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Keywords

forest, wales, structure, over, 60, years, tree, densities, continue, increase, australia, pilliga, forests, changes, south

Disciplines

Life Sciences | Physical Sciences and Mathematics | Social and Behavioral Sciences

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Changes in forest structure over 60 years: tree densities continue to increase in the Pilliga forests, New South Wales, Australia

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Abstract. Studies of long-term vegetation changes are critical for enhancing our understanding of successional dynamics in natural ecosystems. By comparing forest inventory data from the 1940s against field data from 2005, we document changes in stand structure over 60 years in forests co-dominated by *Callitris glaucophylla* J.Thompson & L.Johnson, *Allocasuarina luehmannii* (R.Baker) L.Johnson and *Eucalyptus crebra* F.Muell., in central Pilliga, New South Wales (NSW), Australia. Sampling was stratified across two forest types and across a 1951 wildfire boundary, to assess the effects of initial stand structure and early disturbance on stand dynamics. Stems in the size range tallied in the 1940s (>8.9 cm DBH for *Callitris* and >11.4 cm for *Allocasuarina* and *Eucalyptus*) of each genus increased about three-fold in density and about four-fold in basal area over 60 years, with similar trends in both forest types and fire zones. On average, there were 3638 stems ha^{-1} in 2010, of which 86% were small *Allocasuarina* and *Callitris* (<11.4-cm and <8.9-cm diameter at breast height, DBH, respectively). These results illustrate a continuation of forest encroachment that was initially documented in the late 1800s. However, increases in *Allocasuarina* have received little attention compared with *Callitris* recruitment. In the absence of disturbance, ongoing increases in stand stocking may be expected.

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Introduction

In Australia, as elsewhere in the world, great advances have been made in the past 20–30 years in mapping vegetation patterns and relating these patterns to underlying biophysical gradients (e.g. Specht and Specht 1999; Keith 2004). However, our understanding of how ecosystems have changed over long periods of time is often very crude, largely because of the paucity of accurate historical information (Lunt 2002). Consequently, vigorous debates often occur in public and ecological circles about the putative nature and causes of poorly defined ecosystem changes (e.g. Benson and Redpath 1997; Fensham 2008). As evidenced by climate politics, when scientific uncertainty is high, there is little reason to expect congruence between the political acceptability and ecological plausibility of competing scenarios. Consequently, studies that accurately document long-term and large-scale changes in ecosystem structure and disturbance regimes play a pivotal role in enhancing environmental literacy, influencing land-use policies and informing ecosystem management (e.g. Woinarski and Catterall 2004; Fensham *et al*. 2005; Brook and Bowman 2006; Lunt *et al*. 2006; Fensham 2008).

Many Australian studies of long-term vegetation dynamics compare current conditions against those at (or shortly after) European colonisation, thereby highlighting the dramatic impact of European land uses (Lunt 2002). However, ecosystems change continually, and large changes in structure and composition can occur over decadal periods in response to recent changes to global climate and disturbance regimes, including land clearance, timber harvesting, burning, grazing and reservation (McDougall 2003; Woinarski *et al*. 2006; Mac Nally *et al*. 2009). Arguably, ecosystem responses to current and recent management are more relevant to contemporary land management than changes that occurred over a century ago.

The ecological history of *Callitris–Eucalyptus* woodlands in eastern Australia has received considerable attention and been greatly debated (Rolls 1981, 2000; Mitchell 1991; Norris *et al*. 1991; Benson and Redpath 1997; van Kempen 1997; Griffiths 2002; Lunt *et al*. 2006). In many regions, *Callitris* recruited abundantly in the late 1800s, before rabbit infestations, livestock grazing and drought conditions caused a recruitment hiatus until the 1950s, when wetter conditions returned, the myxomatosis virus was introduced, and rabbits no longer suppressed *Callitris* regeneration (Lacey 1972, 1973; Noble 1997; Fensham *et al*. 2005). However, stands were originally heterogeneous, and often well stocked with other species (Lunt *et al*. 2006), and this generic history is not universal (Fensham 2008; Prior *et al*. 2011). The Pilliga region in north-eastern NSW has received considerable

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attention in debates about *Callitris* encroachment, following responses to Rolls' (1981) environmental history of the region (e.g. Mitchell 1991; Norris *et al*. 1991; Benson and Redpath 1997; van Kempen 1997). However, as in much environmental history, debates have largely focussed on forest dynamics in the late 1800s, with little consideration of more recent forest dynamics (Lunt and Spooner 2005).

