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META-ANALYSIS

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Global synthesis reveals strong multifaceted effects of eucalypts on soils

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Abstract

Aim: Eucalypts have a widespread global distribution owing to their popularity for agroforestry and as environmental plantings. Despite an abundance of site-specific evidence that eucalypts modify soils and soil processes, we lack a quantitative synthesis of their overall effects at the global scale. This limits our capacity to assess the likely impacts of future introductions in any given region of the world.

Location: Global.

Time period: 1986–2021.

Major taxa studied: *Eucalyptus*, *Angophora* and *Corymbia*.

Methods: We used a systematic search to derive a database of empirical data from 227 studies across 33 countries ($n_{\text{effect size}} = 2{,}806$) and tested three predictions about the effects of eucalypts on soil properties and whether these effects varied with plantation age and soil depth.

Results: Compared with (non-eucalypt) native vegetation, eucalypts significantly reduced soil moisture, microbial abundance, nitrogen, cations and anions. Relative reductions in soil microbes and ions were stronger in older eucalypt plantations. A comparison of eucalypts with (non-eucalypt) silvicultural and agropastoral systems revealed similar effects on most soil properties, although eucalypts tended to reduce potassium and enhance carbon to a greater extent than other managed systems. We found no consistent effects of eucalypts on soil pH.

Main conclusions: Our study provides the first extensive global meta-analysis of the effects of eucalypts on soil properties and processes and demonstrates that effects are highly dependent on the community with which they are compared (i.e., natural or managed). In general, our findings reinforce the widely held belief that eucalypts deplete soil nutrients and dominate water resources. Understanding how eucalypts affect soils allows us to assess their global suitability for agroforestry, soil rehabilitation and soil carbon enhancement, while considering the potential environmental costs.

KEYWORDS
acidity, carbon, eucalypt, meta-analysis, nitrogen, nutrients, soil function

1 | INTRODUCTION

Increasing globalization is associated with the spread of many plants and animals beyond their natural ranges (Hobbs, 2000). This trend has occurred naturally or by accident (e.g., zebra mussels; Ricciardi, 2003) or intentionally, whereby a species is actively encouraged in order to meet an agricultural, economic or social objective (e.g., cane toads; Easteal, 1981). The impacts of introduced species on local socio-ecological systems are highly context and organism dependent and range from potentially beneficial (Walther et al., 2009) to environmentally or economically detrimental (Bradshaw et al., 2021). Eucalypts, which include *Eucalyptus*, *Angophora* and *Corymbia* spp., have been hugely successful at establishing beyond their natural range (Stanturf et al., 2013). They occur naturally in Australia and the drier areas of Papua New Guinea and were originally introduced to Europe as ornamental plants before their rapid expansion around the globe, largely attributable to their value as timber, pulp, firewood, charcoal and other products (Stanturf et al., 2013; Turnbull, 1999; Williams & Brooker, 1997). Eucalypt plantations now cover *c*. 19 million hectares across the Americas, Africa, Europe, the Middle East and Asia (Iglesias-Trabado & Wilstermann, 2008; Stanturf et al., 2013; Turnbull, 1999), representing *c*. 6.5% of planted forests globally (FAO, 2020).

