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Coarse Woody Debris Improves Nutrient Cycling in a Rehabilitated Montane Forest

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ABSTRACT

The successful restoration of disturbed ecosystems depends on the ability of below-ground soil decomposer communities to cycle organic matter into soil stocks and available forms for above-ground producers. We investigated the interactions between forest disturbance history, coarse woody debris and leaf carbon-to-nitrogen ratio (C:N) and their impacts on biological activity in soil and litter within a rehabilitated rock spoil and adjacent undisturbed montane forest in Kosciuszko National Park, Australia. We measured rates of soil CO_2 efflux and leaf decomposition, two key measures of soil function, to determine whether proximity to coarse woody debris improved soil function in rehabilitated sites. Coarse woody debris was associated with increased CO_2 efflux and decomposition in the rehabilitated forest (28.1% and 12.6% increase, respectively), but not within nearby undisturbed forest. In the absence of coarse woody debris, leaf mass loss to decomposition was 84.2% lower in the rehabilitated forest compared to the reference forest. Leaf decomposition varied significantly depending on the species from which the litter derived and was greatest in green tea and eucalyptus litter, and least in rooibos tea, with the CWD and forest type effects being consistent among these. However, decomposition of leaf litter of native species did not conform to expectations; leaves with low C:N had lower, rather than higher, rates of decomposition. These findings highlight the positive effects of coarse woody debris addition on soil functioning within rehabilitated forests and its potential in reconstructing nutrient cycles following disturbance.

1 | Introduction

Forest restoration schemes often prioritise the recovery of above-ground vegetation communities. However, the development of below-ground functions, like decomposition and nutrient cycling, is essential to supporting full recovery. Below-ground biotic communities provide ecosystem services including storage of organic C and provisioning of nutrients to above-ground producers (Daufresne and Loreau 2001). The introduction of coarse woody debris (CWD) is thought to improve the development of soil decomposer communities in forest restoration (Goldin and Hutchinson 2013; Gonzalez-Polo et al. 2013). Although studies have explored whether the addition of CWD affects rates of litter decomposition and biological activity in soil (Hamonts et al. 2017; Wang et al. 2023), fewer have studied soil ecology within the context of ecological restoration (Goldin and Hutchinson 2014). The essential role of soil biota in ecosystem stability and nutrient cycles emphasises their significance, especially in a recovering ecosystem.

Dead plant matter is a large portion of the organic soil layer, and the structural and chemical traits of these inputs are

increasingly understood to influence the rates of activity of soil biota (Eisenhauer and Powell 2017). Soil biotic communities, including saprophytic fungi, bacteria and arthropods, subsist on this dead material and convert complex biomolecules into more available forms, which can then become available to above-ground producers and consumers (Daufresne and Loreau 2001). The ability of soil biota to take advantage of dead organic matter partially depends on the structure and chemical composition of above-ground dead matter. Inputs of leaf litter into the soil influence decomposer activity, but the specific traits of leaves differ between species and can impact rates of decomposition. Inputs of CWD, such as fallen trees or dead stumps, are also thought to provide a wide range of beneficial ecological functions to decomposer communities, becoming biological 'hotspots' for soil activity (Bradford et al. 2023; Gonzalez-Polo et al. 2013; Kuzyakov and Blagodatskaya 2015).

Large pieces of woody debris are abundant and significant structural components of mature forest communities and have long-term impacts on nutrient cycling regimes (Harmon et al. 1986; Jia-bing et al. 2005). Despite the toughness of wood, CWD is an important nutrient source and has been demonstrated to promote decomposer communities (Stokland et al. 2012). The habitat provided by woody debris to microbes, fungi, arthropods, and larger animals is well documented (Kwak et al. 2015; Stutz and Lang 2017; Sullivan et al. 2017; van Galen et al. 2019). Coarse woody debris alters microclimates, increasing soil moisture, moderating soil temperature, and balancing pH, all of which can create more favourable conditions for the decomposer system (Goldin and Hutchinson 2014; Kappes et al. 2007) and increase nutrient cycling within and immediately surrounding CWD (Gonzalez-Polo et al. 2013). CWD is associated with increased soil enzyme activity and increased microbial diversity, both indicators of a robust decomposer community (Amaranthus et al. 1994; Gonzalez-Polo et al. 2013; Kwak et al. 2015). Saprophytic fungi surviving on CWD have been found to contain higher concentrations of N and phosphorus compared to their host dead wood (Harmon et al. 1994). This suggests that the higher concentrations of recalcitrant compounds in CWD, such as lignin, serve a role in storing labile material for longer, increasing its longevity as a nutrient sink (Austin and Ballaré 2010; Rehman et al. 2022). It has also been argued that CWD is capable of exerting influence over the decomposition of nearby litter, through fungal transportation of nutrients over fine spatial scales (Corte et al. 2009; Glassman et al. 2017).

CWD may improve ecosystem resilience against some disturbances and is a highly valued resource for forest restoration (Jia-bing et al. 2005; Kitzberger et al. 2012; Parkhurst et al. 2022). In addition to providing a long-term nutrient sink, the recalcitrant compounds in CWD have long residence times in organic soils, which contribute to pedogenesis, the formation of soil (Stutz et al. 2019). The highly porous structure of CWD can improve moisture retention, which can mitigate water stress for nearby plants and soil biota, as well as provide improved shelter from wind erosion and improved soil stability (Grilliot et al. 2019; Jia-bing et al. 2005; Parkhurst et al. 2022). These functions provided by CWD, however, take many years to be realised if CWD must accumulate naturally following ecological disturbance; thus, the addition of CWD in the early stages of ecosystem restoration may accelerate recovery of processes such as decomposition and nutrient cycling.

Fine organic matter such as leaf litter is much more quickly fragmented and decomposed than CWD; its residence time in soil depends partly on the chemical traits of leaves. One such trait is the ratio of carbon and nitrogen content (C:N ratio), which is negatively correlated with litter mass loss and decomposition rates (e.g., Freschet et al. 2011; Santiago 2007). Increased leaf C:N ratios are associated with plant species with a more nutrient-conservative strategy and physiology (Freschet et al. 2011). N and C are often primary foci for studying leaf nutrient economics, as they are high-demand nutrients for biomolecules needed by consumer and decomposer organisms for survival (Corte et al. 2009; Feller et al. 2003; Funk et al. 2013). These traits affect the decomposition of leaves once they become part of the litter, but plants will resorb a large amount of the N and phosphorus within their leaves as they senesce and before they dehisce (Aerts 1996). This means that the C:N of the litter that reaches the soil and decomposer system is generally higher than that of live leaf tissue (Bakker et al. 2011). In ecological restoration, the C:N ratio of planted species' leaves could influence the rate of recovery and functional resilience of the restored ecosystem. Low C:N leaf litters have the capacity to improve nutrient cycling and accelerate litter decomposition (León and Osorio 2014), while high C:N leaf litters may contribute to lower nutrient releases and litter and soil organic matter accumulation (Lyu et al. 2023).