The Pilliga forests (30°46′S, 149°18′E) vary across a south-east–north-west gradient. Average annual rainfall varies from 450 mm year^{-1} in the north-west to 700 mm year^{-1} in the south-east (Forestry Commission of NSW 1986). *C. glaucophylla* and various *Eucalyptus* species dominate the central and western Pilliga, whereas *C. endlicheri* is abundant in heathy forests on poorer soils in the east (Binns *et al*. 2001). Much of the forest (including the areas surveyed) has been harvested for timber since European settlement, especially for *C. glaucophylla* and *Eucalyptus crebra*. More recently, large areas were declared as conservation reserves (NSW Parks and Wildlife Service Western Directorate 2000). Sparse understoreys in the western Pilliga do not support major wildfires, but many large fires have burnt the eastern shrubby forests since the 1950s (Brookhouse *et al*. 1999; State Forests of New South Wales, Curby 2000). The largest wildfire burnt 917 000 ha, including 350 000 ha of State Forest land, under extreme weather conditions in November 1951 (Forestry Commission of NSW 1952; Brookhouse *et al*. 1999). The extent to which recent (post-1950s) disturbances, including widespread timber harvesting, have affected stand dynamics in the Pilliga is unknown.

In the present study, we use historical forest-management data to ask, how have the Pilliga forests changed over the past 60 years? Are stands stable or still changing greatly? We aimed to assess the relative contributions of initial stand structure and early disturbances on subsequent stand development by documenting structural changes across forest types and across the boundary of a major wildfire in 1951. We hypothesised that the three dominant genera (*Allocasuarina*, *Callitris* and *Eucalyptus*) would respond differently to disturbance history. Because *Callitris* and *Allocasuarina* species can recruit densely in undisturbed stands (Lacey 1972, 1973; Lunt 1998), we expected major increases in the density of both genera, particularly *Callitris*. Dense *Callitris* recruitment in the mid-1950s is well documented (Lacey 1972, 1973; Thompson and Eldridge 2005), but little is known of *Allocasuarina* dynamics. By contrast, *Eucalyptus* recruitment is commonly triggered by fires or soil disturbance (Wellington and Noble 1985; Gill 1997; Vesk and Dorrough 2006), so we hypothesised that eucalypt density would remain relatively stable in unburnt areas but would increase in the burnt area. The findings from the present study will provide a firm foundation for predicting how these forests may continue to change in the future.

Materials and methods

1940s survey

Changes in stand structure were documented by resampling transects that were surveyed in the 1940s. The survey methods of the 1940s are described by Whipp *et al*. (2009). In the mid-1940s, trees were tallied in 1-acre (0.404 ha) plots (2 × 5 chains or ~40 × 100 m) along continuous, 40-m-wide strip transects. In each plot, surveyors counted (1) the number of *Callitris* in each 1′-diameter class for all *Callitris* >3.5′ (8.9-cm)-diameter DBH, and (2) the number of *E. crebra* and *A. luehmannii* stems >4.5′ DBH in the following four DBH classes: 5–9′ (11.4–24.0 cm), 10–16′ (24.1–41.8 cm), 17–20′ (41.9–52.1 cm) and 20′+ (>52.1 cm). Hereafter, these trees are referred to as 'tallied trees'. To assess 'small', untallied *Callitris* (<3.5′, 8.9-cm DBH) and *E. crebra* (<4.5′, 11.4-cm DBH), surveyors counted the number of units (each 1/40th acre, 100 m^2) that were 'effectively stocked' in each 1-acre plot (stocking rates of small *A. luehmannii* were not recorded). Effective stocking was defined as more than four to seven stems per unit, or 420–748 stems ha^{-1} (Lindsay 1946). Stands were classified into forest types on the basis of the basal area of the dominant species (Lindsay 1967). Thus, forest type COP was dominated by *E. crebra* (C), *Allocasuarina luehmannii* (O) and *Callitris* (P), in order of decreasing basal area. However, the major timber species, *Callitris*, was listed first (e.g. PCO) wherever it was dense enough to be managed as a commercial stand (Lindsay 1967; Baur 1988).