Eucalypts are highly prized in the silvicultural industry owing to their pest resistance, rapid growth and timber production under a wide range of soil and climatic conditions (Eldridge et al., 1993; Zaiton et al., 2020). They are also valued for their ability to control erosion, reduce waterlogging and rehabilitate saline and sodic soils (Jagger & Pender, 2003; Mishra et al., 2003; Teketay, 2000; Zohar et al., 2008), and have also been promoted widely for their economic benefits to rural smallholders (Jagger & Pender, 2003; Jaleta et al., 2016). Yet, despite these positive benefits, there is increasing anecdotal and empirical evidence that, beyond their native range, eucalypts have substantial negative effects on soils and ecological processes. These negative effects range from soil nutrient (Zhang et al., 2015) and groundwater (Christina et al., 2017) depletion to soil surface hydrophobicity (Burch et al., 1989) and acidification (Jobbágy & Jackson, 2003; Rhoades & Binkley, 1996) and allelopathic effects on native vegetation (Chu et al., 2014; del Moral & Muller, 1970; Zhang & Fu, 2009). The extent to which eucalypts affect soils and soil function, however, is not well understood across their entire range, largely because these effects are strongly context dependent and therefore likely to vary markedly with soil and climatic conditions, tree or plantation age and, potentially, species identity. For example, in pasture systems that were afforested with eucalypts, Turner and Lambert (2000) found a consistent decrease in soil carbon (C) in Australia, whereas Lima et al. (2006) reported the opposite pattern in Brazil. The lack of a global consensus on the effects of eucalypts on soils makes it difficult to characterize their global suitability for agroforestry or rehabilitating degraded soils or their potential to provide solutions to hydrological problems associated with soil salinity and waterlogging. Understanding these soil effects is particularly important when considering the potential for eucalypts outside their native range to increase the likelihood of environmental and ecological damage or reductions in soil functions.

Here, we examine the impacts of eucalypts on soil processes and properties using a synthetic database derived from 227 studies published world-wide between 1986 and 2021. Our study focused on four main hypotheses. First, we expected that eucalypts would reduce soil N, P, K, moisture, pH, cations and microbial activity relative to both native vegetation and agrosilvicultural systems. Many tree taxa resorb N, P and K from the leaves back into the tree before leaf abscission, resulting in little return to the soil via leaf litter decomposition, yet eucalypts have a particularly high retranslocation efficiency, resorbing on average 56% of N and 98% of P (Killingbeck, 1996; Saur et al., 2000). For this reason, we predicted soil beneath eucalypts to be relatively low in N, P and K, although certain management practices, such as fertilization, have the potential to offset this effect (Gonçalves et al., 2004). Likewise, soil moisture would be expected to be lower beneath eucalypts because of their high requirement for water (Madalcho et al., 2019), proliferation of hydrophobic plant residues (Burch et al., 1989) and great ability to extract groundwater through deep root systems, often lowering water table depths by several metres (Christina et al., 2017). There are numerous reports of eucalypts acidifying the soil (Leite et al., 2010; Rhoades & Binkley, 1996; Soumare et al., 2016), through a combination of mechanisms including cation redistribution, root respiration and litter leachates (Jobbágy & Jackson, 2003), and this acidification is likely to drive a reduction in microbial activity (Curtin et al., 1998; Iovieno et al., 2010). Furthermore, the retention of cations in living eucalypt biomass is likely to deplete cations in the soil, although some might be returned to the topsoil via decomposition of leaf litter (Jobbágy & Jackson, 2003).

Our second hypothesis was that soils under eucalypts would be, on average, more C rich than other agrosilvicultural systems owing to higher rates of litter production (Demessie et al., 2012; Paul et al., 2002; Sangha et al., 2006), yet C poor relative to native vegetation with leaf litter that tends to be decomposed more readily (Bernhard-Reversat & Schwartz, 1997; Castro-Díez et al., 2012).

Third, we predicted that certain effects would vary with the maturity of the eucalypt plantation. Older eucalypts have greater canopy coverage and produce more litter than younger eucalypts, resulting in stronger effects on soil C and rainsplash erosion (Chen et al., 2013; Sun et al., 2018; Zou & Bashkin, 1998). The growth rate of eucalypts is also much greater for younger trees, leading to intensified nutrient depletion and water extraction (Forrester et al., 2010).

Fourth, we expected that soil effects relating to C and nutrients (N, P, K, other cations and anions) and their recycling (microbes and enzymes) would be highest in the uppermost soil profile, where litter enters the soil and microbial activity is typically highest (Blume et al., 2002; Fang et al., 2005).