In highly disturbed ecosystems, soil properties can be heavily altered and affect the type of vegetation communities that can be supported. Loss of organic soils can limit the activity of soil biota, reduce soil nutrient availability, and soil water holding capacity, delaying ecosystem recovery (Macdonald et al. 2015). In cases where the soil organic layer has been lost, recovery of the above-ground ecosystem may be tightly coupled with recovery of below-ground ecosystem composition, structure and function (Dorrough et al. 2023; Hu et al. 2022). The protection and retention of soil organic layers is therefore often a priority in ecosystem restoration and rehabilitation (Macdonald et al. 2015; MacPhee 2013). However, this is not always possible in certain disturbed environments, such as former mining sites, as the topmost layers of soil may have been compacted, eroded or covered. In these circumstances, careful species selection and the addition of CWD may be employed to enhance soil biological activity and the accumulation of soil organic matter, and thus support the recovery of these processes where soil functioning has been lost.

We explored the influence of CWD and leaf nutrient traits on soil activity within the context of montane eucalypt forest recovery following major disturbance in Kosciuszko National Park, Australia. The study system is characterised by dominant *Eucalyptus dalrympleana*, *E. viminalis*, and *E. delegatensis*, with acidic clay loam soils and an abundance of ground litter and deadwood (Macphee and Wilks 2013). We tested the role of CWD on soil respiration and litter decomposition rates in an undisturbed reference forest and an adjacent rehabilitated forest. The rehabilitated forest was established in 2008 by reshaping and replanting a rock spoil and had little to no soil or vegetation development prior to intervention. To assess the effect of planted

litter quality on soil organic matter accumulation and decomposition, we measured mass loss of litter bags containing leaf litter from *Acacia dealbata* and a mix of *E. viminalis* and *E. dalrympleana*, which are locally abundant tree species with contrasting N content and that dominate the restoration plantings. Decomposition of these species was compared to a standard: rooibos (*Aspalathus linearis*) and green tea (*Camellia sinensis*; Keuskamp et al. 2013).

Based on the positive effect of CWD on litter decomposition rates found in other systems, we expected greater litter mass loss and increased rates of CO_2 efflux in soils adjacent to CWD (Bradford et al. 2023; Gonzalez-Polo et al. 2013; Marra and Edmonds 1996), with the strongest effect of CWD in the rehabilitated forest. We expected that because N content is often a limiting resource within decomposer communities, the high C:N ratio *Eucalyptus* spp. and rooibos (*A. linearis*) leaves would have slower decomposition compared to the low C:N ratio leaves from *A. dealbata* and *C. sinensis*. We expected low C:N ratio leaves would decompose fastest, and rates would be highest near CWD. Although the impacts of both litter quality and CWD on decomposition rates are established in the literature, there are few studies that specifically test the interaction between litter quality and CWD in ecosystem recovery.

2 | Methods

2.1 | Study System

The experiment was established in a rehabilitated montane eucalypt forest and nearby undisturbed stand (hereafter 'reference') within Kosciuszko National Park, 1050 m ASL in south-eastern Australia (36°17′30″ S, 148°31′07″ E). The reference forest overstorey is dominated by *E. dalrympleana* and *E. delegatensis*, with *E. viminalis* and *E. pauciflora* as sub-dominants. The rehabilitated site was established on an 8 ha, 10-m-deep rock spoil, resulting from the construction works for the Snowy Mountains Hydro-Electric Scheme between 1949 and 1974.

Rehabilitation of the rock spoil was undertaken in 2008–2009 and the recovering forest now has an overstory of *A. dealbata, E. viminalis*, and *E. dalrympleana* (Macphee and Wilks 2013). During this work, the rehabilitation site was treated with 530 m of eucalypt CWD laid in windrows down the slope of the spoil. Tubestock was planted in composted holes, then hay mulch was added at a rate of 11.25 t ha^{-1} (Wilks 2023, personal communication). These treatments were not uniform, and some areas received scarce compost and hay (Macphee and Wilks 2013).

2.2 | Experimental Design and Setup

Both the decomposition and CO_2 efflux experiments were two-way factorial designs replicated over eight experimental blocks. Each block was comprised of one 2 × 2 m plot located within the rehabilitated forest, and another located in the reference forest directly upslope (Figure 1). Each plot location was chosen in relation to a mass of CWD with a volume greater than 0.063 m^3 (minimum 2 m length × 0.2 m diameter). CWD state of decay was estimated using qualitative classes of Spetich et al. (1999); and Woldendorp et al. (2004), the CWD included in this study were between intermediate (intact heartwood, bark sloughed) and advanced stages of decay (loss of structural integrity). Previous definitions of CWD have used lower threshold volumes of 0.009 m^3 (Woldendorp et al. 2004; Yan et al. 2006), but our minimum of 0.063 m^3 was appropriate for the reference forest CWD (primarily fallen trunks) and the rehabilitated forest CWD, which was less varied. Plots were separated by a minimum of 10 m and no two plots were established on the same length of CWD. For consistency, we only used CWD that ran downslope.

To measure the effect of CWD, we established two subplots within each plot: spaced 1 m and 3 m from the centre of the CWD mass (and no closer to any other CWD mass) (Figure 1B). Subplots were established along 2 m lines parallel to the CWD mass, established along the slope. In total, 32 subplots (8 replicate blocks × 2 forest sites × 2 CWD treatments) were established, spanning over 2 ha.

2.3 | Vegetation, Litter and Soil Characterisations

We measured the basal area of stems, canopy cover and the volume of CWD at the plot level, and we measured soil temperature, soil moisture, litter ground cover and litter C:N within each sub-plot. All measurements were undertaken from November 2022 to March 2023 in spring, summer, and autumn.

We estimated the basal area of woody stems per hectare around each plot using a dendrometer with a factor of 1 in the rehabilitated forest and a factor of 4 in the reference forest (Kramer 1982). We ignored the minimum diameter at breast height (DBH) standards of 10 cm in the rehabilitated forest in favour of a minimum of 5 cm, due to the high proportion and density of small diameter trees. Basal area was calculated as the number of included stems multiplied by the basal factor. Additionally, we measured the DBH of included stems and noted the species.

Canopy cover was estimated using a vertical photo taken at 0.5 m height above the centre of each subplot using a Google Pixel 4a (24 mm wide lens; Google, Mountain View, CA, USA). Photos were processed using ImageJ (Schneider, Rasband and Eliceiri, 2012) into binary black-and-white images, where black pixels were closed canopy and white pixels were sky. Through visual inspection, image artefacts from sun glare or mistaken grouping were removed. Average canopy cover for each plot was estimated using the proportion of black pixels across subplots.

Litter cover was estimated with two parallel point-transects along each subplot. We made point observations of the ground surface every 5 cm along a 2 m transect, generating 80 observations per subplot. Leaf litter was collected from three 0.25 m × 0.25 m quadrats next to each subplot and oven dried at 60°C for 72 h. Leaf litter was then analysed for total C and N content through combustion using a CHN Skalar Primacs SNC 100 combustion analyser (Skalar, Breda, Netherlands).