2005 sampling

Stands co-dominated by *C. glaucophylla*, *E. crebra* and *A. luehmannii* in the central Pilliga were selected for resampling in 2005, using the following criteria: 1940s data existed and transects could be relocated; stands supported PCO or COP forest types in the 1940s; and stands were within 10 km of the boundary of the 1951 wildfire and had not been burnt since. In total, 61 stands were selected (Fig. 1). Approximately half were in each forest type (PCO and COP), and half of the patches in each forest type were burnt in 1951. A 400-m section of a 1940s transect was selected near the centre of each selected forest patch. Three 10 × 10 m plots were spaced 100 m apart along each 400-m strip. In each plot, the species and DBH of all live trees was recorded. Each *Callitris* was allocated to one of the following two cohorts: pre-1905 (hereafter termed '1800s *Callitris*') and 1950s or more recent ('post-1950s *Callitris*') on the basis of size and growth-form. Whereas forest types were randomised, the sampling strategy was pseudo-replicated with respect to fire, because only one fire (1951) was examined. Thus, results document species responses to the 1951 fire in the surveyed area, and are not necessarily representative of potential responses to other fire events in different areas (Oksanen 2001; Cottenie and De Meester 2003).

Data analysis

Data collected in 2005 from the three plots at each site were pooled, and density data were converted to per hectare values, for comparisons against the 1940s data. Basal area in the 1940s was calculated using the midpoint of each DBH class, with 13′ (33 cm) being arbitrarily used for the largest (12′+) size class for *Callitris* and 22′ (55.9 cm) for the largest (20′+) class for eucalypts. Wilcoxon rank-sum tests with Bonferroni corrections were then used to compare the mean density and basal area of tallied trees of each species between the 1940s and 2005.

Changes in the density and basal area of tallied trees of each species were also analysed using repeated-measures general

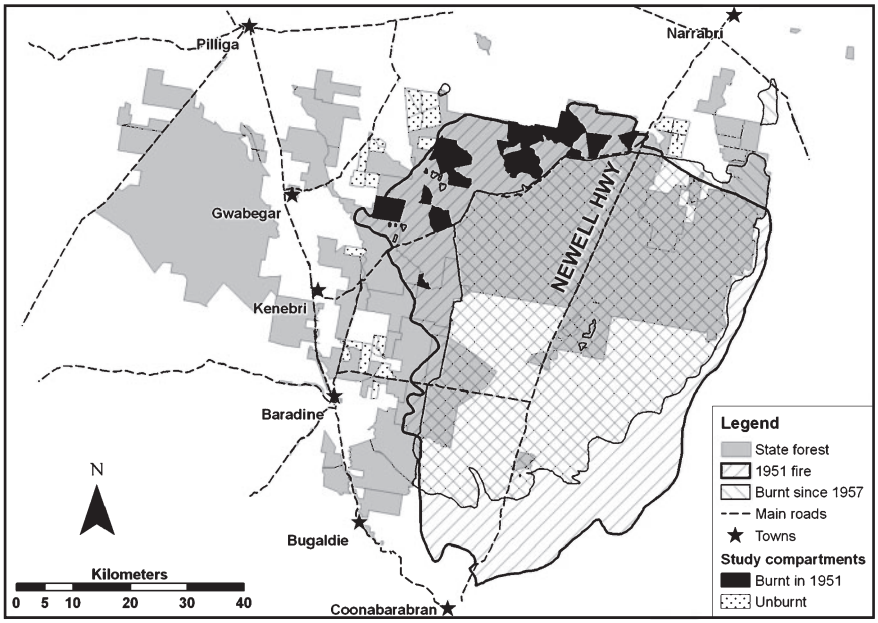

Fig. 1. Locality of sample areas and fire boundaries in the Pilliga forests, New South Wales. Sample sites were placed in each Study Compartment (compartments burnt in 1951 shown in black, unburnt compartments shown in stippled white).