Despite the fact that eucalypts have an extensive global distribution and are highly prized commercially, there has been no quantitative global synthesis of their effects on specific soil properties. Some effects of eucalypts on broad ecosystem services (e.g., soil formation) were examined in a synthesis by Castro-Díez et al. (2021), yet this study spanned several tree genera and, consequently, had limited data on eucalypt soil effects ($n_{\text{effect size}} = 141$). Here, we apply the latest rigorous meta-analytical techniques (Nakagawa et al., 2017; Noble et al., 2017) to an extensive global dataset focused solely on eucalypts *sensu lato* ($n_{\text{effect size}} = 2{,}806$) and their soil effects. The large extent of our data enables us to produce a more powerful, nuanced and globally meaningful synthesis of the effects of eucalypts on individual soil properties, such as soil carbon and phosphorus. Our meta-analysis also offers two new extensions to the current understanding of eucalypt effects; that is, the importance of plantation age and soil depth as drivers of variation in these effects, and comparisons not only with other silvicultural systems, but also with agropastoral systems and native vegetation. These advances in knowledge will provide important information to guide policy-makers and practitioners in pursuit of improved environmental outcomes in areas where eucalypt plantings continue outside their native range.

2 | METHODS

2.1 | Literature search

We searched two electronic databases (Web of Science and Scopus) on 25 August 2021 for published studies, using the following search terms: ((eucalypt*) NEAR/5 (soil* OR microbe* OR plant* OR animal* OR invertebrate*)). Search terms were sought in the title, abstract and keywords, and all studies up to the search date were included. The "NEAR/5" term and its Scopus equivalent ("PRE/5") were used to limit the number of studies to a feasible amount, while maintaining reproducibility. Note that additional search terms and unrestricted distance between terms could have captured additional relevant studies; therefore, our search strategy could be considered systematic but not entirely comprehensive. Although a systematic and reproducible approach is essential for minimizing bias, true comprehensiveness is not necessary in meta-analysis and can be very difficult to achieve in large fields (Nakagawa et al., 2017).

Our search yielded 5,731 results from Web of Science and 3,948 results from Scopus. One study conducted by the authors that was not identified in this search was also added. A total of 3,933 duplicates between search-engine results were removed, resulting in 5,747 total records for screening. This list was refined manually, based on titles and abstracts, to remove items that focused on unrelated fields (e.g., genetics, modelling, remote sensing, plant physiology), resulting in 1,449 studies remaining for full-text screening. With a large number of studies remaining, we decided to narrow our focus solely to soil characteristics, thereby excluding the animal, plant and macrofungus studies that we initially sought in the keyword search. We also chose to focus on eucalypt plantations and exclude native eucalypt forests, which differ markedly in their land-management history. After full-text screening (including removal of animal, plant and macrofungus studies), 227 studies remained for data extraction (a list of the data sources is provided in the Supporting Information Appendix S1). A PRISMA checklist and diagram are included in the Supporting Information and detail the screening process and adherence to best practice reporting guidelines (Table S1; Figure S1; Page et al., 2021). It is worth noting that additional search terms (e.g., "edaphic", "bacteria") have the potential to capture additional relevant studies; therefore, our review is unlikely to be wholly comprehensive.

2.2 | Data extraction

Assessing the effects of eucalypts requires a comparison with a eucalypt-free community. One option is to adopt a repeated measures approach to compare soil properties before and after eucalypt afforestation (e.g., Epron et al., 2009). An alternative is to compare eucalypts with nearby eucalypt-free communities that experience similar climatic conditions and are likely to share a similar soil-forming history (e.g., Guedes et al., 2016). Our initial searches revealed that the latter approach, requiring no long-term commitment, was far more common and would therefore yield a larger dataset with which to test our predictions. Accordingly, we decided to use non-eucalypt communities (e.g., pine plantations, native vegetation, pastures, croplands) as the "control" in our analyses.

For each reported soil property (Table 1), we extracted the mean value, sample size and a measure of the variance (SD, SE or confidence interval), where provided, for the eucalypt community and control community. Given that some studies took replicate measurements within sites and among sites, we chose to consider within-site replicates as pseudoreplicates and extracted variance and sample size only when they were reported at the site level. Owing to differences in what was considered a "site", we followed the definition of the authors of each study. Generally, sites were defined as separate, non-contiguous communities, but in some cases, multiple sites were contained within the same community, although separated by several kilometres. If studies reported only within-site replicates, we recorded no variance and a conservative sample size of one. When a study reported repeated measures over time, we extracted only the most recent value to maintain the independence of effect sizes. Values not reported in the text were extracted from figures using ImageJ software, v.1.53e (Abràmoff et al., 2004). Where no measure of variance (at the site level) was reported in the text, we used imputation to estimate these values (see Section 2.3 below) after compilation of the final dataset.