We estimated CWD volume from measures of diameter and length taken in the field, and approximated using the volume of a cylinder ($\pi r^2 h$).

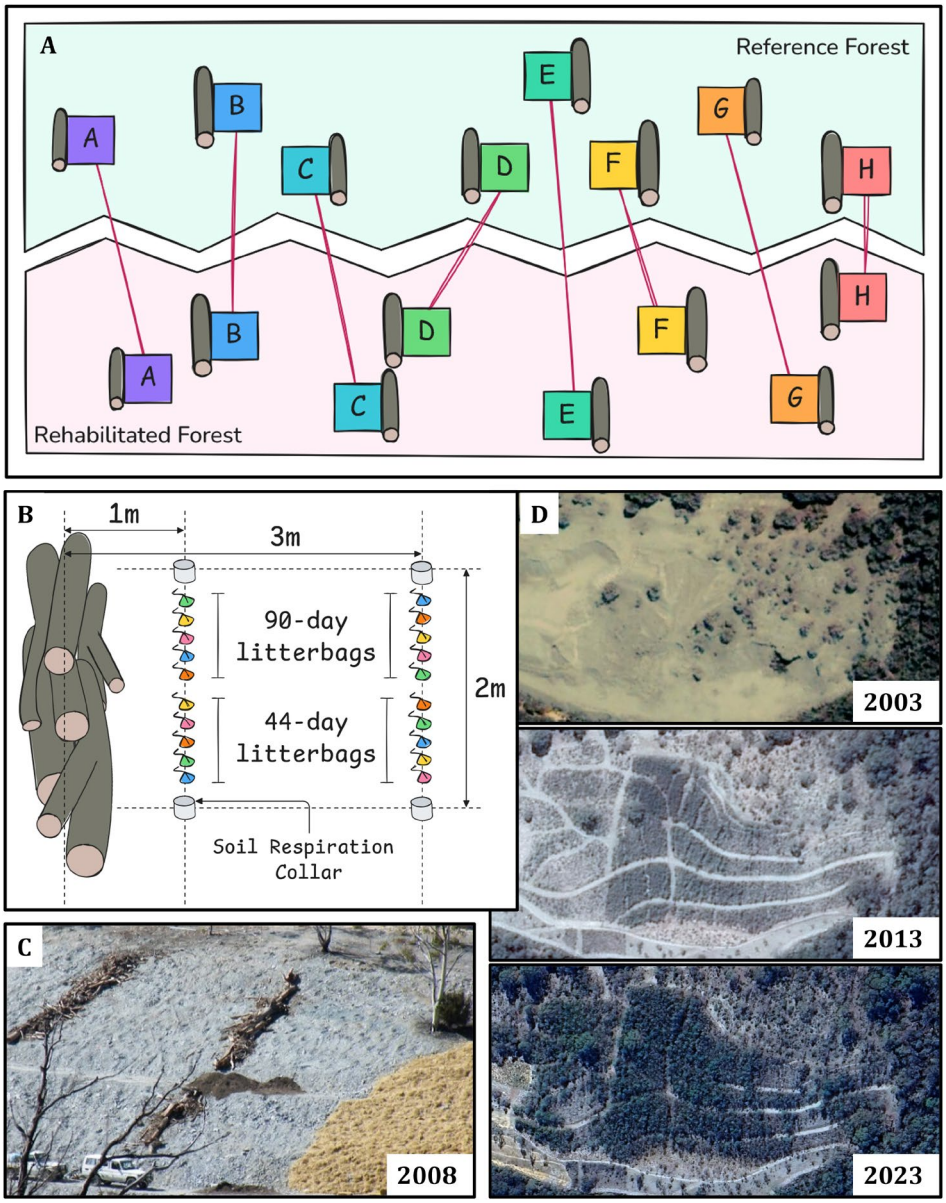

FIGURE 1 | Experimental design and rehabilitation site images. Schematic of the experimental blocks, with paired plots within blocks indicated by letters (A). An individual plot setup, indicating the location of subplot 1 m and 3 m from the centre of the CWD, the litter bags (in 90 and 44-day groups) and two soil respiration collars (B). Rehabilitation in progress in 2008, with linear piles of CWD and hay (photo: G. Wilks) (C). Aerial photographs of the Snowy Adit site, from 2003 prior to rehabilitation (top), in 2012 post-rehabilitation with linear CWD windrows evident, and in 2018 (all images Google Earth 7.3, 2023) (D).

2.4 | Respiration Experiment

Soil CO_2 efflux was measured using a LI-6400 with a soil chamber attachment (LI-COR Biosciences, Lincoln, NE, USA). PVC collars (11 cm diameter, length = 5 cm) were installed in December 2022 within a 20 cm radius of both ends of each subplot, without disturbing the decomposition experiment (Figure 1B). We measured soil efflux rates within each collar on three separate occasions (February 2–3, March 2–3, April 18 of 2023; $n = 576$). The target CO_2 concentration was set at 410 ppm, with a measurement frame (delta) of 15. Soil moisture was measured with a time-domain reflectometer (TDR) moisture probe (Spectrum Technologies, Aurora, IL, USA), at three points within a 10 cm radius of each soil collar and then averaged. Soil temperature was measured with the LI-6400 soil temperature probe inserted vertically 10 cm from the soil collar. Soil efflux was measured between 10 am and 4 pm to minimise diurnal effects, and blocks were measured sequentially.

2.5 | Decomposition Experiment

For the decomposition experiment, we adapted methods from Keuskamp et al. (2013) using commercially available green tea (Product code: 070177 26186 3; Twinings) and rooibos tea (Product code: 6009636 040002; Just Rooibos). Additionally, we gathered fresh leaves from *E. dalrympleana*, *E. viminalis* and *A. dealbata* trees within the rehabilitated forest. Leaves were oven-dried for 48 h at 60°C, then ground until they passed through a 2 mm sieve but did not pass through a 0.5 mm sieve, creating

a particle size similar to the commercial teabags. Preliminary analyses of both *Eucalyptus* spp. indicated that they had similar total C and N content (Appendix S1). Because of this, leaves from *E. dalrympleana* and *E. viminalis* were bulked prior to drying and grinding. The leaf material from each species was then weighed to 2.0 g, transferred into empty nylon mesh teabags, and sealed to create five different litters: Green, Rooibos, *Eucalyptus* (combined *E. viminalis* and *E. dalrympleana*), *Acacia* (*A. dealbata*) and Mixed (*Eucalyptus* and *Acacia* leaves in a 1:1 ratio). Grinding, drying and use of nylon mesh teabags provided a standardised approach; however, we expect that the actual rates of litter decomposition may differ from those observed in fresh litter. The nylon mesh bags excluded mesofauna, macrofauna and root access, potentially reducing decomposition (Bradford et al. 2002); the dried litter may have lower decomposition rates than fresh litter (Taylor 1998), while grinding does increase surface area and may increase decomposition rates (Rinkes et al. 2014). Decreased access to litter for mesofauna, macrofauna and roots is a known limitation of litterbag experiments and can underestimate true decomposition rates, as macrofauna mechanically fragment litter and can play a large role in total decomposition (Frouz 2018; Njoroge et al. 2023). Combined mass of bag and litter was recorded. TC and TN were determined for three random samples of each litter type using a CHN Skalar Primacs SNC 100 combustion analyser.

