

## Fire alters soil labile stoichiometry and litter nutrients in Australian eucalypt forests

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**Abstract.** Ecological stoichiometry may be used to investigate the impacts of fire regime, as fire regime can influence the cycling and balance of elements within forest ecosystems. We investigated the effects of fire history on soil and litter stoichiometry in four forest sites in Queensland, Australia. Soil and litter in recently burned areas were compared with those in areas with no recent fire. Effects of burning on concentrations and ratios of multiple pools of carbon (C), nitrogen (N) and phosphorus (P) in soil varied between sites, indicating that site and fire regime characteristics regulate these responses. Labile pools of soil C, N and P were more responsive to burning than total pools, and labile soil C : P and N : P ratios tended to be lower in recently burned areas, consistent with our expectations. These changes suggest that the disparate volatilisation temperatures of these elements influence post-fire soil stoichiometry, and that P cycling may be enhanced in some post-fire environments. Fire-induced changes to litter chemistry were not consistent with soil effects, although litter was generally nutrient-enriched in recently burned areas. Our results reveal the potential for fire to alter elemental balances and thus modify C and nutrient cycling in the plant–soil system.

**Additional keywords:** labile carbon, nitrogen, phosphorus.

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### Introduction

Forest fire represents a critical agent of disturbance in many ecosystems globally, and fire-affected elemental cycling may influence the structural and functional responses of plant and microbial communities to burning (Chen and Xu 2010). Enhanced plant growth due to increased availability of nutrients like nitrogen (N) and phosphorus (P) in the post-fire environment is a well-known example of this effect (e.g. Chambers and Attiwill 1994), and fire-induced changes to nutrient availability have been studied extensively (e.g. Debano and Conrad 1978; Adams *et al.* 1994; Giardina *et al.* 2000; Certini 2005). However, fire may also alter the stoichiometric balance between N, P and carbon (C) in ecosystem components (Toberman *et al.* 2014; Dijkstra and Adams 2015), and these effects may be just as important as changes in the absolute amounts of elements, given that stoichiometry often influences ecological patterns and processes owing to the specific proportions of elements required by organisms (Serner and Elser 2002).

Despite their potential influence over ecosystem properties, the stoichiometric responses of soil and the forest floor to burning have not usually been investigated explicitly, although they have received some recent attention (e.g. Pellegrini *et al.* 2015). The few previous investigations into fire's impacts on stoichiometry have usually occurred in grasslands that were

likely N-limited (e.g. Cui *et al.* 2010; Pellegrini *et al.* 2015; Zhang *et al.* 2015). However, primary productivity may be limited by P rather than N in approximately half of all terrestrial ecosystems (Elser *et al.* 2007), and research into the stoichiometric effects of fire in P-limited systems will thus be critical to understanding the impacts of the increasing occurrence of fire associated with climate change (Westerling *et al.* 2006; Liu *et al.* 2010). There also appears to be a tendency for fire-induced stoichiometric shifts to favour P (Toberman *et al.* 2014; Zhang *et al.* 2015), such that fire may be particularly significant for biological communities associated with low-P soils (Wardle *et al.* 2003, 2004; Close *et al.* 2009). Recently, Butler *et al.* (2017) reported that burning in a potentially P-limited eucalypt forest was associated with lower foliar N : P ratios in several plant species and lower foliar P resorption proficiency in the grass tree *Xanthorrhoea johnsonii*. However, further consideration of the stoichiometric responses of other ecosystem components (e.g. soil, plant litter) to a variety of fire regimes is warranted, to better understand the effects of fire on biogeochemical cycling and the soil–plant system.

Previous studies have focused on the concentrations and stoichiometry of total or plant-available (i.e. soluble and readily soluble inorganic) pools of nutrients (e.g. Zhang *et al.* 2015). However, to fully appreciate the impacts of burning on

biogeochemical cycling, it is also necessary to consider the 'labile' pools of C, N and P, which include inorganic (i.e. carbonate-C,  $\text{NO}_3^-$ -N,  $\text{NH}_4^+$ -N,  $\text{PO}_4^{3-}$ -P) and easily soluble organic forms (e.g. simple polysaccharide-C, amino acid-N, RNA- and DNA-P) that are rapidly cycled, readily biologically available and potentially more easily volatilised or transformed during fires compared with complex or refractory forms (González-Pérez *et al.* 2004; Muqaddas *et al.* 2015). Labile C : N : P stoichiometry may be more dynamic than total C : N : P stoichiometry, and is highly influential over below-ground, biologically mediated processes, including microbial activity and nutrient mineralisation (Sinsabaugh *et al.* 2009, 2013); however, labile pools have rarely been considered in the contexts of fire-altered biogeochemistry or stoichiometry.