We also retrieved the following additional information for each soil property record: control context (i.e., silviculture, native vegetation or agropastoral), age of eucalypt plantation, soil depth, and the identities of the eucalypt and control species where known. Owing to the wide variation in soil profiles globally, we extracted soil depth as a binary variable (upper or lower) according to the discretion of the original authors. In the vast majority of studies, the upper soil profile corresponded to the top 10 cm, while the lower soil profile generally corresponded to anywhere from 10 to 50 cm. When soil properties from more than two different soil depths were reported, we extracted only the uppermost and lowermost values to minimize the risk of non-independence.

TABLE 1 Original soil properties within each broad group (with number of effect sizes in parentheses; all abbreviations are standard chemical elements)

Soil property group	Original soil properties
Anions	Carbonate (4); chloride (4); S (14); sulphate (4)
Cations	Al (49); B (8); bases (9); base saturation (26); Ca (117); cation exchange capacity (83); cations (9); Co (1); Cu (11); Fe (19); Hg (1); Mg (114); Mn (13); Na (42); Na absorption ratio (4); Ni (1); Pb (1); V (1); Zn (12)
Conductivity	Electrical conductivity (64); salinity (4)
Soil C	C fractions (20); C stock (53); C (113); organic C (227); organic matter (67)
Soil density	Bulk density (211); compaction (4); hardness (14); porosity[a] (61)
Soil enzymes	Aminopeptidase (2); cellobiosidase (7); chitinase (2); dehydrogenase (3); glucosidase (14); *N*-acetylglutamate (1); peroxidase (4); phenoloxidase (4); phosphatase (14)
Soil erosion	Sediment production (2); erosion (14); stability[a] (15)
Soil K	K (152)
Soil microbes	Bacterial abundance (1); microbial activity (6); microbial biomass (110); microbial composition (13); microbial respiration (24); microbial richness (15); soil respiration (7)
Soil N	Ammonium (16); N (242); N fixation (4); N loss[a] (2); N mineralization (12); N stock (34); nitrate (17); nitrification (10); organic N (6)
Soil P	P (184); P leaching[a] (24)
Soil pH	pH (269)
Soil temperature	Temperature (27)
Soil moisture	Evaporation[a] (5); infiltration (9); moisture (112); repellency[a] (4); runoff[a] (9); water-holding capacity (25)

[a]Attribute was coined (multiplied by minus one).

The wide range of reported soil properties were grouped into 14 main properties: C, N, P, K, anions, cations, conductivity, density, enzymes, erosion, microbes, temperature and moisture (Table 1).

2.3 | Data analysis

We used the natural log response ratio (lnRR) as the effect size in our meta-analysis (Hedges et al., 1999), calculated as $\ln RR = \log(\bar{x}_{eucalypt}/\bar{x}_{control})$ where $\bar{x}$ is the mean value of a soil property beneath eucalypts or the control community. The sampling error variance in lnRR, the inverse of which was used to weight effect sizes in our meta-analytical models, was calculated according to the formulas presented by Hedges et al. (1999). The lnRR was chosen because it is simple to interpret and largely unaffected by non-independent samples (Noble et al., 2017). The lnRR is positive when the magnitude of a soil property is greater beneath eucalypts relative to the control community, and vice versa. Values of zero in the means of specific soil properties occurred in 0.1% of cases and were managed using single imputation (Lajeunesse, 2013; Nakagawa, 2015). To do this, we set zeroes in means recorded in eucalypt plantations to the value that would produce the lowest lnRR value in the dataset, and vice versa for means recorded in control communities. The lnRRs of some original properties were coined (multiplied by minus one; Table 1), meaning that all properties within a group were expected to respond in the same direction. For example, within the soil density group, soil porosity was multiplied by minus one to match bulk density, such that greater values corresponded to reduced porosity. We used imputation to derive values of standard deviation that were not reported for 43% of eucalypt means and 48% of control means. Standard deviations are used in the weighting of effect sizes, which, if associated with high variance, are downweighted in the meta-analytical models. The type of imputation we chose uses the relationship between the $\log_{10}$-transformed means and $\log_{10}$-transformed standard deviations to back-calculate suitable values (Lajeunesse, 2013). In our case, the relationship used in imputation was strong (R^2 = .81), implying that imputation is likely to be reliable for this dataset despite large amounts of missing data (but see section 2.4. *Publication bias and sensitivity analyses*).

