address as most temperate woodlands in southern Australia have been cleared for agriculture, and only small remnants, most of which are highly degraded, remain in many regions (Hobbs & Yates, 2000).

Two polarized views exist. Traditionally, environmental histories have stated that woodlands were originally densely stocked with trees but were rapidly cleared for agriculture in the late 1800s and early 1900s. Tree clearance combined with heavy grazing led to catastrophic ecosystem changes, including widespread soil erosion, rising water tables, dryland salinity, and biodiversity losses (Bolton, 1981; Adamson & Fox, 1982; Hobbs & Hopkins, 1990; Young, 2000). In contrast, a number of recent environmental histories have claimed that, rather than being densely timbered, woodlands were originally very open, with few, scattered trees (Rolls, 1981, 1999, 2000; Barr & Cary, 1992; Ryan *et al.*, 1995; Jurskis, 2000). Rolls (1999, p. 197), for instance, stated that temperate woodlands were originally 'dotted with a dozen or so… trees to the hectare' (Fig. 1). Under this model, low tree densities were originally maintained by frequent burning by indigenous peoples. After European settlement, fires were suppressed and tree densities increased (rather than decreased). Proponents of this model have asserted that current remnants are considerably denser than at the time of settlement, and that many current approaches to vegetation management and conservation are misguided (Ryan *et al.*, 1995; Jurskis, 2000). Not surprisingly, many of these claims have been vigorously disputed (Mitchell, 1991; Norris *et al.*, 1991; Benson & Redpath, 1997).

To complicate this polarized debate, there is little dispute that some native trees did increase in density shortly after European settlement in some regions, especially the fire-sensitive native conifer *Callitris glaucophylla* J. Thompson & L. Johnson (Harrington *et al.*, 1979; Rolls, 1981; Noble, 1997; Griffiths, 2002). However, hardly any information is available on pre-settlement stand structures for *Callitris* or co-occurring *Eucalyptus* species. In an influential paper, Walker *et al.* (1993) estimated that 6.3 billion trees were cleared from woodlands in the agricultural Murray–Darling Basin region in south-eastern Australia. This figure was calculated by estimating the degree of clearance of each vegetation type and counting tree densities in current remnants. The authors acknowledged, however, that errors may have arisen as a result of post-settlement increases in tree densities, and called for 'more historical research' to improve their estimates.

This debate has important implications for regional land-management planning. State and regional policies on vegetation clearance, salinity management and regional restoration works are largely predicated on the traditional understanding of widespread historical clearance. Some recent vegetation histories, however, question many of the principles upon which these strategies have been developed. Unfortunately, resolution of this debate is greatly impeded by the paucity of accurate information on pre-settlement tree densities and stand structures. In the absence of accurate information,

Figure 1 Photograph of an open woodland grazing property in central Victoria taken in the 1920s. Rolls (1999) presented this photograph with the caption, 'this photograph… gives a good idea of tree cover in the temperate regions of Australia 200 years ago'. Tree density appears to be considerably < 5 trees ha^{-1}. (Reproduced with permission of the State Library of New South Wales, Reference number PXB301 No.39).

protagonists have often overgeneralized from selected archival and ecological information, of dubious spatial referability (Lunt, 2002).

The aim of this study is to provide quantitative estimates of historical stand structures in *Eucalyptus–Callitris* woodlands in central New South Wales, Australia. Specifically, we document: (1) variations in tree density, composition, basal area and canopy cover at the time of European settlement, and (2) post-settlement changes in these attributes. In contrast to previous studies that have used archival information, we recorded physical evidence of pre-settlement trees (including stumps, stags and veteran trees) in relatively undisturbed remnants in order to obtain spatially explicit, quantitative data on pre-settlement stand structures.

METHODS

Terminology

Following at least 40,000 years of indigenous occupation, Australia was first settled by Europeans in 1770. Central New South Wales was not settled until the mid-1800s, however, and widespread tree clearance and dense regeneration of *Callitris* occurred from the 1870s onwards (Gammage, 1986; Allen, 1998; Lunt & Spooner, 2005). In this paper, the term *pre-settlement trees* refers to trees that existed when Europeans first settled in the region in the mid-1800s, and the term *post-settlement trees* refers to trees that established after this date. In practice, however, pre- and post-settlement trees were often distinguished by comparing trees against the abundant *Callitris* that regenerated in the 1870s and 1880s. Trees that established before this cohort were classed as pre-settlement and those that established with or after this cohort were called post-settlement. At least 20 years elapsed between the first European settlement of the region and the late-1800s *Callitris* regeneration pulse. This interval is unlikely to influence the results obtained, however, since any trees that regenerated after the 1850s are unlikely to be distinguished from those that established in the 1870s, and any pre-settlement trees that were felled during this 20-yr period would still have been identified as being of pre-settlement origin. Two other terms require definition: *pre-settlement evidence* refers to all evidence of pre-settlement trees, including living and dead standing trees, fallen trees, and stumps, and *current trees* refer to all sampled living trees, including trees of pre- and post-settlement origin.

Site selection

The study was carried out in the *Eucalyptus–Callitris*-dominated woodland belt of central New South Wales (NSW), an area of *c.* 100,000 km^2 stretching from Nyngan in the north (31°32′ S, 147°10′ E) to Corowa in the south (35°59′ S, 146°23′ E), and from Forbes in the east to Lake Cargellico in the west (Fig. 2). Over 95% of central NSW has been cleared for agriculture (Sivertsen & Clarke, 2000), and most vegetation remnants are small and isolated. Consequently, sampling was restricted to the least disturbed remnants in the region. State Forests were selectively sampled since these areas have been managed in a consistent fashion since European settlement and past management is often well documented (e.g. Curby, 1997; Allen, 1998). Furthermore, fire has been excluded from most State Forests throughout the 20th century, which has helped to preserve evidence of pre-settlement trees.