In response to these research gaps, the following study was conducted in four eucalypt forest sites on low-P soils in south-east Queensland, Australia. The effects of fire history on soil and litter chemistry and stoichiometry in total and labile pools were investigated, based on the hypotheses that (1) recent fire would be associated with lower soil C : P and N : P ratios in labile pools, with total pools being affected less; and (2) changes in litter stoichiometry would be consistent with changes in soil stoichiometry.

## Materials and methods

### Study sites and sampling

Four dry eucalypt forest sites were selected based on their fire histories, with two situated within Toohey Forest, near Brisbane (Toohey Forest A and B, 500 m apart; Table 1), and two in the White Rock–Spring Mountain Conservation Estate (WRSMCE) near Ipswich (WRSMCE A and B, 2900 m apart; Table 1). Toohey Forest is an open eucalypt forest on shallow, sandy Leptosols (Food and Agriculture Organization, United Nations classification; Beckman 1967), with mean average precipitation (MAP) of 1030 mm and mean annual temperature (MAT) of 20.5°C (1981–2015). Vegetation in the WRSMCE is shrubby-to-tall open eucalypt forests occurring on Cainozoic and Mesozoic sediments. The WRSMCE has a MAP of 955 mm and MAT of 23.4°C (1981–2015). Soils in the WRSMCE are sandy, and have been described as Lixisols (Ipswich City Council 2014). All four sites contained recently, frequently burned (RFB) areas of forest, and adjacent areas that had remained undisturbed for at least a decade when sampled (no recent fire, NRF areas; Table 1).

Samples were collected from Toohey Forest in February 2014 and from WRSMCE sites in November 2013. At all sites, the RFB and NRF areas were separated by vehicle or walking tracks. Within sites, five sampling locations were established in both areas along transects running parallel to these tracks, such that there were five pairs of sampling locations between the RFB and NRF areas, spaced 15–20 m apart. Ten litter samples (leaf, humus and fermentation layers combined) were sampled at each site using a 25-cm<sup>2</sup> quadrat, with each consisting of three combined quadrat subsamples. Ten surface soil samples (0–10 cm depth, each comprising five bulked subsamples) were then collected at each site using a soil corer (6.5 cm diameter) after litter removal. Additional soil samples were collected for soil bulk density estimations. This study design is somewhat limited because the fire histories were pseudo-replicated within

sites and because the effects of fire frequency were confounded with those of time since fire. The former limitation was not overly problematic as the NRF and RFB areas were highly comparable in aspects other than fire history, whereas the latter was essentially unavoidable for our sites.

### Sample preparation and chemical analyses

Soil samples were sieved at 2 mm and air-dried, whereas litter samples were oven-dried (105°C for 2 h, then at 65°C for 1 week). Total C and N of finely ground soil and litter were determined by dry combustion (LECO TruMac TCN). Soil total P was measured using molybdenum-blue spectrophotometry after combustion at 550°C and extraction with 0.5 M  $\text{H}_2\text{SO}_4$  (Saunders and Williams 1955), whereas litter total P was determined after nitric–perchloric acid digestion (Jackson 1958). Soil total inorganic P ( $P_i$ ) was measured spectrophotometrically after 0.5 M  $\text{H}_2\text{SO}_4$  extraction without prior combustion, and soil total organic P ( $P_o$ ) was calculated as the difference between soil total P and  $P_i$  (Saunders and Williams 1955).

Soil and litter hot-water-extractable (HWE) C, N and P were measured to represent the labile fractions of these elements (Sparling *et al.* 1998; Chen *et al.* 2005; Tutua *et al.* 2013). Samples were incubated in water at 70°C for 16 h, then shaken for 5 min and filtered using Whatman 42 filter papers. Extracts were analysed for HWE organic C and total N using a Shimadzu TOC-VCPH/CPN analyser, which is fitted with a total N unit (Chen *et al.* 2005), and for HWE total P using spectrophotometry after sulfuric digestion in an autoclave.