A large proportion of the included studies (55%) compared the same eucalypt plantations with multiple plant communities. To manage this non-independence in treatment means, we divided the analyses into three separate comparisons: eucalypt versus silvicultural plantations (e.g., *Pinus*), eucalypt versus native vegetation and eucalypt versus agropastoral systems (e.g., cropland, managed pasture). By separating many of the shared eucalypt (treatment) means among the three analyses, we were able to use 929 (33%) additional effect sizes than if we had included all comparisons in the same model. To manage shared control means (e.g., native forests compared with two sets of eucalypt plantations), we constructed variance–covariance matrices for each comparison, in which the diagonals represented the sampling error variance in lnRR and the off-diagonal cells represented the covariance resulting from shared controls (Noble et al., 2017). In other words, off-diagonal cells were set to zero unless there was a shared control, in which case the covariances were calculated according to the method of Lajeunesse (2011).

We used study identity and eucalypt species as random factors in the intercept models and meta-regressions. Within this model structure, study identity accounted for the variance explained by study-specific phenomena, such as methodology or multiple measurements of soil properties. Three moderators were used in meta-regression: soil property (categorical, 14 levels), eucalypt plantation age (continuous, $\log_{10}$-transformed before analysis) and soil depth (categorical, two levels). Age and soil depth were structured as an interaction with soil property in separate meta-regression models because each was associated with a different and reduced subset of effect sizes. If soil property, age and soil depth were included in the same model (i.e., as a three-way interaction), the number of effect sizes would be reduced by 69% (n = 1,937 fewer effect sizes) and the interpretation of results would become highly complex. All estimated coefficients are presented as true values rather than relative to a reference group. The native vegetation comparison contained the highest number of effect sizes (n_{total} = 1,239, n_{age} = 718 and n_{soil} = 690; Supporting Information Table S2), followed by the silvicultural comparison (n_{total} = 913, n_{age} = 451 and n_{soil} = 365; Supporting Information Table S2) and agropastoral comparison (n_{total} = 654, n_{age} = 429 and n_{soil} = 445; Supporting Information Table S2). Thus, the total number of effect sizes used in our analyses was $n_{effect\ size}$ = 2,806. All models were conducted using the *rma.mv* function in the *metafor* R package v.3.0-2 (Viechtbauer, 2010), and we calculated a marginal R^2 for each meta-regression that represented the variance explained by moderators (Nakagawa & Schielzeth, 2013). The overall meta-analytical mean, derived from the intercept model, is virtually meaningless in ecological meta-analyses, where different groups, such as soil properties, often have opposing effects and where heterogeneity (I^2; Higgins & Thompson, 2002) is typically high (O'Dea et al., 2021). We therefore use the intercept model only to evaluate the heterogeneity among effect sizes, which, when high, can reduce statistical power and therefore make estimates more conservative (Valentine et al., 2010). We considered an effect significant when the 95% confidence interval did not cross zero.