The least disturbed forests, and stands within these forests, were selected for study. Where possible, three stands were sampled across the major topographic or edaphic gradient

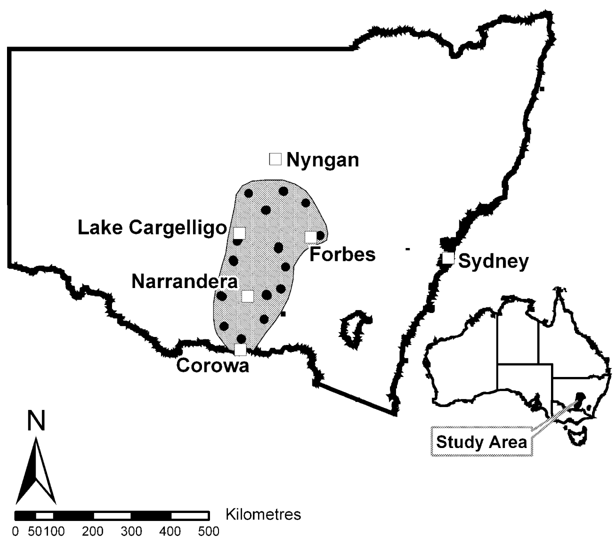

Figure 2 Location of study region and sample sites in central New South Wales, Australia.

within each forest. In total, we sampled 39 stands from 16 forests, evenly spaced across the region (Fig. 2). Sampling was restricted to woodlands dominated by *Callitris glaucophylla*, *Eucalyptus microcarpa* Maiden (Grey Box) and *E. populnea* L. Johnson & K. Hill (Bimble Box). Small proportions of *Allocasuarina luehmannii* (R.T. Baker) L. Johnson (Buloke), *Eucalyptus melliodora* A. Cunn. ex Schauer (Yellow Box), *E. blakelyi* Maiden (Blakely's Red-gum) and *E. sideroxylon* A. Cunn. ex Woolls (Red Ironbark) occurred at some sites.

Stand sampling

In each stand, all evidence of pre-settlement trees was recorded in a 1-ha (100 × 100 m) quadrat, and all current living trees (including those of pre- and post-settlement origin) were recorded in a nested 900-m^2 quadrat. Each 1-ha quadrat was divided into 100 sub-plots of 10 × 10 m, within which the following types of evidence of pre-settlement trees were recorded: (1) live trees, (2) dead standing stags, (3) dead fallen trees, (4) cut stumps, and (5) soil depressions remaining from highly decayed stumps. A number of attributes were recorded to help to differentiate between stumps of pre- and post-settlement trees, including the degree of stump decomposition, the approximate cutting period, and type of cutting equipment (e.g. axes or mechanical saws). Living trees of pre- and post-settlement origin could usually be easily distinguished, as most forests were extensively ringbarked in the late-1800s and surviving pre-settlement trees usually possessed a distinctive growth-form. We identified pre-settlement evidence conservatively, and coded all evidence as 'uncertain cohort' whenever any uncertainty existed. All 'uncertain cohort' evidence was excluded from calculations of pre-settlement values in order to minimize errors. Thus, our results provide estimates of the *minimum* density, basal area and cover of trees at the time of settlement, and actual values are likely to have exceeded these estimates.

Girth was measured overbark at breast height (GOBBH) for stags and standing and fallen trees, and near ground level for stumps and depressions. To determine basal area and canopy coverage of past stands, all stump measurements were converted to girth over bark at breast height based on allometric relationships documented from live trees and freshly cut stumps sampled across the region (I. Lunt & K. Ross, unpubl. data). Since sapwood and bark had disappeared from most stumps, allometric relationships were used to add sapwood and bark diameters to stump measurements where required.

Crown cover at time of settlement

Crown cover at the time of settlement was calculated to classify pre-settlement stands using Walker & Hopkins' (1990) structural scheme, and to illustrate the range of stand structures that existed at the time of settlement. Crown cover was not assessed in current stands. The crown cover of each pre-settlement tree was estimated based on allometric relationships between GOBBH and canopy diameter (I. Lunt & K. Ross, unpubl. data). In order to estimate accurately the total crown cover in each 1-ha quadrat, the position of all pre-settlement evidence must be accurately recorded in the field. However, we recorded the position of pre-settlement evidence to a 10 × 10 m grid resolution only. To estimate the total crown cover in each 1-ha quadrat, the location of all pre-settlement evidence was randomly plotted within each 10 × 10 m grid cell. Schematic crown maps were then generated for each 1-ha quadrat using bubbleplot charts in Microsoft Excel, with the bubble diameter scaled to the estimated canopy diameter. The cover of each and all tree species in each quadrat was then estimated by counting intercepts between plotted tree crowns and a grid of 400 points overlaid on each bubbleplot chart. To minimize errors resulting from randomized locations, tree locations were re-randomized, and cover values were re-calculated five times for each quadrat. The mean values were used to provide estimates of pre-settlement canopy cover within each 1-ha quadrat.

Post-settlement disturbance index

Despite attempts to sample the least disturbed stands in the region, the amount of post-settlement human disturbance varied greatly amongst sites. To assess whether estimated tree densities at the time of settlement were negatively correlated with the degree of post-settlement disturbance, post-settlement disturbance was estimated using an index comprising five attributes: (1) number of harvesting and thinning events (0–4; high scores indicate high impact), (2) cover of exotic weeds (0–3), (3) abundance of rabbit warrens (0–2), (4) evidence of soil disturbance by ripping or upturned stumps (0–2), and (5) presence of old tracks within the quadrat (0–1). The site disturbance index was obtained by summing these five scores.

Statistical analyses

Associations between tree densities in current stands and at the time of European settlement, and between tree densities at the time of settlement and other environmental variables were investigated for *Eucalyptus*, *Callitris*, *Allocasuarina* and combined species. Paired-samples *t*-tests were used where variables were significantly correlated, and two-independent-samples *t*-tests were used when no significant correlations existed. Where necessary, variables were log-transformed in order to satisfy assumptions of normality, and outliers were excluded from analyses. For *Allocasuarina*, however, assumptions for normality could not be met, and equivalent non-parametric Wilcoxon signed ranks tests were used. Relationships between the post-settlement disturbance index and the density, basal area and crown cover of each and all species at the time of settlement were explored using Pearson's correlation coefficient using SPSS version 11.5.