### Data analyses

Data distributions were tested for normality using the Shapiro–Wilk test and log-transformed where necessary. Paired Student's *t*-tests were used to compare soil and litter properties between the NRF and RFB areas within sites (statistical significance at  $P < 0.05$ ). To evaluate the consistency of the size of the effects of fire history on soil and litter stoichiometric ratios across all sites, we calculated mean response ratios (RRs) on a percentage basis with 99% confidence intervals, based on the means of RFB and NRF plots ( $\text{RR}\% = \left( \frac{\bar{X}_{\text{RFB}} - \bar{X}_{\text{NRF}}}{\bar{X}_{\text{NRF}}} \right) \times 100$ ). Where confidence intervals did not overlap zero, effect size was considered significant. This meta-analytical approach was adopted in order to account for potential inherent differences in site properties (see Wan *et al.* 2001; Dijkstra and Adams 2015). Analyses were conducted using *Statistix 8.0*.

## Results and discussion

### Soil chemistry and C : N : P ratios

Fire history did not appear to affect soil pH or bulk density at our sites (data not shown). Similarly, soil total C and N were generally not affected (Table 2). Hot-water-extractable soil C and N appeared somewhat more responsive; however, these effects were generally not significant for HWE C and were inconsistent for HWE N (Table 2). Soil total P concentrations were higher in RFB areas at Toohey Forest B and WRSMCE B, but lower at WRSMCE A, whereas soil HWE P was only higher at WRSMCE B (Table 2). The variability in the effects of fire on soil C, N and P is likely a reflection of the differing site and fire

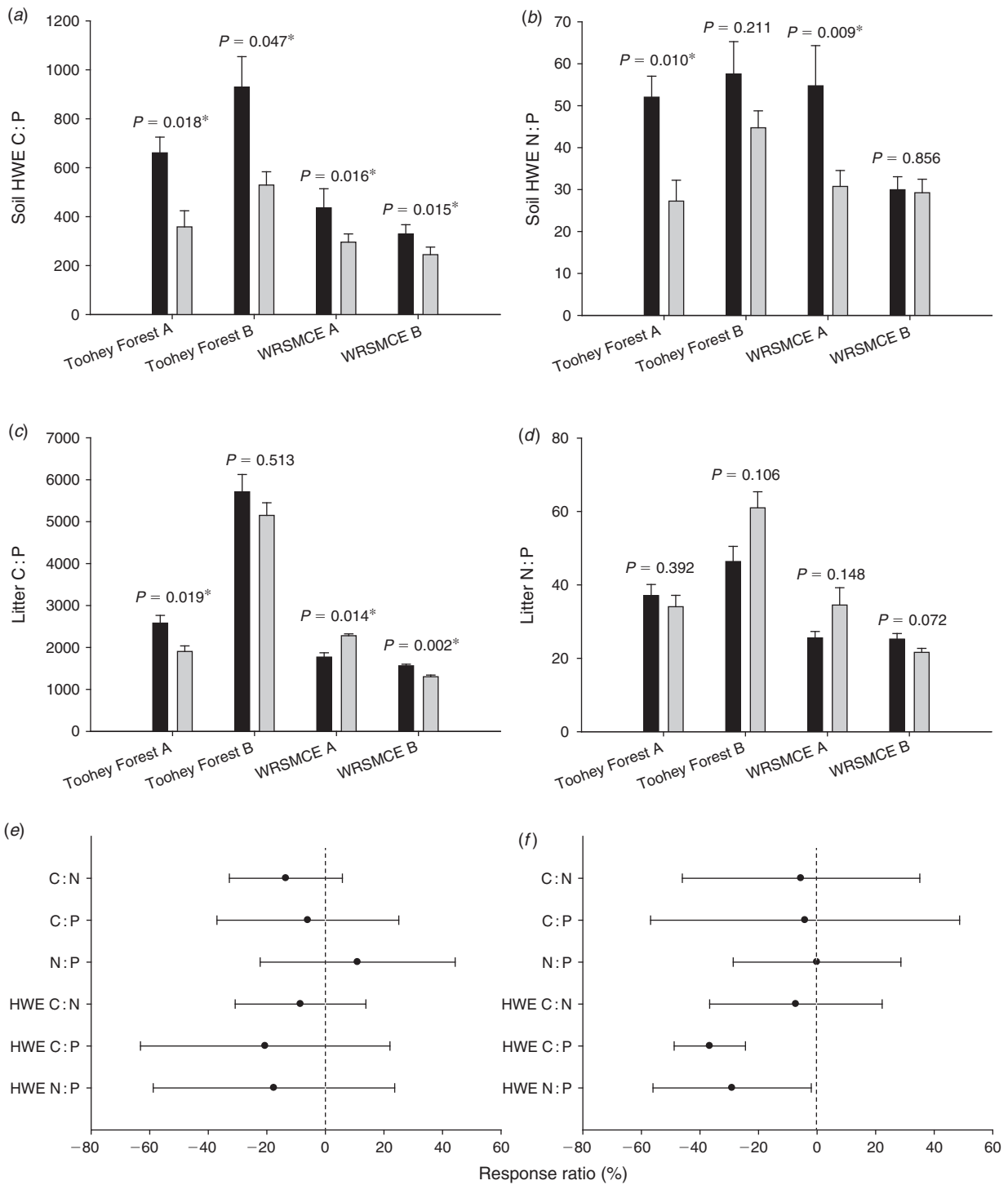
**Table 1. General site characteristics and fire histories of recently, frequently burned (RFB) and no recent fire (NRF) areas at Toohey Forest and White Rock Spring Mountain Conservation Estate (WRSMCE) sites**