linear models (GLMs) in SPSS 16.0 for Windows (SPSS Inc. 2008). Where necessary, data were transformed to meet assumptions of equality of covariance matrices as measured by Box's M test, and homoscedasticity as measured by Levene's test of equality of error variances. The density and basal area in 2005 of each *Callitris* cohort (1800s and post-1950s) were compared between the two forest types and two fire zones using two-way ANOVA tests for unequal sample sizes (Kutner *et al*. 2005; Insightful Corporation 2007). In 2005, plots that contained ≥4–7 saplings of *Callitris* and *E. crebra* were defined as 'effectively stocked', following Lindsay's (1946) definition. A linear regression was used to examine the relationship between the density of post-1950s *Callitris* regeneration and the basal area of 1800s *Callitris* at each site.

Results

In 2005, stands consisted of sparse large eucalypts amidst dense, predominantly small *Allocasuarina* and *Callitris* (Fig. 2*a*). The mean density of all species was 3638 stems ha^{-1} (±311 s.e.), of which 86% were small *Allocasuarina* (<4.5′, 11.4-cm DBH) or *Callitris* (<3.5′, 8.9-cm DBH). *E. crebra* made up only 5%, and 'other species' 1% of total stems. However, average basal area was almost equally distributed among *Allocasuarina*, *Callitris* and *E. crebra*, with the remaining 10% contributed by other species, most of which were eucalypts (Fig. 2*b*). The high basal area of *E. crebra* and 'other species' reflected the large size of eucalypt stems compared with those of *Allocasuarina* and *Callitris*.

The average density of tallied stems of all species increased significantly from 188 stems ha^{-1} (±11 s.e.) in the 1940s to 537 stems ha^{-1} (±26 s.e.) in 2005; almost a three-fold increase over ~60 years. Contrary to our expectations, the density of each species (*Allocasuarina*, *Callitris* and *E. crebra*) increased by a

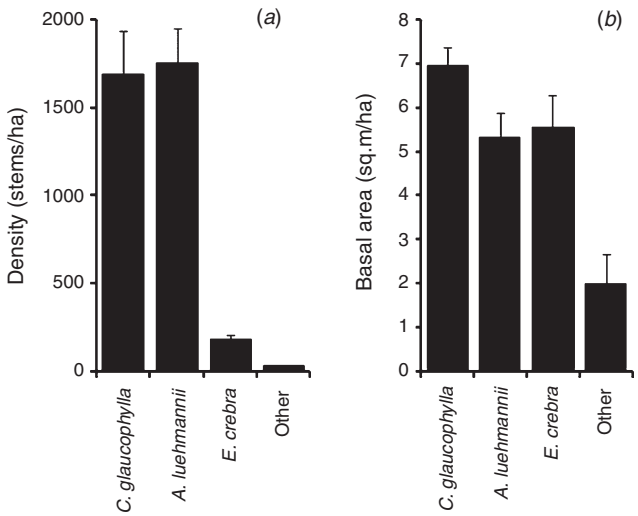

Fig. 2. Mean (*a*) density and (*b*) basal area of stems of all sizes in 2005. Error bars show standard error of the mean.

similar magnitude, and the proportion of stems of each species was similar in both periods (Fig. 3*a*). The mean basal area of tallied stem sizes increased almost four-fold from 4.2 m^2 ha^{-1} to 15.9 m^2 ha^{-1}, and basal area of *Allocasuarina*, *Callitris* and *E. crebra* increased significantly (Fig. 3*b*). The increase in density and basal area of 'other species' was not significant ($P > 0.05$), probably because of their sparseness.