Stepwise linear regressions were also performed on the pre-settlement density, basal area and crown cover of *Eucalyptus*, *Callitris*, *Allocasuarina* and combined species, in order to investigate associations with geographic locality (latitude and longitude) and site disturbance. The five components of the

Table 1 Mean stand attributes in current stands and at the time of European settlement for *Eucalyptus–Callitris* woodlands in central New South Wales

Attribute	Time of European settlement	Current stands, all trees	Current stands, large trees (> 60 cm GOBBH)
Density (trees ha^{-1}) all species	39	**1474**	**198**
Density (trees ha^{-1}) *Eucalyptus*	24	**52**	19
Density (trees ha^{-1}) *Callitris*	14	**1387**	**176**
Density (trees ha^{-1}) *Allocasuarina*	1.6	**29**	2.6
Basal area (m^2 ha^{-1}) all species	10.7	**15.6**	11.4
Basal area (m^2 ha^{-1}) *Eucalyptus*	8.3	**3.0**	**2.8**
Basal area (m^2 ha^{-1}) *Callitris*	2.2	**12.3**	**8.4**
Basal area (m^2 ha^{-1}) *Allocasuarina*	0.3	0.2	**0.1**

GOBBH: Girth over bark at breast height.
Values for current stands that are significantly different ($P > 0.05$) from those at the time of settlement are shown in bold.

Figure 3 Typical current forest structure within sampled State Forests in central New South Wales. Stands were dominated by *Callitris glaucophylla*, which regenerated in the late 1800s, with scattered *Eucalyptus* species and *Allocasuarina luehmannii*. Tall stumps of pre-settlement *Callitris* are visible in the foreground.

Figure 4 Pooled size structure of current trees in 39 *Eucalyptus–Callitris*-dominated stands in State Forests in central New South Wales. Saplings smaller than 10-cm girth represented 59% of all trees and are not shown for reasons of clarity. Column labels show the upper value for each decile, for example 20 = 11–20 cm, 30 = 21–30 cm, etc.

site disturbance index were entered separately and collectively (as the site disturbance index). Again, outliers were removed, and where necessary data were log-transformed to achieve normality. Stepwise linear regressions were performed on each variable, with all variables initially entered (F entry = 0.05, removal = 0.10), using default options in SPSS 11.5.

RESULTS

Current tree densities

The density of living trees in current stands averaged 1474 trees ha^{-1}, but varied greatly from 256 to 7433 trees ha^{-1} (Table 1). Most stands were dominated by *Callitris* (94% of trees; Figs 3 & 4), with minor *Eucalyptus* (4%) and *Allocasuarina* (2%). Most trees were small (Fig. 4); 59% of trees were < 10 cm GOBBH, and 96% of these were *Callitris*. By contrast, most large trees were eucalypts, including 89% of trees > 150 cm GOBBH.

Pre-settlement evidence

In total, 26% of all potential pre-settlement evidence was classed as 'uncertain cohort' and was excluded from the following calculations to minimize errors. In the worst-case scenario, in which all uncertain evidence did originate before European settlement (which is unlikely), estimates of pre-settlement tree densities would represent 74% of actual pre-settlement densities, based on surveyed evidence.

Evidence of pre-settlement trees was found at all sites. Overall, stumps were the most frequent source of evidence of pre-settlement trees (51%), followed by stags (20%), fallen trees (11%), soil depressions (10%) and live trees (8%). Most pre-settlement evidence (87%) ranged from 60 cm to 250 cm GOBBH (estimated GOBBH at time of death), and only 1.1% of pre-settlement evidence was smaller than 60 cm GOBBH (Fig. 5). The paucity of evidence of small trees could reflect either: (1) actual pre-settlement patterns, or (2) faster decomposition of small stumps before sampling occurred. The latter explanation is likely since small *Callitris* saplings are known to have been thinned from many forests in the early 1900s

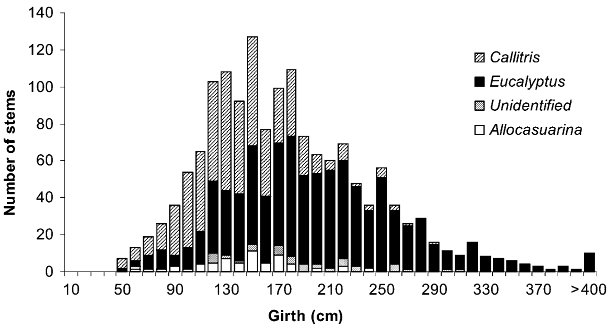

Figure 5 Pooled size structure of pre-settlement evidence for each genus in *Eucalyptus–Callitris* woodlands in central New South Wales. Column labels show the upper value for each decile, for example 50 = 41–50 cm, 60 = 51–60 cm, etc.

(Curby, 1997; Allen, 1998), but few small thinning stumps were observed. Thus, results may greatly under-estimate actual densities of small trees at the time of settlement. Consequently, in subsequent comparisons of tree densities in current stands and at the time of settlement, comparisons are made against trees > 60 cm GOBBH (or 20 cm diameter at breast height) in current stands to increase the reliability of comparisons. For brevity, trees > 60 cm GOBBH are called 'large trees'.

Pre-settlement tree densities and species composition

On average, we estimated that there were 39 trees ha^{-1} at the time of European settlement (Table 1), but values varied greatly amongst stands, from 17 to 81 trees ha^{-1}. *Eucalyptus* was the most abundant genus at the time of settlement, accounting for 58% of all evidence, followed by *Callitris* (35%), *Allocasuarina* (4%) and unidentified species (3%; Fig. 5). Virtually all unidentified species were from shallow soil depressions where no wood remains could be found. From their advanced state of decomposition and frequent large size, it is assumed that most if not all were *Eucalyptus*. On this assumption, *Eucalyptus* accounted for 61% of all trees at the time of settlement. *Eucalyptus* was numerically dominant at most sites, and accounted for > 50% of trees at the time of settlement at 74% of sites.