Site	Coordinates	Major plant species	Soil bulk density (g cm <sup>-3</sup> )	Soil pH	Soil clay (%)	Slope	Fire history of RFB area	Fire history of NRF area
Soil (0–10 cm) bulk density, pH and clay content values are for NRF areas (means ± s.e.; n = 5). TSF, time since fire								
Toohey forest A	-27.5392, 153.0451	<i>Eucalyptus acmenoides</i> , <i>Corymbia citriodora</i> , <i>Acacia leiocalyx</i>	1.0 (±0.08)	4.9 (±0.1)	11.0 (±1.0)	10–15°	Low-intensity prescribed burns in Aug. 2013 (TSF 0.5 years), July 2005 and Aug. 1998	No fires since at least 1998 (date of last fire unknown; TSF > 15 years)
Toohey forest B	-27.5400, 153.0501	<i>E. crebra</i> , <i>Allocasuarina littoralis</i> , <i>Xanthorrhoea johnsonii</i>	1.1 (±0.04)	4.3 (±0.3)	13.3 (±0.4)	0–5°	Low-intensity prescribed burns in September 2009 (TSF 4.4 years), April 2008, May 2003 and c. 1995	Low-intensity prescribed burn in June 1999 (TSF 14.7 years)
WRSMCE A	-27.7186, 152.8645	<i>C. citriodora</i> , <i>E. crebra</i> , <i>Lophostemon confertus</i>	1.1 (±0.03)	5.9 (±0.04)	7.2 (±1.2)	25–30°	Moderate- to high-intensity wildfire in October 2012 (TSF 1.1 years) and medium-intensity wildfires in August 2004 and c. December 2000	No fires since at least 1998 (date of last fire unknown; TSF > 15 years)
WRSMCE B	-27.6957, 152.8510	<i>C. henryi</i> , <i>E. crebra</i> , <i>E. siderophloia</i>	1.2 (±0.07)	5.2 (±0.03)	10.4 (±0.4)	0–10°	Low- to medium-intensity wildfire in October 2012 (TSF 1.1 years), a prescribed burn in July 2010 and a medium-intensity wildfire in December 1998	Medium-intensity wildfire in December 1998 (TSF 14.9 years)

**Table 2. Pairwise comparisons of selected litter and soil properties (0–10 cm; means ± s.e.) between NRF and RFB areas at Toohey Forest and White Rock Spring Mountain Conservation Estate (WRSMCE) sites**

P values from Student's paired *t*-tests provided, with statistical significance (*P* < 0.05) denoted \*; n = 5; NRF, no recent fire; RFB, recent, frequent fire; TC, TN and TP, total C, N and P respectively; P<sub>i</sub>, P<sub>o</sub> and C<sub>o</sub>, inorganic P, organic P and organic C respectively; HWE N, P and C<sub>o</sub>, hot-water-extractable (i.e. 'labile') forms of total N, total P and organic C