In December 2022, we buried teabags 4–6 cm below the soil surface (Keuskamp et al. 2013) along a 2 m transect parallel to the CWD within each subplot, ensuring teabags were spaced 15 cm apart. Two of each teabag were buried in each 2 m transect (adjacent and 3 m from CWD), one to be retrieved after 44 days and the other after 90 days, and randomly ordered to account for the effects of slope and adjacency of teabags. In total, we buried 320 teabags across the 32 subplots (10 bags per subplot across 8 replicates of 2 forest zones, and 2 CWD treatments). We lost 30 teabags due to animal disturbance over the course of the experiment ($n = 290$), primarily in the reference forest. After the incubation period, we retrieved the teabags and removed soil particles and root growth, then oven-dried the teabags at 60°C for 48 h prior to weighing. We used an additional 40 teabags to estimate mass loss due to handling, and the averaged loss (0.038 g) was excluded from the loss of each buried teabag.

2.6 | Statistical Analyses

All analyses were performed in R statistical software (v4.2.1, R Core Team, 2022), using the tidyverse, ggpubr, lmerTest, ggResidpanel, and emmeans packages (Kuznetsova et al. 2017; Wickham et al. 2019; Kassambara 2023; Lenth 2023).

To test for stand differences between forests, we used generalised linear mixed models. For soil moisture, temperature, ground litter cover, and subplot ground litter C:N, we analysed the interaction between forest and CWD treatment. Basal area, canopy cover, and volume of CWD were analysed with a one-way effect of forest type. All models included block as random intercepts.

The effects of CWD and forest on soil CO_2 efflux were modelled using a gamma-distributed generalised linear mixed model, due to positive-skewed data distribution and funnelling of Pearson's residuals (heteroscedasticity) when using a standard linear mixed model with a normal distribution. Three outliers were identified in a Q-Q plot of the preliminary gamma model fit; one measurement was less than 0.02 μmol CO_2 $m^{-2} s^{-1}$, and two measurements exceeded 100 μmol CO_2 $m^{-2} s^{-1}$. These outliers were likely due to machine errors and were excluded from further models. The initial model included the interaction of forest type and CWD, with soil moisture and soil temperature as additional covariates. Plot and block were included as nested random intercepts, and day as a crossed random intercept. We compared this model with alternative models that (i) included additional interactions between forest type and either moisture or temperature, and (ii) models in which temperature and moisture were excluded, and selected the model with the lowest Akaike Information Criterion (AIC; Akaike 1974; Appendix S3). The final model included interactions between forest type and CWD, and between forest type and moisture. Temperature was not included in the final model as there was no evidence of a main effect of soil temperature or an interaction with forest type.

To test our predictions about the effects of forest type and CWD on litter mass loss, we used a single linear mixed effects model which included a four-way interaction between forest type (reference or restored), CWD treatment (presence or absence), litter type (green, rooibos, *Eucalyptus*, *Acacia*, mixed) and burial period (as a two-level factor: 44 and 90 days) as fixed effects in the model, with plot as a random intercept. Interaction terms with $p > 0.1$ were excluded, and the final model included all main effects and the interaction between CWD and forest type. The effect estimates, standard error, and significance were gained via the summary function in base R, applied to the model.

3 | Results

3.1 | Comparison of Reference and Rehabilitated Forest Structure

The reference forest had a greater stem basal area, a denser canopy, lower soil temperature, and higher soil moisture than the rehabilitated forest (Figure 2, Table 1). Mean stem basal area in the reference forest was approximately three times greater than the rehabilitated forest (reference forest = 38.2 m^2; rehabilitated forest = 12.9 m^2; $p < 0.001$). Canopy cover in the reference forest was also significantly more closed, with the predicted means differing by 14.5% (Table 1). Soil temperatures ranged from 13°C to 19°C and were on average 2.2°C warmer in the rehabilitated forest than the reference forest ($p < 0.001$). Soil moisture in the rehabilitated forest was on average less than half that of the reference forest (ref. mean = 10.7%, rehab. mean = 4.0% volumetric moisture content; $p < 0.001$).

Leaf litter cover was lower in the rehabilitated forest, but only slightly (62% in the reference forest and 59% in the rehabilitated forests; $p < 0.05$) and did not differ among CWD treatments (Figure 3c). The C:N ratio of leaf litter did not differ between forest plots when CWD was absent (Figure 3d). However, there was a 5.21% decrease in the C:N ratio in reference forest plots with CWD, and a 4.68% increase in the C:N ratio in rehabilitated forest plots with CWD (Table 1; both

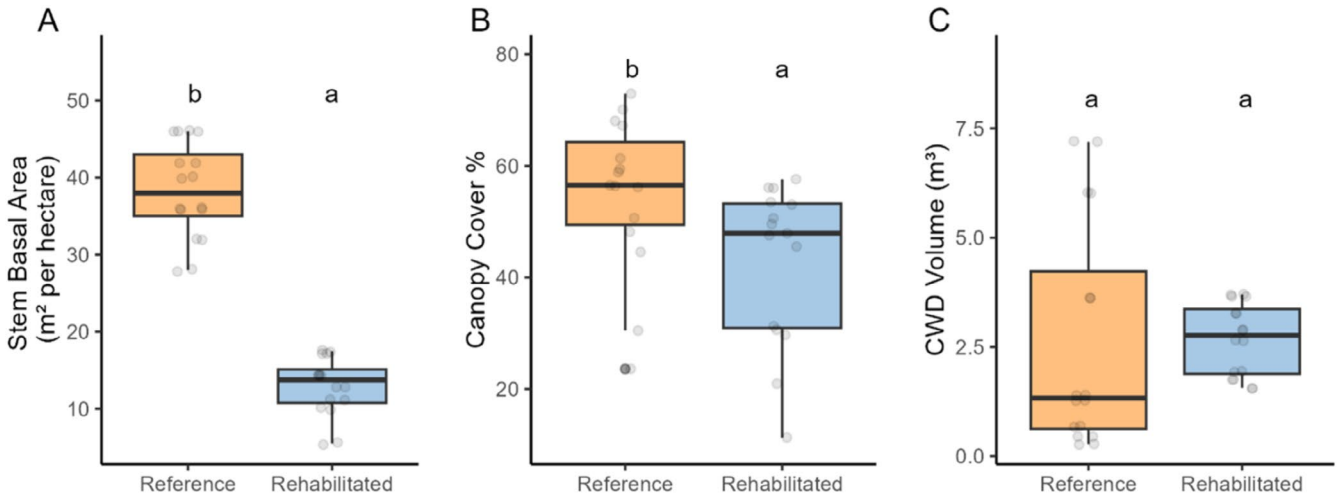

FIGURE 2 | Boxplots of stem basal area (A), canopy cover (B), and CWD volume (C) within reference and rehabilitated forest. All boxplots have raw data overlaid (jittered points). Groups that are not significantly different share a letter.