Comparison of pre-settlement and current tree densities

On average, tree density was over 37 times greater in current stands than at the time of settlement when all trees were compared, and five times as great when trees > 60 cm GOBBH were compared (Table 1; both $P < 0.01$). The higher density of large trees (> 60 cm GOBBH) in current stands was almost totally due to *Callitris*, which has increased significantly since settlement ($P < 0.01$; Table 1). By contrast, there was no significant difference between the estimated density of *Eucalyptus* at the time of settlement and the density of large *Eucalyptus* in current stands ($P > 0.05$). There was also no significant correlation between the density of trees at the time of settlement and the current density of large trees (> 60 cm GOBBH) at each site for any or all species (all $P > 0.05$, $n = 39$).

Basal area comparisons

The relative basal areas of *Callitris* and *Eucalyptus* have almost completely reversed since European settlement (Table 1). *Eucalyptus* comprised 78% of average site basal area at the time of settlement, compared with just 19% in current stands. By contrast, *Callitris* accounted for 79% of average site basal area in current stands, compared with 21% at the time of settlement. A similar result emerged when the comparison was restricted to large trees in current stands (Table 1). Consequently, *Callitris* basal area was significantly greater in current stands than at the time of settlement ($P < 0.01$), whereas *Eucalyptus* basal area was significantly lower in current stands ($P < 0.01$). Total basal area was significantly greater in current stands than at the time of settlement when all current trees were analysed ($P = 0.01$), but there was no significant difference in total basal area between current and pre-settlement stands when current trees < 60 cm GOBBH were excluded ($P > 0.05$).

The basal area of large eucalypts (> 60 cm GOBBH) has declined since settlement by 5.1 $m^2\ ha^{-1}$ at each site on average, and has increased at only three sites (8%). Given the high potential for eucalypt stumps to have decayed before the survey was conducted, the real rate of decline is likely to be underestimated. There was no significant correlation ($P > 0.05$) between basal area at the time of settlement and in current stands for all species, *Callitris* or *Eucalyptus*.

Crown cover at time of settlement

Estimated crown cover at the time of settlement averaged 29% (range 10–47%), which is classified as 'woodland' in Walker & Hopkins' (1990) structural scheme. Crown cover was dominated by *Eucalyptus* (mean = 24%), with low cover of *Callitris* (5%) and *Allocasuarina* (1%). Fig. 6 illustrates the range of observed pre-settlement crown patterns, and highlights the variations in canopy cover amongst sites. To some extent this variation may encompass 'lost' data, since the most disturbed sites had lower tree densities (Fig. 7). Apparent 'gaps' may have been occupied by trees that decomposed some time ago. Evidence of small saplings, in particular, is unlikely to have persisted through time. The crown-cover maps highlight the degree of *Eucalyptus* dominance at the time of settlement. *Eucalyptus* crown dominance reflects the larger average stem girth of *Eucalyptus* than *Callitris* and the wider canopy of *Eucalyptus* than *Callitris* trees at a given stem girth.

Post-settlement disturbance

Despite attempts to select the least disturbed study sites possible, all areas displayed evidence of post-settlement disturbance. In total, 67% of quadrats contained evidence of

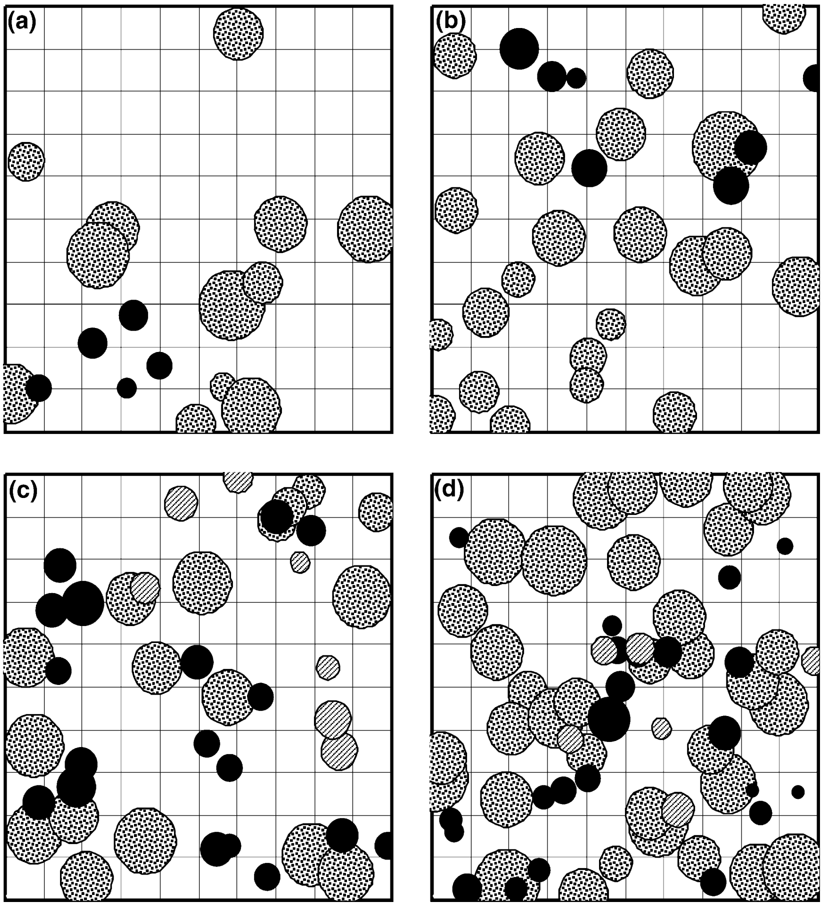

Figure 6 Estimated tree canopy cover at the time of European settlement in four representative 1-ha quadrats that encompass the range of documented pre-settlement tree densities. Tree locations were randomly plotted within each 10 × 10 m grid cell. Dotted circles: *Eucalyptus*; solid circles: *Callitris*; and hatched circles: *Allocasuarina*.

ringbarking in the late 1800s or early 1900s. All but one plot contained evidence of subsequent timber harvesting, and all areas had been grazed by European stock.