2.4 | Publication bias and sensitivity analyses

Publication bias was assessed using a modified version of Egger regression (Sterne & Egger, 2006), trim-and-fill tests (Duval & Tweedie, 2000) and a visual assessment of the funnel plot of precision (inverse standard error) of lnRRs against the meta-analytical residuals (*sensu* Nakagawa & Santos, 2012), which were extracted using the *MCMCglmm* R package v.2.32 (Hadfield, 2010; Hadfield & Nakagawa, 2010). We performed three types of sensitivity analysis to test the robustness of estimated effects. First, we removed the five studies contributing the highest number of effect sizes in each data subset. Second, we removed extreme values of lnRR and sampling error variance. Third, we ran unweighted meta-regressions, which are unbiased but less precise than weighted models (Morrissey, 2016; Nakagawa & Lagisz, 2016), using the *lmer* function in the *lme4* package v.1.1-27.1 (Bates et al., 2015). Effects were considered robust if they remained quantitatively similar to the original analysis, allowing for qualitative differences in significance owing to loss of statistical power.

3 | RESULTS

The 227 studies in our database were located across five continents, in both tropical and sub-tropical ecosystems (Figure 1), with more than half of the studies conducted in Brazil (74 studies), China (38 studies) and India (16 studies). A total of 13 studies, comprising 105

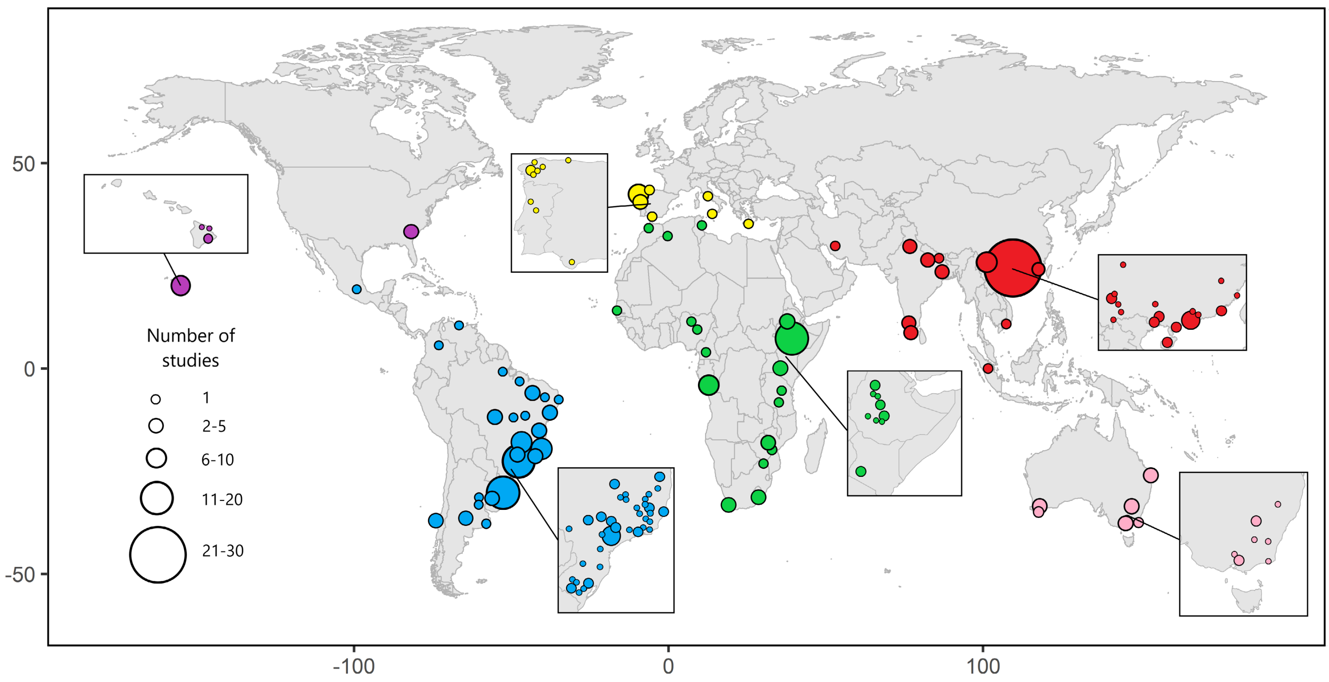

FIGURE 1 Global map (latitude and longitude) showing locations of included studies, coloured by continent