TABLE 1 | Summary of models testing effects of forest and CWD treatments for stand measures.

Measurement	Fixed Effect	Intercept	Forest (rehab)	CWD (+)	Forest (rehab): CWD (+)
Stem Basal Area ($m^2\ h^{-1}$)	Estimate (se)	38.25 (1.51)	−25.38 (0.25)***	—	—
Canopy (%)	Estimate (se)	55.79 (4.60)***	−14.57 (0.64)***	—	—
CWD Volume (m^3)	Estimate (se)	2.62 (0.41)***	0.06 (0.13)	—	—
Soil Temperature (°C)	Estimate (se)	14.16 (0.44)***	2.53 (0.26)***	−0.20 (0.25)	−0.64 (0.36)
Soil Moisture (%VMC[a])	Estimate (se)	10.30 (1.54)***	−6.71 (0.62)***	0.82 (0.62)	−0.096 (0.88)
Litter Cover (%)	Estimate (se)	0.62 (0.03)***	−0.034 (0.014)*	−0.0031 (0.014)	−0.023 (0.020)
Litter C:N	Estimate (se)	57.86 (2.09)***	1.20 (0.84)	−3.02 (0.84)***	5.78 (1.19)***

Note: Different stand measurements are reported with the effects of forest and, if applicable, effects of CWD and their interactions. Intercept refers to a measurement taken from a plot in the reference forest with no CWD.
*< 0.05 significance is denoted with asterisks.
**< 0.01 significance is denoted with asterisks.
***< 0.001 significance is denoted with asterisks.
[a]%VWC = % volumetric water content.

$p < 0.05$). C:N measurements were highly variable across all treatments, with high standard deviations in the CWD plots (reference forest Std. dev = 7.36; rehabilitated forest Std. dev = 10.14).

3.2 | Rates of CO_2 Efflux From Soils

We selected the model which included interactions between forest type and CWD treatment, as well as interactions between moisture and CWD treatment. Rates of efflux were significantly higher in the reference forest than in the rehabilitated forest regardless of CWD presence; however, the magnitude of difference between forests was more pronounced in the absence of CWD (Figure 4a). Efflux values ranged from 0.323 to 18.902 μmol CO_2 $m^{-2}s^{-1}$ and the mean efflux within the reference forest was approximately double that within the rehabilitated forest when CWD was absent (mean difference = 2.74 μmol CO_2 $m^{-2}s^{-1}$). CWD had a positive effect on efflux in rehabilitated forests and differences between forests declined to an average of 1.15 μmol CO_2 $m^{-2}s^{-1}$ when CWD was present. Soil moisture did not have a significant main effect on efflux but was associated with a positive effect within the rehabilitated forest (Table 2).

In the final model, the fixed effects of forest type, CWD treatment, and moisture explained 43% of the variance in soil CO_2 efflux, and an additional 15% was explained by the random effects of plot, block and date.

3.3 | Litter Mass Loss

Mass loss due to decomposition was greater in the reference forest subplots, although only in the absence of CWD (Table 3; Figure 4b). On average, mass loss was similar in reference and rehabilitated forest when CWD was present (mass loss = 0.310 and 0.300 g/g for reference and rehabilitated respectively; $p = 0.8072$). Leaf mass loss after 90 days burial differed among species; greatest loss was observed in green tea and eucalyptus litter (green tea predicted mean loss = 0.431 g/g, *Eucalyptus* predicted mean loss = 0.362 g/g), and least in rooibos tea (predicted mean loss = 0.172 g/g). Both *Acacia* and Mixed teabags

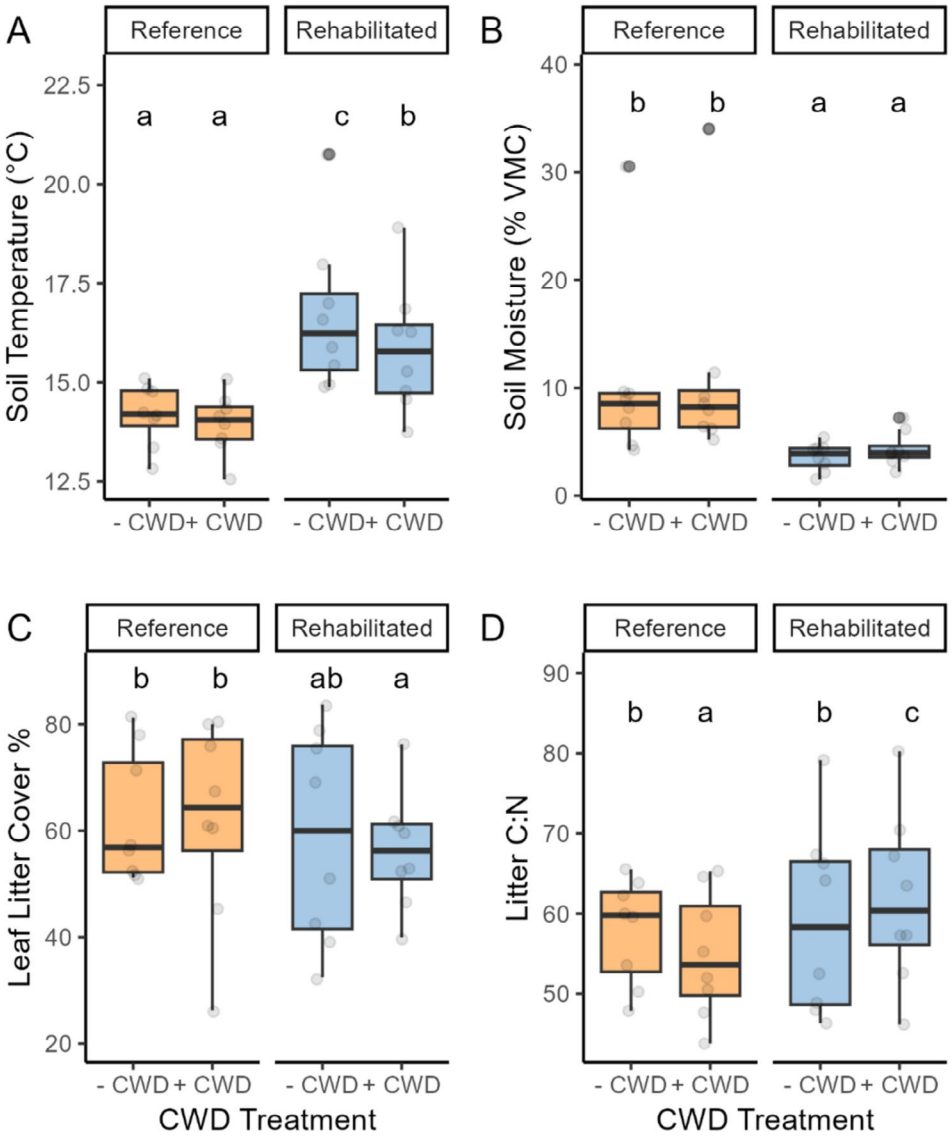

FIGURE 3 | Boxplots of soil temperature (A), soil moisture (B), leaf litter cover (C), and litter C:N (D) in subplots with and without CWD in rehabilitated and reference forest. All boxplots have raw data overlaid (jittered points). Groups that are not significantly different share a letter.

lost similar proportions, with predicted mean losses of 0.238 and 0.294 respectively (Figure 5). Across all teabags, on average 79.3% of the total mass loss occurred in the first 44 days (Figure 4).