For all species combined, there was a significant negative correlation between the post-settlement disturbance index and the estimated density ($r = -0.46$, $P = 0.01$, $n = 39$), basal area ($r = -0.44$, $P = 0.01$; Fig. 7a) and crown cover ($r = -0.407$, $P = 0.012$) of trees at the time of settlement. This relationship was largely driven by *Eucalyptus* species (Fig. 7b), and there was a significant negative correlation between the disturbance index and the estimated density ($r = -0.46$, $P = 0.01$), basal area ($r = -0.53$, $P = 0.01$; Fig. 7b) and crown cover ($r = -0.373$, $P = 0.023$) of *Eucalyptus* at the time of settlement. In contrast, there was no significant correlation between the disturbance index and the estimated density ($r = -0.209$, $P > 0.05$), basal area ($r = -0.160$, $P > 0.05$; Fig. 7c) or crown cover ($r = -0.090$, $P > 0.05$) of *Callitris* at the time of settlement. These results imply that the density, basal area and crown cover of trees at the time of settlement may be underestimated in the most disturbed sites, especially for *Eucalyptus*.

Regression analyses

Stepwise regression was used to identify the range of factors that contributed to patterns for each dependent variable. However, only one variable was found to contribute to the best model for each dependent variable (Table 2). In general, results confirmed those obtained from previous *t*-tests and correlation analyses. The site disturbance index was significantly negatively associated with estimated basal area and crown cover at the time of settlement for all species and *Eucalyptus*. Interestingly, longitude was significantly positively associated with the estimated density of all species, and with the estimated density, basal area and crown cover of *Allocasuarina* at the time of settlement (Table 2). In contrast, *Callitris* density, basal area and crown cover at the time of settlement were not significantly related to geographic location or post-settlement disturbance. The individual components of the site disturbance index did not contribute to any of the models. Thus, in general, tree densities at the time of settlement were found to be significantly greater in the east of the region, and in relatively undisturbed sites.

DISCUSSION

This study provides the first quantitative data from any region of Australia on regional patterns of tree density, basal area and crown cover at the time of European settlement. A number of Australian studies have documented pre-settlement tree density and species composition (e.g. Lunt, 1997b; Fensham & Holman, 1998; Stubbs & Specht, 2002; Martin, 2005), but only

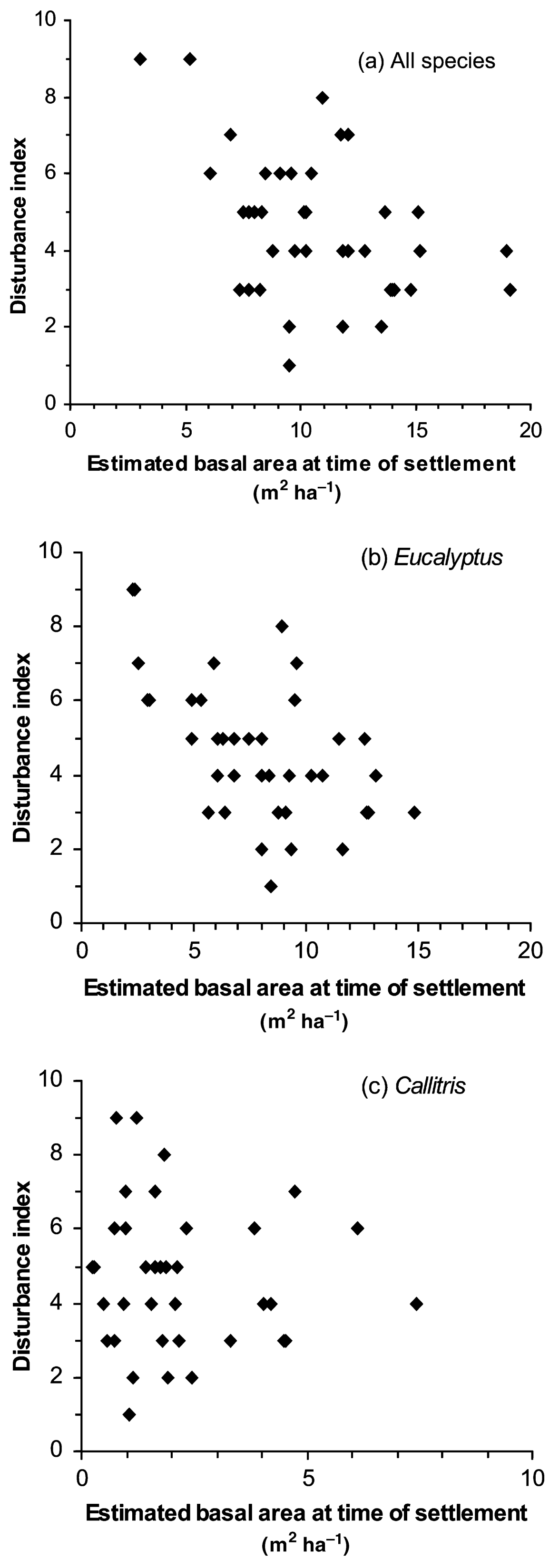

Figure 7 Relationships between the post-settlement site disturbance index and estimated basal area at the time of European settlement for (a) all species, (b) *Eucalyptus* and (c) *Callitris*.

one study has documented regional variations in pre-settlement canopy cover (Fensham & Holman, 1998) and none has documented pre-settlement basal area. Furthermore, this is the first large-scale Australian study to use field evidence of pre-settlement trees rather than archival data.