effect sizes, were conducted on eucalypt plantations within their native range. The earliest published study was in 1986, but most were published after 2000, with a consistent increase in the number of publications to the present day (Supporting Information Figure S2a). The median age of the eucalypt plantations in our analyses was 11 years. The most represented species were *Eucalyptus grandis*, *Eucalyptus globulus*, *Eucalyptus urophylla*, *Eucalyptus camaldulensis*, *Eucalyptus saligna* and *Eucalyptus tereticornis*, six of the "big nine" cultivated eucalypt species (Stanturf et al., 2013), but 22% of studies did not identify eucalypts to species level (Supporting Information Figure S2b).

3.1 | Main effects on soil properties

About 3–6% of the variation in eucalypt effects was explained by soil property (shown by R^2 values in Supporting Information Table S3), with significant effects for soil moisture, microbes, anions, cations, conductivity, C, N and K (Figure 2; Supporting Information Table S4). Most of these effects represented declines when eucalypts were compared with plantations, native vegetation or agropastoral systems, although soil C increased in one comparison. Furthermore, eucalypt species identity explained very little of the variance in soil effects (<6% of the variance in all but one meta-regression model; Supporting Information Table S3), and we found high heterogeneity in our intercept models (I^2_{total}>.98; Supporting Information Table S5).

Eucalypt effects, however, varied markedly depending on the community with which they were compared (i.e., silvicultural, native vegetation or agropastoral). Soil moisture and soil microbes were significantly lower (by an average of 23% and 47%, respectively) under eucalypts relative to native vegetation, but there were no significant differences when eucalypts were compared with managed systems (Figure 2; Supporting Information Table S4). Likewise,