Mass loss was not correlated with either C:N ratio or total N content of the litter (Figure 5). C:N for green tea and rooibos litter was both similar to published values (Keuskamp et al. 2013; Appendix S1). Mass loss after 90 days was highest in low C:N green tea. Even though the *Acacia* leaves had a C:N ratio similar to green tea, and *Eucalyptus* had a C:N ratio similar to rooibos (38.8) their mass loss was not consistent with expectations (Figure 5). The mixed tea had an intermediate C:N ratio but had mass loss more similar to that of the *Acacia* litter.

4 | Discussion

We investigated the interactions between forest disturbance history, coarse woody debris and leaf C:N and their impacts on biological activity in soil and litter within a rehabilitated rock spoil and adjacent undisturbed montane forest in Kosciuszko National Park, Australia. We predicted that litter decomposition and soil CO_2 efflux would be higher adjacent to CWD, and we observed this in the rehabilitated forest. This is consistent with evidence that CWD serves as an important long-term C and moisture store, and habitat for decomposers and soil biotic communities. In the reference forest, soil biological activity was higher, but there was no positive effect of CWD. These results highlight the potential benefits of CWD addition for recovery of soil biological processes during forest ecosystem rehabilitation, but also suggest that benefits may wane as the stand matures.

We also predicted that the effects of CWD on litter decomposition would be greatest among local litter with low leaf C:N. However, while the rooibos and green tea standards decomposed according to expectations, trends among local leaf litters were the inverse, with the high C:N ratio *Eucalyptus* leaves losing more mass than the low C:N ratio *Acacia* leaves. Our project was focused on a single restoration site in a broadleaf evergreen

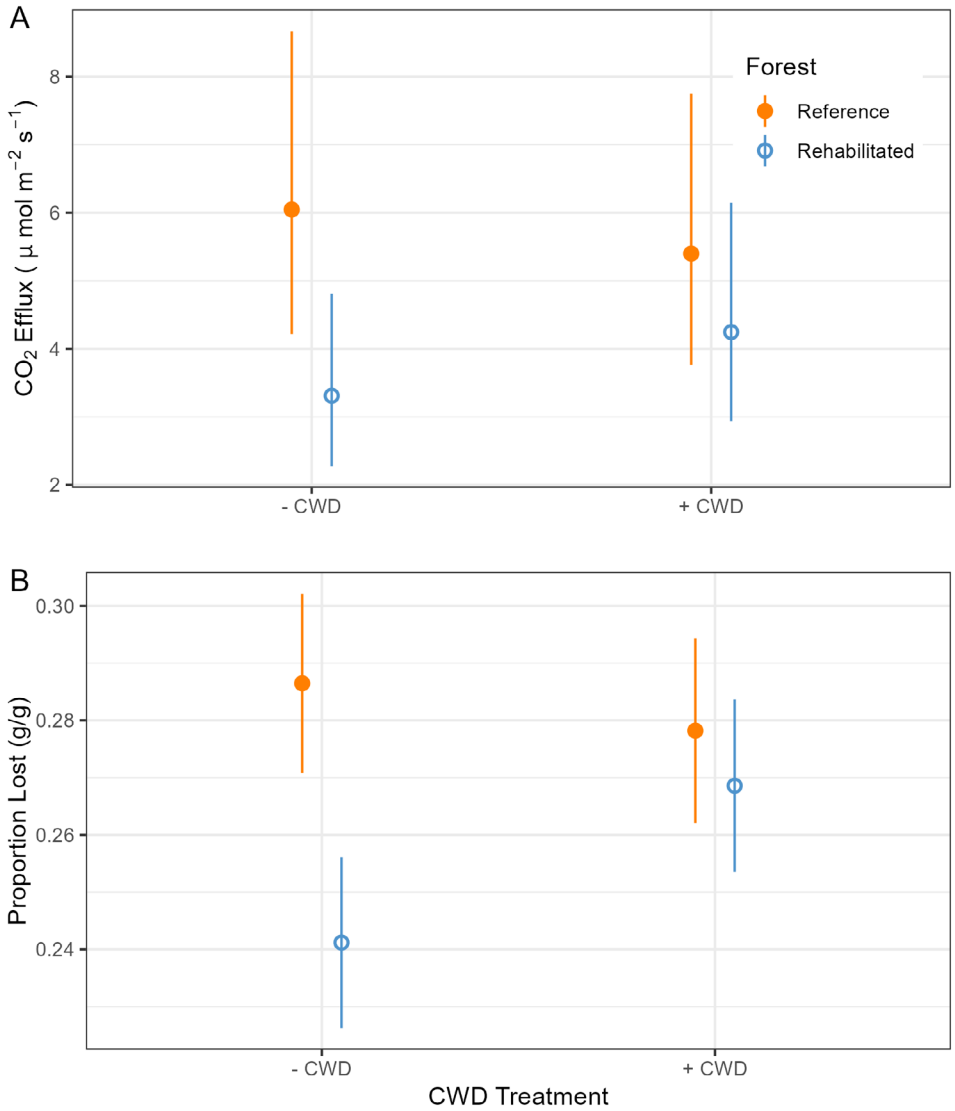

FIGURE 4 | Predicted mean CO_2 efflux (A) and mean mass loss of litter by decomposition (B) in rehabilitation (open blue points) and reference forests (orange solid points) with and without CWD. Lines are 95% confidence intervals.

sclerophyll forest in the Australian Alps; thus, our findings may be specific to this site. However, as we argue below, the findings may be generally applicable to understanding the role of CWD in soil function and warrant further examination across other similar restoration efforts. Below we explore the interplay between CWD, efflux, and drivers of decomposition rates in more detail.

4.1 | CWD Increases CO_2 Efflux and Decomposition Within the Rehabilitated Forest

The positive effects of CWD in the rehabilitated forest support findings that CWD improves the productivity of nearby soils (Gonzalez-Polo et al. 2013; Kwak et al. 2015). Despite prior evidence of the positive effects of CWD in mature temperate forests (e.g., Gonzalez-Polo et al. 2013), there was no evidence of increased rates of CO_2 efflux or decomposition around CWD in the reference forest. This finding suggests that soil decomposer communities in the reference forest may not be dependent on islands of CWD as a nutrient source; within the reference forest, soil biological activity was generally high, regardless of proximity to CWD, suggesting substrate is not limiting (Harmon et al. 1986; Stutz and Lang 2017).