	Litter biomass (kg ha <sup>-1</sup> )	Litter N (%)	Litter P (%)	Soil TC (%)	Soil TN (%)	Soil TP (µg g <sup>-1</sup> )	Soil TP <sub>i</sub> (µg g <sup>-1</sup> )	Soil TP <sub>o</sub> (µg g <sup>-1</sup> )	Soil HWE C <sub>o</sub> (µg g <sup>-1</sup> )	Soil HWE N (µg g <sup>-1</sup> )	Soil HWE P (µg g <sup>-1</sup> )
Toohey Forest A	8703 (±754)	0.71 (±0.04)	0.019 (±0.001)	2.31 (±0.25)	0.080 (±0.011)	74 (±5)	6.9 (±0.4)	66.9 (±5.0)	690 (±51)	54.5 (±3.9)	1.1 (±0.1)
RFB area	5247 (±361)	0.95 (±0.06)	0.028 (±0.002)	2.64 (±0.17)	0.075 (±0.005)	86 (±6)	9.2 (±1.3)	77.1 (±7.1)	578 (±43)	44.0 (±3.2)	1.8 (±0.3)
P value	0.003*	0.034*	0.004*	0.096	0.362	0.255	0.108	0.407	0.069	0.071	0.110
Toohey Forest B	10610 (±838)	0.43 (±0.02)	0.009 (±0.001)	2.34 (±0.20)	0.038 (±0.005)	35 (±3)	4.0 (±0.4)	30.7 (±2.4)	401 (±30)	25.0 (±1.8)	0.5 (±0.1)
RFB area	8801 (±811)	0.58 (±0.03)	0.010 (±0.000)	1.91 (±0.22)	0.057 (±0.006)	64 (±5)	6.0 (±0.3)	57.4 (±4.7)	346 (±25)	29.3 (±1.6)	0.7 (±0.1)
P value	0.077	0.001*	0.879	0.070	0.019*	0.002*	0.002*	0.003*	0.022*	0.006*	0.051
WRSMCE A	7944 (±1075)	0.72 (±0.03)	0.028 (±0.001)	1.70 (±0.17)	0.066 (±0.006)	168 (±6)	41.0 (±2.8)	127.2 (±7.6)	433 (±36)	54.0 (±4.0)	1.1 (±0.2)
RFB area	3047 (±169)	0.80 (±0.11)	0.023 (±0.000)	1.63 (±0.07)	0.057 (±0.004)	111 (±3)	27.0 (±2.0)	83.8 (±1.1)	354 (±24)	37.1 (±3.1)	1.2 (±0.1)
P value	0.014*	0.600	0.030*	0.677	0.341	0.002*	0.002*	0.005*	0.087	0.014*	0.304
WRSMCE B	7065 (±390)	0.81 (±0.05)	0.032 (±0.001)	1.50 (±0.10)	0.058 (±0.007)	121 (±3)	25.6 (±1.7)	94.9 (±3.6)	339 (±20)	30.2 (±0.7)	1.1 (±0.1)
RFB area	3763 (±533)	0.85 (±0.03)	0.039 (±0.001)	1.72 (±0.11)	0.072 (±0.006)	148 (±7)	36.8 (±3.1)	111.2 (±7.1)	406 (±38)	48.4 (±3.3)	1.7 (±0.2)
P value	0.015*	0.460	0.004*	0.265	0.224	0.008*	0.035*	0.044*	0.244	0.004*	0.019*



**Fig. 1.** Comparisons of (a) soil hot-water-extractable (HWE; i.e. 'labile') C:P; (b) soil HWE N:P; (c) litter total C:P; (d) litter total N:P (observed means + s.e.;  $n = 5$  in all cases) between 'no recent fire' (NRF; black bars) and 'recently, frequently burned' (RFB; grey bars) areas at Toohey Forest and White Rock Spring Mountain Conservation Estate (WRSMCE) sites (Student's paired  $t$ -test  $P$ -values provided and statistical significance denoted \*), and effects of recent, frequent burning on (e) litter; and (f) soil total and HWE C:N:P ratios, expressed as the mean response ratios (RRs) of the four study sites ( $\% \pm 99\%$  confidence intervals;  $n = 4$ ; effect sizes were considered significant where confidence intervals did not overlap zero).

characteristics (e.g. slope, time since fire). For example, we suspect that the significantly lower concentrations of soil total P,  $P_i$ ,  $P_o$  and HWE N in the RFB area at WRSMCE A ( $P$ -values  $< 0.05$  in all cases; see Table 1) were due to the site's steep slope, which may have promoted rapid losses of soluble nutrients after burning (Lane *et al.* 2011).

The effects of fire history on soil total C : N and C : P ratios were varied and inconsistent between sites, while soil total N : P was not significantly affected by fire at any site. In contrast, we found remarkable consistency in the effects of fire on soil HWE C : P and N : P ratios (Fig. 1a, b). Recent occurrence of fire was associated with significantly lower soil HWE C : P ratios at all sites, and significantly lower HWE N : P at Toohey Forest A and WRSMCE A. Accordingly, the mean RRs of soil HWE C : P and N : P across all sites were significantly less than zero (Fig. 1f). To our knowledge, this is the first study to demonstrate that soil labile stoichiometry is highly responsive to fire, even where total C : N : P stoichiometry is not. This novelty is enhanced by the low-P status of our study system, as most prior research into fire-induced stoichiometry shifts has been conducted in N-limited grasslands (Cui *et al.* 2010; Pellegrini *et al.* 2015).