Our results illustrate the well-documented increase in *Callitris* densities that occurred in the late 1800s (Lindsay, 1967; Rolls, 1981; Noble, 1997). Actual increases in *Callitris* densities would have far exceeded the densities documented here, as many *Callitris* undoubtedly died or were felled during the preceding century (Lunt *et al.*, 2001). Dense *Callitris* recruitment, combined with selective removal of *Eucalyptus*, effectively transformed State Forests from *Eucalyptus* to *Callitris* dominance. The degree of original *Eucalyptus* dominance was unexpected. Whilst a decline in *Eucalyptus* is acknowledged by foresters (e.g. Lindsay, 1967; Lacey, 1973; Forestry Commission of New South Wales, 1988), few observers have highlighted the magnitude of this transformation.

Thus, these results incorporate elements from both traditional and recent vegetation histories. Tree densities certainly did increase greatly after European settlement, as highlighted by recent histories (Ryan *et al.*, 1995; Rolls, 1999, 2000) and acknowledged by earlier foresters and ecologists (Lindsay, 1967; Harrington *et al.*, 1979; Forestry Commission of New South Wales, 1988). However at the time of European settlement, stands were much denser than is acknowledged by these recent histories. These results show that pre-settlement tree densities in the *Callitris*–*Eucalyptus* zone were at least three times the 'dozen or so… trees to the hectare' proposed by Rolls (1999, p. 197). Actual densities may have been even greater again, given likely losses of historical evidence, particularly small trees. Importantly, the average tree density we obtained (39 trees ha^{-1}) is far greater than that shown in Fig. 1 (from Rolls, 1999).

By contrast, we present Fig. 8, which shows a small, uncleared woodland dominated by *Eucalyptus microcarpa* on a travelling stock reserve near Forbes in central NSW. Uncleared sites dominated by pre-settlement trees like this are now extremely rare. We recorded 43 large trees (> 60 cm GOBBH) from a 1-ha quadrat at this site, which is similar to the average density of trees at the time of settlement that we recorded in this study (39 trees ha^{-1}). Based on our results, this well-wooded view is more typical of stand structures in temperate *Eucalyptus*–*Callitris* woodlands at the time of European settlement than the open pastoral landscape presented by Rolls (1999; Fig. 1).

Recent histories by Ryan *et al.* (1995) and Rolls (1999, 2000) have suggested that, following European settlement, open park-like landscapes (as in Fig. 1) were transformed to dense forests (Fig. 3). Such changes may perhaps have occurred in other Australian landscapes, but, according to our data, they did not commonly occur in *Callitris*–*Eucalyptus* woodlands in central NSW. In this ecosystem, a more appropriate model is to view most open pastoral landscapes (Fig. 1) and dense *Callitris* forests (Fig. 3) as both having been derived from past

Table 2 Factors contributing to the estimated density, basal area and cover of each and all species at the time of European settlement, based on stepwise regression analyses. Only one independent variable contributed significantly to each model

Dependent variable	Independent variable (s)	Beta	*t*	*P*	Constant	Model summary	
						F	*P*
Density							
All species	Longitude	0.000	2.960	0.005	−14.863	8.763	0.005
Allocasuarina	Longitude	0.000	6.718	0.000	−2.575	45.135	0.000
Callitris	–			n.s.			
Eucalyptus	–			n.s.			
Basal area							
All species	Disturbance index	−0.806	−2.975	0.005	14.440	8.853	0.005
Allocasuarina	Longitude	0.000	4.935	0.000	−3.011	24.358	0.000
Callitris	–			n.s.			
Eucalyptus	Disturbance index	−0.750	−3.303	0.002	11.732	10.909	0.002
Crown cover							
All species	Disturbance index	−1.882	−3.025	0.005	37.158	9.150	0.005
Allocasuarina	Longitude	0.000	4.454	0.001	−2.137	19.837	0.001
Callitris	–			n.s.			
Eucalyptus	Disturbance index	−1.807	−2.785	0.008	32.525	7.756	0.008

Figure 8 An uncleared woodland dominated by *Eucalyptus microcarpa* on a travelling stock reserve near Forbes in central NSW. There were 43 large trees ha^{-1} (> 60 cm girth) at the site, which is close to the average pre-settlement tree density recorded in this study (39 trees ha^{-1}). This structure appears to have been typical of *Eucalyptus–Callitris* woodlands at the time of European settlement.

clearing of former *Eucalyptus*-dominated woodlands (Fig. 8). This suggestion does not deny the existence of considerable variability in woodland tree densities at the time of European settlement (as shown in Fig. 6). However, our data demonstrate that the woodland in Fig. 8 is more representative of average pre-settlement tree densities in the study area. More open landscapes certainly occurred in other regions (Fensham, 1989; Barr & Cary, 1992; Croft *et al.*, 1997; Lunt, 1997a,b; Morcom & Westbrooke, 1998), and possibly within other ecosystems in this region, but they were not dominant in *Eucalyptus–Callitris* woodlands across central NSW.

Conversely, some recent studies based on traditional vegetation histories appear to have overestimated pre-settlement woodland tree densities. Walker *et al.* (1993) estimated that 6.3 billion large trees were cleared from woodlands in the Murray–Darling Basin, based on a mean density of 189 large trees (> 60 cm GOBBH) per hectare in current remnants. In calculating the number of trees cleared, Walker *et al.* (1993, p. 269) assumed that 'present-day vegetation… has a similar structure to pre-European vegetation', although they recognized that this assumption was problematic. Walker *et al.*'s (1993) estimated pre-settlement tree density is almost five times the mean pre-settlement tree density that we obtained (189 vs. 39 trees ha^{-1}). Even if we arbitrarily assume that the real density of large pre-settlement trees was double the mean density we recorded (i.e. 78 trees ha^{-1}), Walker *et al.*'s (1993) estimate is still 2.4 times greater than this potentially inflated estimate. Based on this coarse calibration, we suggest that 1–3 billion large trees have been cleared from the Murray–Darling Basin, rather than the 6.3 billion large trees suggested by Walker *et al.* (1993).