This pattern of results could be specific to our site; however, later successional ecosystems tend to have higher soil respiration rates than early successional ecosystems, due to the contribution of higher quantities of larger roots and robust soil biotic communities, though the specific contribution of each can be highly dependent on additional factors like soil temperature and moisture (Huang et al. 2016; Luo et al. 2012; Wang et al. 2014). Mature montane eucalypt forests are associated with high rates of litter fall that outweigh losses due to decomposition, and in the absence of fire can accumulate deep continuous litter layers (Raison et al. 1986). Other important sources of C for microbes are root turnover and root exudation. The belowground input of C through these pathways is likely to be higher in mature forests compared to young forests due to large differences in biomass. Soil microbial activity is therefore likely to be higher in the reference forest due to an abundance of accumulated organic substrates, including labile

TABLE 2 | Summary table of coefficients for the fixed effects on CO_2 efflux from generalised linear mixed model with a gamma error distribution.

Fixed effects	Estimate	(Std. error)
Intercept	1.81	(0.19)***
Forest (Rehabilitated)	−1.16	(0.19)***
CWD (+ CWD)	−0.11	(0.042)**
Moisture	−0.0019	(0.0067)
Forest (Rehab): CWD (+)	0.36	(0.060)***
Forest (Rehab): Moisture	0.076	(0.014)***
	Conditional $R^2 = 0.580$	
	Marginal $R^2 = 0.430$	
Random effects	**Variance**	**Std. dev**
Plot: Block	0.027	0.16
Block	0.0047	0.069
Date	0.016	0.13
Residual	0.13	0.36

Note: Intercept refers to a measurement taken in the reference forest without CWD.
*< 0.05 significance is denoted with asterisks.
**< 0.01 significance is denoted with asterisks.
***< 0.001 significance is denoted with asterisks.

TABLE 3 | Table of coefficients for the fixed effects on litter mass loss due to decomposition from linear mixed model.

Fixed effects	Estimate	(Std. error)
Intercept	0.38	(0.010)***
Forest (Rehabilitated)	−0.045	(0.011)***
CWD (+ CWD)	−0.0076	(0.0089)
Litter (*Acacia*)	−0.18	(0.0095)***
Litter (Mixed)	−0.13	(0.0094)***
Litter (*Eucalyptus*)	−0.076	(0.0094)***
Litter (Rooibos)	−0.26	(0.0092)***
Burial (90 days)	0.062	(0.0060)***
Forest (Rehab): CWD (+)	0.036	(0.012)**
	Conditional $R^2 = 0.78$	
	Marginal $R^2 = 0.77$	
Random effects	**Variance**	**Std. dev**
Plot	0.000165	0.0128
Residual	0.00261	0.0511

Note: Intercept refers to a Green teabag buried for 44 days in the reference forest distal to CWD. Higher level interactions with p-values > 0.05 were removed. The model explained 77.2% of the proportion of variance in litter mass loss, 75.7% explained by the fixed effects and approximately 2% by the random effects.
*< 0.05 significance is denoted with asterisks.
**< 0.01 significance is denoted with asterisks.
***< 0.001 significance is denoted with asterisks.

leaf and root material as well as root exudates (Gaudinski et al. 2000). The importance of C derived from CWD is likely minimised in mature forests due to an abundance of substrate. Additionally, high levels of CO_2 efflux in the reference forest relative to the rehabilitated forest in the absence of CWD may be due to autotrophic respiration, which we expect would be higher in the mature forest given the greater tree basal area, canopy cover and soil development (de Godoy et al. 2021).

Both moisture availability and temperature are important determinants of the rates of litter decomposition and soil respiration (Krishna and Mohan 2017; Wang et al. 2013). However, only moisture was an important explanatory factor in explaining variation in our soil respiration measurements, and then only within the rehabilitated forest. Soil moisture was lower within the rehabilitated forest's soils, as has been found in other rehabilitated rock spoils (Ngugi et al. 2015). Our findings suggests that moisture wasn't limiting soil biological activity within the reference forest but low moisture retention may have constrained respiration rates within the rehabilitated forest. We did not observe any differences in soil moisture or temperature in response to CWD treatments although CWD can be a valuable store for moisture (Klamerus-Iwan et al. 2020). These effects might be more apparent in drier years but this project was undertaken in a La Niña year, where rainfall was 157% of the 1996–2024 average (daily rainfall sourced from Cabramurra weather station ID 072161, Bureau of Meteorology 2024).

While the C:N ratio of the ground leaf litter was similar across forests when CWD was absent (Figure 3), when CWD was present, the C:N ratio of litter was greater in the rehabilitated forest and lower in the reference forest relative to when CWD was absent. This may suggest a higher rate of N mobilisation within the rehabilitated forest's soils in proximity to CWD, but not in the reference forest. These patterns mirror the results seen in the decomposition experiment and broadly support the prediction that decomposer communities are mobilising more nutrients in the microbial hotspot surrounding CWD (Kuzyakov and Blagodatskaya 2015; Stutz and Lang 2017). However, the ecological impact of CWD in mature forests may be much subtler and less important as a C store, habitat, or moisture store in ecosystems with well-developed organic soils and in wetter years.

4.2 | C:N Ratio of Leaves Does Not Predict Mass Loss From Decomposition

Although decomposition rates in the standard litter (green and rooibos teas) conformed to expectations (Keuskamp et al. 2013), mass loss of the native litter was not negatively correlated with increasing C:N. This was surprising, both given the wider literature on leaf stoichiometry and associations between leaf C:N and decomposition (Santiago 2007; Freschet et al. 2011; Rosenfield et al. 2020), and also because of the wider literature that describes the decomposition of similar *Acacia* and *Eucalyptus*