Significantly lower soil labile C : P and N : P ratios in RFB areas were consistent with our hypothesis of fire-induced C : N : P stoichiometry shifts in favour of P in labile pools. This supports the idea that the high volatilisation temperature of P influences post-fire soil chemistry and stoichiometry in labile pools, but not necessarily in total pools, which may contain various complex, recalcitrant forms of organic matter that may be resistant to volatilisation or oxidation (González-Pérez *et al.* 2004). Hot-water-extractable forms of C, N and P are regarded as highly labile and therefore readily available for use by microbes (Sparling *et al.* 1998). Thus, changes in the stoichiometry of HWE C, N and P may regulate the relative rates of release or occlusion of these elements in the soil system (Sinsabaugh *et al.* 2009), and in particular may lead to greater rates of available P release and C and N immobilisation. Thus, the significantly lower HWE C : P and N : P ratios in RFB areas may lead to, or be indicative of, enhanced or 'less-conservative' P cycling in fire-affected soils. Further, our results indicate that changes to soil labile C : N : P stoichiometry can persist for up to 4 years post fire in some cases (i.e. at Toohey Forest B). Previous studies in the same forest landscape indicate that the soil microbial biomass could rapidly occlude post-fire increases in available P and thereby act as a sink to prevent P losses from the P-poor system (Huang *et al.* 2013). A similar effect may underlie the apparent longevity of the reduced labile C : P ratios in our study, particularly given that soil microbial biomass is closely coupled to the HWE C pool (Sparling *et al.* 1998).

#### Litter chemistry and C : N : P ratios

Recent fire was associated with higher total litter N concentrations at both Toohey forest sites, but WRSMCE sites were not similarly affected (Table 2). Total litter P concentrations were higher in RFB areas at the Toohey Forest A and WRSMCE B sites, lower in the RFB area at WRSMCE A and unaffected at Toohey Forest B (Table 2). Litter HWE pools of C, N and P were generally not affected (Table S1 in supplementary material available online). These effects were not necessarily qualitatively consistent with soil effects, suggesting that litter nutrient

concentrations were not particularly sensitive to the fire-induced changes to soil nutrients at our sites. This effect may be influenced by the large proportions of nutrient-poor compounds in *Eucalyptus* litter (i.e. lignin in bark and stems; Scalenghe *et al.* 2015), such that responses of litter nutrient concentrations may become more apparent when only leaf material is considered.

Fire history had no consistent effects on litter HWE or total C : N : P stoichiometry (Fig. 1c, d, e). Litter total C : N ratios were lower in RFB areas at both Toohey forest sites, whereas litter total C : P ratios were lower in RFB areas at Toohey Forest A and WRSMCE B and not significantly different at Toohey Forest B. Litter N : P ratios did not differ between RFB and NRF areas at any site (Fig. 1d), suggesting that the fire-altered soil nutrient concentrations did not disproportionately alter rates of foliar N and P resorption on a community level. Numerous factors may influence the potential for fire-induced decoupling of N and P cycling, but much remains unclear. For instance, Toberman *et al.* (2014) reported reduced N : P ratios in eucalypt litter in biennially burned areas, but not quadrennially burned areas, suggesting that fire frequency regulates litter stoichiometry shifts. However, other studies have reported reduced total N and increased or unchanged total P in litter following single fire events (e.g. Bhandari *et al.* 2000; Cade-Menun *et al.* 2000), indicating that frequency is not the only factor, and that further research is required to understand how fire affects the biogeochemical functioning of the soil–plant system.

#### Conclusions

The effect of fire on soil and litter chemistry and stoichiometry varied between our sites, indicating that site or fire history characteristics influence fire-induced C : N : P stoichiometry shifts. Nevertheless, the balances of HWE (i.e. labile) pools of C, N and P in soil were frequently shifted in favour of P, consistent with our hypothesis. This effect may be attributed to the different volatilisation temperatures of these elements. These effects may be associated with, or indicative of, altered patterns of elemental cycling, and particularly enhanced P cycling, in recently burned ecosystems.

#### Conflict of interest

The authors declare that they have no conflict of interest.

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