Comparisons against other methods

This study provides invaluable data on pre-settlement stands that could not be obtained by any other means, especially on stand size structures and basal area. Most large-scale regional studies of pre-settlement tree densities from Australia have analysed historical survey plans from the late 1800s, many of which include tables showing distances between witness trees and allotment corners (e.g. Lunt, 1997b; Fensham & Holman, 1998; Stubbs & Specht, 2002; Martin, 2005). Historical tree densities can be calculated from these data using the plotless closest-neighbour method of Cottam (1949) and Cottam & Curtis (1956).

Studies based on closest-neighbour analyses of witness-tree distances on historical plans provide 'ballpark' estimates of minimum densities of pre-settlement trees, owing to a number of biases in this method. Surveyors selectively marked large, permanent and conspicuous trees rather than the closest tree to each corner, and systematically ignored small trees and certain species (Fensham & Holman, 1998; Lunt, 1998; Stubbs & Specht, 2002). Stubbs & Specht (2002) suggested that trees < 30–40 cm diameter were too small to be blazed and recorded by early surveyors. Thus, closest-neighbour analyses of witness-tree distances provide *minimum* estimates of the actual density of large trees > 30–40 cm diameter. By contrast, our field measurements include evidence from many pre-settlement trees that were > 20 cm diameter (60 cm GOBBH). Consequently, stump assessments may enable more accurate estimates of the density of medium-sized trees than studies of corner-to-witness-tree distances on old survey plans. If this is the case, then higher densities would be expected from studies based on field evidence, provided that the field evidence was well preserved.

Martin (2005) used witness-tree distances to estimate pre-settlement tree densities in the Boona Mount area in the far north of our study region, and recorded an average of 19.5 trees ha^{-1} (range 9.3–31.4, $n = 16$ parishes). Eight of our 1-ha quadrats (from four State Forests) were within Martin's (2005) study area. On average, we estimated that there were 41 trees ha^{-1} (range = 17–65 trees ha^{-1}) at the time of settlement, which, as expected, is significantly higher than Martin's estimate (independent-samples t-test, $t = 3.312$, $P = 0.01$). However this difference could be the result of different sampling areas rather than different methods.

Van der Ree & Bennett (2001) estimated the density of pre-settlement trees in northern Victoria by counting the number of large trees (> 70 cm diameter at breast height) along roadsides. On average, they recorded fewer pre-settlement trees than this study (21 cf. 39 trees ha^{-1}). However, their method would be expected to underestimate the true density of pre-settlement trees, because many pre-settlement trees are likely to have died and fallen during the past 150 years, and some trees smaller than 70 cm diameter may have originated before settlement (A. Bennett, pers. comm. 2005; I. Lunt, unpubl. data).

In contrast to many settlement surveys in the USA (Whitney & DeCant, 2000), in Australia surveyors were not instructed to record the diameter of blazed witness trees (Stubbs & Specht, 2002; Spooner, 2005), and thus it is not possible to obtain estimates of tree-size classes or basal area from survey plans. Thus, the information we obtained on pre-settlement size structures, basal area and canopy cover cannot be obtained from any other source.

Study limitations

Our results indicate the *minimum* density, basal area and crown cover of trees at the time of European settlement. Actual values are likely to have exceeded these estimates for a number of reasons. Many pre-settlement trees were cut down over 100 years before our study, and many stumps and dead trees are likely to have disappeared in the interim. Rates of loss are likely to be influenced by initial tree size, soil moisture and climatic conditions, species-specific wood properties, and the degree of site disturbance.

Estimated *Eucalyptus* densities at the time of settlement were negatively correlated with the intensity of post-settlement disturbance, but no such association existed for *Callitris*. This pattern suggests that *Eucalyptus* stumps are more likely to have disappeared from disturbed sites than decay-resistant *Callitris* stumps. *Eucalyptus* wood decomposes faster than *Callitris* wood, as *Callitris* wood is highly resistant to decay and attack by insects, including termites (Lacey, 1973). Furthermore, large old *Eucalyptus* trees often have hollow trunks, and many stumps consist of a thin outer shell that is easily broken. Selective loss of *Eucalyptus* stumps implies that *Eucalyptus* originally dominated stands to an even greater extent than the results indicate.

Few stumps of small (< 60 cm GOBBH) pre-settlement trees were detected. This pattern is consistent with many historical reports that state that the region originally supported a relatively open understorey (e.g. Rolls, 1981, 1999; Ryan *et al.*, 1995). However, the pattern also reflects preferential decomposition and loss of small stumps, which break easily at ground level. Few stumps of small, post-settlement saplings were found even in forests that are known to have been silviculturally thinned in the early 1900s. Consequently, the paucity of evidence of small pre-settlement trees is likely to be a methodological artefact. Thus, this method cannot be used to settle debates over the density of small trees and saplings at the time of European settlement (e.g. Norris *et al.*, 1991; Benson & Redpath, 1997 vs. Rolls, 1981; Ryan *et al.*, 1995).

Pre-settlement tree densities were also underestimated as a result of difficulties in conclusively identifying all pre-settlement trees and stumps; 26% of all evidence that may have been from pre-settlement trees was excluded from estimates for this reason. However, many of these stumps were probably from post-settlement rather than pre-settlement trees. Unfortunately, this is the only source of error that can be quantified. Consequently, the extent to which we have underestimated actual values cannot be determined.

Regional vs. State Forest tree densities

Most of the sampled forests were small remnants (< 500 ha) that occupied soils and topographic positions similar to those in the surrounding, cleared agricultural areas. These forests exist because of early government policies to retain timber reserves in agricultural regions, not because these areas were unsuitable for agricultural production (Curby, 1997; Allen, 1998). Consequently, selective sampling of State Forests is unlikely to have led to biased sampling of particular soils or topographic positions that are unrepresentative of *Eucalyptus*–*Callitris* forests across the wider region. Importantly, however, these results cannot be extrapolated to other forest types that occupy other environmental positions within the region (e.g. riparian forests).