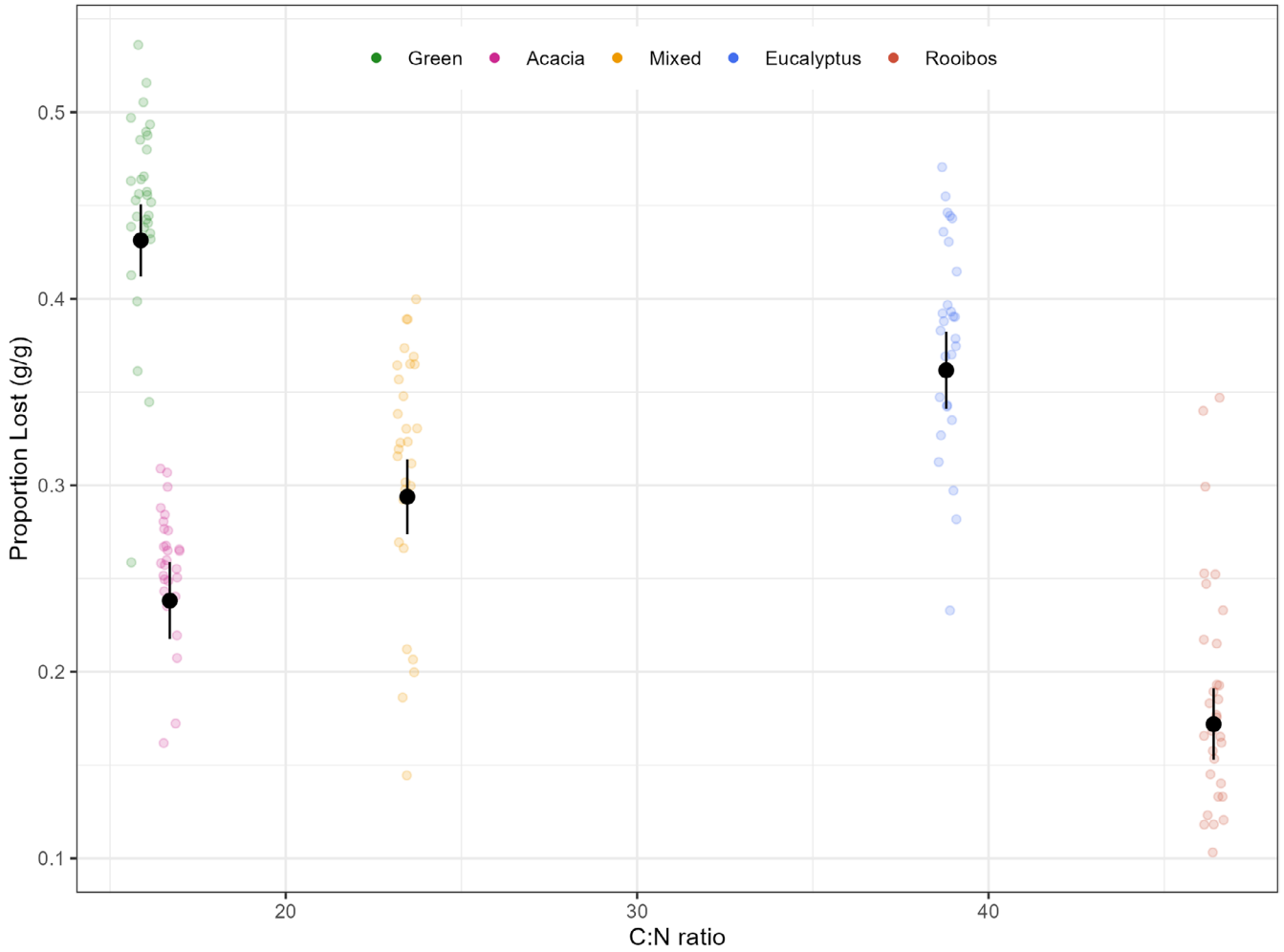

FIGURE 5 | Predicted mean mass loss of litter by decomposition after 90 days and C:N ratio of the litter. The mean proportion of mass loss due to decomposition is indicated by points, with 95% CIs indicated by vertical lines. Transparent coloured points show the proportion loss of each litter bag.

species (Pilar Castro-Díez et al. 2012; Bini et al. 2013; Buettel et al. 2019). Instead, we saw the inverse trend, with *Eucalyptus* litterbags losing greater mass and *Acacia* teabags losing less mass. Additionally, the mixed teabags had similar mass loss to the Acacia teabags, which suggests that *Acacia* leaves were able to inhibit the decomposition of *Eucalyptus*. Others have found that mixed *Acacia* and *Eucalyptus* leaf litters increased nutrient cycling and therefore soil biotic activity, compared to monocultures (Forrester et al. 2006). The reason we did not see a similar pattern in the *Eucalyptus*, *Acacia* and Mixed litters may be due to variation in unmeasured litter traits such as lignin content, Lignin:N ratio (Mukamparirwa et al. 2024), or the presence of anti-microbial extracts in *Acacia* litter (Borges et al. 2020; Krishna and Mohan 2017).

4.3 | Connections to Restoration Practice

This research is the first to provide quantitative evidence of the value of CWD in improving soil functioning within a disturbed montane forest ecosystem and supports the wider view of CWD as a 'hotspot' for stimulating biological activity within a recovering ecosystem. The lack of CWD effect seen in the reference forest may, however, lead to further questions about the partitioning of hetero- and autotrophic respiration around CWD and whether this result is generalisable to other restoration projects. Some latter successional forests have been found to have greater soil respiration, often attributed to greater root biomass, soil microbial biomass and increased humidity (Yan et al. 2009). Whether CWD helps contribute to increased heterotrophic respiration may be obscured by the effect of autotrophic respiration in our study's mature reference forest.

In a restoration context, planting species with litter resistant to decomposition may contribute high proportions of organic matter into soil humus, which speeds the build-up of organic soil horizons and provides better habitat to soil biotic communities (Descheemaeker et al. 2009; Macphee and Wilks 2013). Evidence from other rehabilitated mine spoils suggests that plantings aid in soil recovery and the build-up of humus, compared to natural succession (Abakumov et al. 2013). Our study would suggest that the inclusion of *A. dealbata* in montane rehabilitation plantings may contribute to the accumulation of soil organic matter, although further research is necessary to determine if our findings are consistent in other Australian montane forests.

Additionally, using CWD as a large buffer of recalcitrant organic material can provide long-term support for a recovering

ecosystem, at least at a fine scale. The results suggest several interesting directions for further investigation. For example, the cost/benefit equations around adding CWD require further quantification, as does the assessment of how far from CWD benefits are measurable. At present, the broader potential for managing CWD in other recovering ecosystems (e.g., systems that have more established soils) remains less clear, and whether the benefits to the decomposer system are realised in those contexts may depend heavily on climatic variation (Kwak et al. 2015; Ngugi et al. 2015; Parkhurst et al. 2022; Petraglia et al. 2018). Future studies in other Australian montane forests as well as other ecosystems will improve our understanding of the role of CWD in restoration management and assess whether our findings are generalisable. Here we have shown the role of CWD in nutrient cycling in a rehabilitated forest, providing evidence for the application of CWD in soil-building processes in reforestation projects. Our findings indicate that recalcitrant leaf litters from species like *Acacia dealbata* can increase the accumulation of the organic soil layer, which is needed to recover degraded soils.

Author Contributions

Jack C. J. Vernon: conceptualization, data curation, formal analysis, investigation, methodology, supervision, visualization, writing – original draft, writing – review and editing. **Adrienne B. Nicotra:** conceptualization, formal analysis, funding acquisition, methodology, project administration, resources, supervision, validation, writing – review and editing. **Josh Dorrough:** conceptualization, formal analysis, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, writing – review and editing. **Zachary A. Brown:** conceptualization, methodology, resources, supervision, validation, writing – review and editing.

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Data Availability Statement

The data that support the findings of this study are available at DOI:10.6084/m9.figshare.29277890.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.