The proportion of each site that was recorded as 'effectively stocked' with small *Callitris* increased from an average of 12% in the 1940s to 48–65% in 2005. Small *E. crebra* stems were very sparse in both periods. On average, 1% of plots were 'effectively stocked' with small *E. crebra* in the 1940s, compared with 3–6%

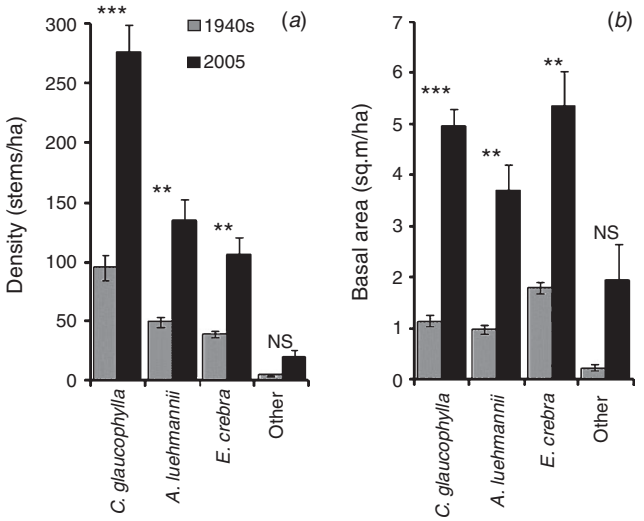

Fig. 3. Mean (*a*) density and (*b*) basal area in the 1940s and in 2005 for stems >3.5′ (8.9 cm) for *Callitris glaucophylla* and >4.5′ (11.4 cm) for other species. Error bars show standard error of the mean. ***$P < 0.001$, **$P < 0.01$, NS = $P > 0.05$.

of plots in 2005. Stocking levels for small *Allocasuarina* were not recorded in the 1940s.

Regression analysis showed a weak, but significant, negative relationship between the density of post-1950s *Callitris* and the basal area of 1800s *Callitris*, as assessed in 2005 ($r = 0.407$, $F = 11.496$, $P = 0.001$). Post-1950s regeneration was consistently low where the basal area of 1800s *Callitris* was high, but was highly variable where the basal area of 1800s *Callitris* was low (Fig. 4).

Repeated-measures GLM analyses showed no significant three-way interactions (time × fire history × forest type) or interactions between fire history and forest type for density or basal area (Tables 1, 2). Consequently, the effects of forest type and fire history are considered separately. Tallied *Callitris* were significantly denser in PCO stands and *E. crebra* in COP stands in both periods (Table 1). The density of tallied *Allocasuarina* did not differ significantly between forest types. The density and basal area of tallied trees of all three species increased significantly over time (Tables 1, 2), and a significant forest type × time interaction indicated that the density of tallied *Callitris* increased more substantially in COP than in PCO stands (Table 1). The number of tallied *Callitris* trees approximately doubled in PCO stands, and increased more than five-fold in COP stands, although the actual number of new tallied stems was very similar in both forest types (+170 *v.* +190 stems ha^{-1}). The basal area of tallied stems of all three species also increased over time (Table 2). *Callitris* basal area was significantly greater in PCO than in COP stands in both periods, but the basal area of other species did not differ between forest types.

Contrary to expectations, there were no significant relationships between fire history and the density of tallied stems for any species, although a greater density of tallied *Callitris* at burnt than at unburnt sites in both time periods approached statistical significance ($P = 0.09$; Table 1). Surprisingly, *Callitris* basal area was also significantly greater in burnt than unburnt areas in both periods (Table 2). There were no significant time × fire history interactions; however, near-significant interactions for *E. crebra* and *Allocasuarina* basal area ($P = 0.08$ and 0.07, respectively) suggest that basal area of both species may have increased more at unburnt than at burnt sites (Table 2).

In 2005, there were over three times as many 1800s *Callitris* in PCO than in COP stands, and over twice as many post-1950 *Callitris* in COP than in PCO stands (both $P < 0.05$; Table 3). Basal area followed a similar pattern but the difference was not quite significant for 1800s *Callitris* ($P = 0.07$; Table 3). In 2005,