Selective sampling of State Forests could, however, have led to an inflated estimate of the *regional* density, basal area and cover of *Callitris* at the time of European settlement. This problem arises because State Forests were only declared in places that supported relatively high volumes of merchantable, mature *Callitris* (Allen, 1998). In the late 1800s and early 1900s the region was rapidly developed for agriculture, and early foresters fought a (largely losing) battle to declare reserves for future timber supplies. Large areas of high-quality timber were cleared for agriculture (Curby, 1997; Allen, 1998). The key factor driving potential forest reservation was the density of pre-settlement *Callitris*. *Eucalyptus* and dense post-settlement *Callitris* regrowth did not influence reservation decisions (Allen, 1998). In many of the sampled forests (especially those in the south of the region), virtually all *Eucalyptus* trees were ringbarked in the late 1800s and 1900s to promote growth of *Callitris* and grasses for forest grazing (Lindsay, 1967; Curby, 1997; Allen, 1998). Consequently, selective sampling of State Forests is unlikely to have led to an overestimation of regional pre-settlement *Eucalyptus* densities. It may, however, have led to an overestimation of regional, pre-settlement *Callitris* densities.

Given that State Forests were declared in areas that contained relatively high densities of timber-bearing pre-settlement *Callitris* trees (Allen, 1998), the pre-settlement *Callitris* densities recorded here are surprisingly low (mean = 14 *Callitris* ha^{-1}), especially given the good preservation of large *Callitris* stumps. It is possible that many pre-settlement *Callitris* were relatively small when cut in the late 1800s, and that their stumps have not been preserved over the past century. However, the results suggest that the density of *Callitris* that was required to justify forest reservation in the late 1800s was not particularly high when compared with the high densities of post-settlement trees in current forests.

Selective quadrat sampling within State Forests

Selective sampling of undisturbed stands within State Forests undoubtedly led to biased estimates of current stand structures. We selected stands that were dominated by *Callitris* that regenerated in the late 1800s, to minimize the impact of recent timber harvesting on pre-settlement evidence. By contrast, stands that we avoided because they had been harvested intensively in recent decades were usually dominated by dense young *Callitris* regeneration with few old *Callitris* (Forestry Commission of New South Wales, 1988). Thus, our estimates of current *Callitris* densities are not representative of State Forests as a whole. Current *Callitris* densities across all State Forests are probably considerably greater than our data suggest (since recently logged areas often contain dense young *Callitris*), and current *Callitris* basal area is probably considerably lower than our data suggest (because intensively logged areas contain fewer mature *Callitris*). Importantly, current stand structures are primarily determined by recent harvesting of post-settlement trees, and recent harvesting patterns are not related to pre-settlement stand structures, as was shown by the absence of correlation between pre-settlement and current stand structures. Thus, the selection of relatively undisturbed stands is likely to have led to biased estimates of current stand structures, but is unlikely to have led to biased estimates of pre-settlement stand structures.

Pre-settlement trees and arboreal fauna

Clearance of the original temperate *Eucalyptus* woodlands to form the agricultural 'wheat–sheep' belt had a dramatic impact on the native biota (Yates & Hobbs, 1997; Lunt & Bennett, 2000). Many species are now restricted to small patches of remnant vegetation, and fragmentation and isolation continue to contribute to population decline for many woodland species (Ford *et al.*, 2001; Bennett, 2003). Many of the largest remnants on the agricultural plains are in State Forests, and State Forests, travelling stock reserves and roadside verges now collectively contain most remnant vegetation (Sivertsen & Clarke, 2000).

In addition to landscape clearing, European settlement also triggered major vegetation changes within remnants (Lunt & Spooner, 2005), as highlighted by the change from *Eucalyptus* to *Callitris* dominance in State Forests. Most State Forests now have lower densities of pre-settlement *Eucalyptus* trees than other uncleared remnants (such as travelling stock reserves) owing to widespread ringbarking in the 1800s and ongoing removal of *Eucalyptus* during the 1900s. This structural change presumably had a large impact on arboreal fauna.

Flowering *Eucalyptus* trees provide an important nectar source for birds and some arboreal mammals, and flower and nectar production increase with tree size and age (MacNally & MacGoldrick, 1997; Wilson & Bennett, 1999). Thus, the loss of old *Eucalyptus* trees is likely to have caused a major decline in nectar provision in state forests. Mature *Eucalyptus* trees also form hollows that many birds, arboreal mammals and reptiles use for nesting and shelter (Bennett *et al.*, 1994; Gibbons & Lindenmayer, 2002). Large hollows take over a century to develop and are extremely rare in *Eucalyptus* trees that established after European settlement (Gibbons & Lindenmayer, 2002). Consequently, hollow availability limits the abundance of arboreal mammals in many production forests (Bennett *et al.*, 1994; Gibbons & Lindenmayer, 2002; Seddon *et al.*, 2003). In contrast, *Callitris* trees do not produce nectar and rarely form hollows (Bennett *et al.*, 1994). Thus, the conversion from *Eucalyptus* to *Callitris* dominance is likely to have had a substantial negative impact on arboreal fauna that depend on *Eucalyptus* nectar and hollows.

CONCLUSIONS

Notwithstanding a number of caveats, this study greatly refines our understanding of post-settlement changes in vegetation structure in *Eucalyptus–Callitris* woodlands in central New South Wales. The results provide a more accurate benchmark of woodland stand structures at the time of European settlement than was previously available, or that could be obtained by any other means. These findings will strengthen the foundation for future land-management policies that incorporate historical benchmarks of landscape vegetation changes. Our results encompass elements of traditional and recent vegetation histories, and may help to integrate these two polarized views. Both views provide partial explanations of the complex vegetation dynamics that have occurred since European settlement. A comprehensive understanding must incorporate elements from both views, and be supplemented by novel findings not fully appreciated previously (such as the high degree of *Eucalyptus* dominance at the time of settlement).

More generally, this study highlights the value of quantitative, spatially explicit, large-scale, historical ecology studies for refining our understanding of long-term ecosystem changes and human impact on natural ecosystems across the world (Swetnam *et al.*, 1999; Bowman, 2001; Foster *et al.*, 2003; Lunt & Spooner, 2005). This long-term context is critical for the development of both ecological theory and sustainable land management.

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