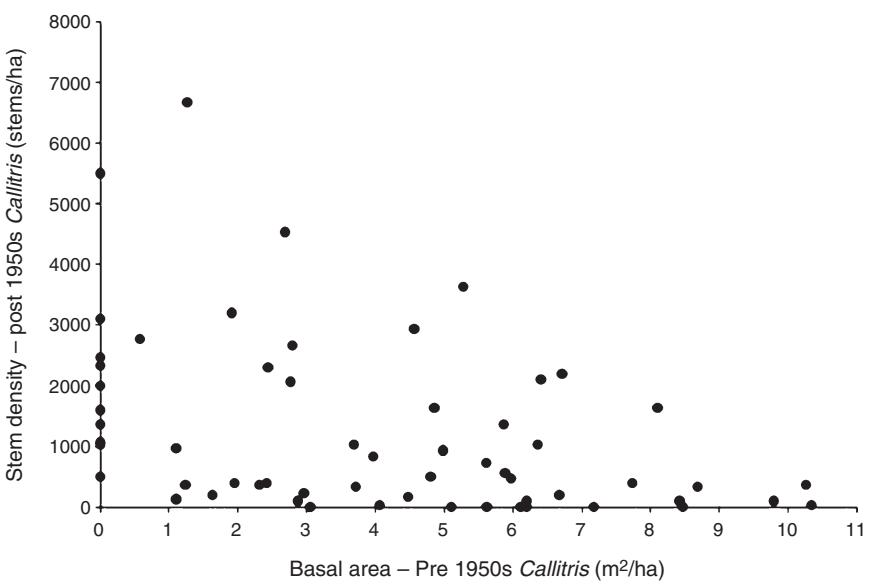

Fig. 4. Relationship between the basal area of 1800s *Callitris* trees and the density of post-1950s *Callitris* regeneration in 2005.

Table 1. Changes in density (stems ha^{-1}) of each species from the 1940s to 2005 in each forest type and fire zone

Mean values above are untransformed. *P*-values refer to transformed data as follows: $\log_e(x+1)$ for *Callitris glaucophylla*, square root for *Eucalytpus crebra* and not transformed for *Allocasuarina luehmannii*. *P*-values for main effect refer to variables that were significantly different at both dates. *P*-values for interact × time indicate changes over time in the relationship between stem density and fire history or forest type. See text for definition of PCO and COP. Significant *P*-values are in bold

Variable	*C. glaucophylla* stems >8.9-cm DBH				*E. crebra* stems >11.4-cm DBH				*A. luehmannii* stems >11.4-cm DBH			
	1940s mean (s.e.)	2005 mean (s.e.)	Main-effect *P*	Interact × time *P*	1940s mean (s.e.)	2005 mean (s.e.)	Main-effect *P*	Interact × time *P*	1940s mean (s.e.)	2005 mean (s.e.)	Main-effect *P*	Interact × time *P*
Time	96 (11)	276 (22)	**<0.001**		39 (3)	106 (15)	**0.001**		49 (4)	135 (17)	**<0.001**	
Forest type												
PCO	147 (16)	317 (26)	**<0.001**	**0.01**	33 (3)	73 (14)	**0.04**	0.08	50 (6)	152 (24)	0.35	0.33
COP	43 (5)	233 (23)			45 (5)	140 (26)			48 (5)	118 (25)		
Fire history												
Burnt in 1951	102 (16)	303 (37)	0.09	0.43	43 (5)	103 (19)	0.66	0.69	59 (7)	133 (23)	0.68	0.50
Unburnt	90 (15)	249 (24)			35 (4)	109 (24)			40 (4)	137 (26)		
Forest type × fire			0.27	0.99			0.35	0.47			0.51	0.71

Table 2. Changes in basal area (m^2 ha^{-1}) of each species from the 1940s to 2005 in each forest type and fire zone

Mean values above are untransformed. *P*-values refer to square-root-transformed data for all three genera. *P*-values for main effect refer to variables that were significantly different at both dates. *P*-values for interact × time indicate changes over time in the relationship between stem density and fire history or forest type. See text for definition of PCO and COP. Significant *P*-values are in bold

Variable	*Callitris glaucophylla* stems >11.4-cm DBH				*Eucalyptus crebra* stems >11.4-cm DBH				*Allocasuarina luehmannii* stems >11.4-cm DBH			
	1940s mean (s.e.)	2005 mean (s.e.)	Main-effect *P*	Interact × time *P*	1940s mean (s.e.)	2005 mean (s.e.)	Main-effect *P*	Interact × time *P*	1940s mean (s.e.)	2005 mean (s.e.)	Main-effect *P*	Interact × time *P*
Time	1.1 (0.1)	4.9 (0.4)	**<0.001**		1.8 (0.1)	5.3 (0.7)	**0.004**		1.0 (0.1)	3.7 (0.5)	**<0.001**	
Forest type												
PCO	1.6 (0.2)	5.6 (0.5)	**0.001**	0.50	1.8 (0.1)	6.5 (1.0)	0.45	0.44	1.0 (0.1)	3.6 (0.8)	0.48	0.44
COP	0.7 (0.2)	4.2 (0.4)			1.8 (0.1)	4.2 (0.9)			1.0 (0.1)	3.8 (0.6)		
Fire history												
Burnt in 1951	1.3 (0.2)	5.6 (0.5)	**0.03**	0.39	2.0 (0.1)	5.3 (0.9)	0.34	0.08	1.3 (0.1)	3.2 (0.6)	0.98	0.07
Unburnt	1.1 (0.1)	4.3 (0.5)			1.6 (0.1)	5.4 (1.0)			0.7 (0.3)	4.2 (0.8)		
Forest type × fire			0.38	0.16			0.49	0.15			0.58	0.94

Table 3. Density (stems ha^{-1}) and basal area (m^2 ha^{-1}) of pre-1900s and post-1950s cohorts of *Callitris glaucophylla* in each forest type and fire zone in 2005

See text for definition of PCO and COP. Significant *P*-values are in bold

Variable	*Callitris* density (stems ha^{-1})				*Callitris* basal area (m^2 ha^{-1})			
	Pre-1900 cohorts		Post-1950 cohorts		Pre-1900 cohorts		Post-1950 cohorts	
	Mean (s.e.)	*P*	Mean (s.e.)	*P*	Mean (s.e.)	*P*	Mean (s.e.)	*P*
Fire history								
Burnt in 1951	233 (52)	0.98	1801 (429)	**0.02**	4.4 (0.6)	0.12	3.5 (0.6)	0.11
Unburnt	288 (59)		1020 (290)		3.9 (0.4)		2.1 (0.5)	
Forest type								
PCO	398 (65)	**0.03**	832 (251)	**<0.01**	5.5 (0.5)	0.07	1.7 (0.5)	**0.01**
COP	120 (25)		1996 (440)		2.7 (0.4)		3.9 (0.6)	
Fire × forest type		0.33		0.66		0.16		0.87

post-1950 *Callitris* was 1.8 times denser in burnt than in unburnt areas ($P = 0.02$; Table 3). By contrast, the density and basal area of 1800s *Callitris* was not significantly different between burnt and unburnt areas (Table 3).

Discussion

In summary, these results illustrate a three- to four-fold increase in the density and basal area of all three genera over 60 years. The increase in the density and basal area of *Callitris* and

Allocasuarina was consistent with hypotheses, but the large increase in *Eucalyptus* density and basal area was not expected. Similar changes occurred in both forest types, although post-1950s *Callitris* saplings are now more than twice as dense in the forest type in which *Callitris* was initially least abundant. Few legacies of the 1951 fire could be detected in 2005.

The documented increase in tree densities since the 1940s is consistent with many accounts of dense *Callitris* regeneration in the 1950s, 1970s and more recently, in the Pilliga and other regions (Curby 1997; Allen 1998; Thompson and Eldridge 2005). The three-fold increase in the density of *Callitris* >8.9-cm DBH recorded here is largely due to the 1950s regeneration pulse, because many more recent recruits are still smaller than 8.9 cm. In addition to an increased density and basal area of *Callitris* >8.9-cm DBH, stocking levels of small *Callitris* saplings (<8.9-cm DBH) have also increased greatly, following major recruitment events in the 1950s, 1970s and more recently.

Whereas dense regeneration of *Callitris* was expected, the level of regeneration by *Allocasuarina* and *Eucalyptus* was unexpected. Regeneration of these species has received comparatively little attention (Morcom and Westbrooke 1998). Dense *Allocasuarina* regeneration has been described anecdotally in forestry reports (Lindsay 1967; Baur 1988), although levels have not been quantified previously. *A. luehmannii* can regenerate from seed and by root suckering, with suckers forming from damaged roots (Murdoch 2005). However, the relative abundance of seedlings and root suckers in the Pilliga is unknown.

Compared with *Callitris*, very little information is available on rates of eucalypt recruitment in dry woodlands in south-eastern Australia. *Eucalyptus* recruitment is commonly promoted by fire or soil disturbance (Wellington and Noble 1985; Gill 1997; Vesk and Dorrough 2006), but can occur during high-rainfall periods, provided that competition from ground plants is low (Vesk and Dorrough 2006). The extent to which *Allocasuarina* and *Eucalyptus* recruitment in the study area has occurred in pulses or continually is also unknown. Other studies have documented ongoing increases in density of *Allocasuarina* species in the absence of fire (Lunt 1998; Kirkpatrick 2004). Because seedling recruitment by both genera is likely to be promoted by high rainfall in this dry climate (Chesterfield and Parsons 1985; Fensham *et al*. 2005; Westbrooke and Florentine 2005), we assume that all three genera may have recruited during similar periods of high rainfall. Even though drought conditions prevailed in the 2000s, there was no evidence of widespread, drought-induced tree mortality, as has been observed in semiarid, savanna woodlands in Queensland (Fensham *et al*. 2009).

Effects of 1951 fire

The 1951 Pilliga wildfire burnt 917 000 ha, including 350 000 ha of State Forest land, under extreme-fire weather conditions (Forestry Commission of NSW 1952; Brookhouse *et al*. 1999). We expected that the density of 1800s *Callitris* would be low in the burnt area in 2005, because *Callitris* is readily killed in high-intensity fires (Lacey 1973; Cohn *et al*. 2011). However, in 2005 we recorded a mean number of 1800s *Callitris* trees as 233 ha^{-1} in the area that was burnt in 1951, which suggests that fire intensity in the areas sampled was far lower than expected. Low fire severity is the most parsimonious explanation for the paucity of differences in stand structure between areas that were burnt and unburnt in 1951. Unfortunately, fire intensity was not mapped in 1951. The lack of spatially explicit records of fire intensity highlights the challenges inherent in attempting to deduce the mechanisms that underlie past stand dynamics by using archival records (Swetnam *et al*. 1999).

Differences between forest types

Forests were mapped in the 1940s to identify areas supporting merchantable timber, and the two sampled forest types (PCO and COP) occurred in similar environmental conditions, but were differentiated on the basis of the amount of merchantable *Callitris* (Lindsay 1967). In 2005, PCO stands contained significantly more pre-1900s *Callitris* trees than did COP stands, as expected. However, many sites in each (former) forest type exceeded the 1940s stem-density threshold, and therefore could now be mapped as PCO stands, if the 1940s mapping methods were repeated. In terms of the basal area of all three species, PCO stands in the 1940s were more similar to COP stands in the 1940s than they were to PCO or COP stands in 2005. Thus, changes in stand structure over time far exceed differences in stand structure between forest types at either point in time.

Although both forest types underwent similar changes over time, the density of *Callitris* regeneration was over twice as great in the forest type in which *Callitris* was initially least abundant (COP). This reflected the broader pattern for greater recruitment of *Callitris* in stands with less competition from existing trees. The high density of *Callitris* saplings in both forest types suggests that stand structure may change greatly in the future, depending on disturbance regimes. Unless thinned mechanically or by fire, locked stands of dense, small *Callitris* are likely to form in both forest types (Lacey 1973; Horne 1990*a*, 1990*b*; Ross *et al*. 2008), and earlier differences between the two forest types are likely to disappear.

Conclusions

In summary, the present results demonstrate major changes in forest structure over a 60-year period. All dominant tree genera have increased in density and basal area since the 1940s. Whereas increases in *Callitris* are well documented, concurrent increases in co-dominant species have been largely over-looked in the ecological literature. The magnitude of the changes that have occurred over time far exceed the differences between mapped forest types time at any point in time. These long-term changes can be documented only because of the existence of detailed forest-survey information from the 1940s (Whipp *et al*. 2009). Such long-term inventory data are immeasurably valuable for understanding the long-term impacts of forest succession and ecological disturbances on Australian ecosystems.

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