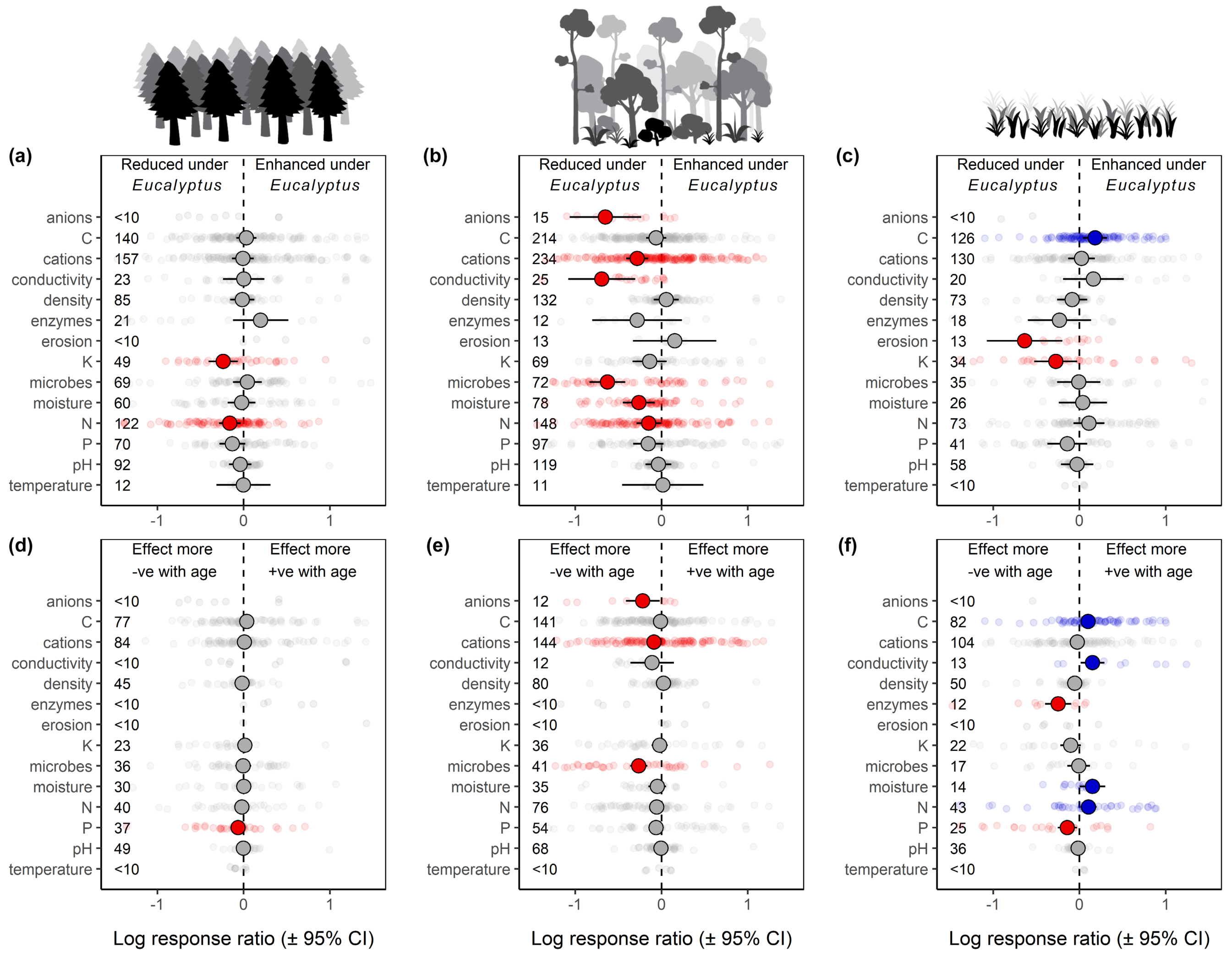

FIGURE 2 (a, b, c) Main effects of eucalypts on soil properties and (d, e, f) interaction slopes with eucalypt plantation age (−ve = negative, +ve = positive) when compared with (a, d) silvicultural systems, (b, e) native vegetation and (c, f) agropastoral systems; confidence intervals are represented by a black bar extending from each estimated mean. Significant results are highlighted in colour. Sample sizes are indicated by numbers along the vertical axis (results based on <10 effect sizes are excluded from the figure owing to unreliability). Raw effect sizes (within the −1.5 to +1.5 range) are shown as background points eucalypts significantly reduced soil N relative to both silvicultural systems and native vegetation. Soils beneath eucalypts had significantly lower amounts of K, but only when compared with managed systems (i.e., not native vegetation). The only positive effect of eucalypts (soil C) was significant only when eucalypts were compared with agropastoral systems.

3.2 | Effects vary with plantation age

Several effects varied with the age of eucalypt plantations. For example, the reductions in soil cations and microbes beneath eucalypts (relative to native vegetation) intensified over time (Figures 2 and 3; Supporting Information Table S4). In contrast, positive effects of eucalypts on soil C, relative to agropastoral systems, increased with plantation age (Figure 2; Supporting Information Figure S3).

3.3 | Effects vary in strength among soil depths

Finally, our meta-regression models also indicated that some effects were significant only at a particular soil depth (upper or lower; Figure 4). For example, when compared with agropastoral systems, eucalypts enhanced soil cations and carbon, but only in the upper soil profile. In contrast, negative effects of eucalypts on soil P and K, relative to agropastoral systems, were significant only in the subsoil (Figure 4).

3.4 | Publication bias and sensitivity analysis

We found some evidence of publication bias in the silvicultural (Egger: $z = -3.13$, $p = .002$; trim-and-fill: four missing studies detected) and agropastoral (Egger: $z = -3.16$, $p = .002$; trim-and-fill: two missing studies detected) data subsets, though these results were driven by a few extreme outlying values (Supporting Information Figure S4). Meta-regression results were quantitatively similar to those obtained from sensitivity analyses (Supporting Information Figures S5–S9), although some changed in significance as power was lost.

4 | DISCUSSION

Our global meta-analysis revealed that eucalypts have mostly negative effects on soil properties and associated processes in comparison to other plantation forests, native vegetation and agropastoral systems. However, the effects of eucalypts were highly dependent on the community with which they were compared. Reductions in soil microbes, moisture and cations in eucalypt soils were evident only when compared with native vegetation, but not managed

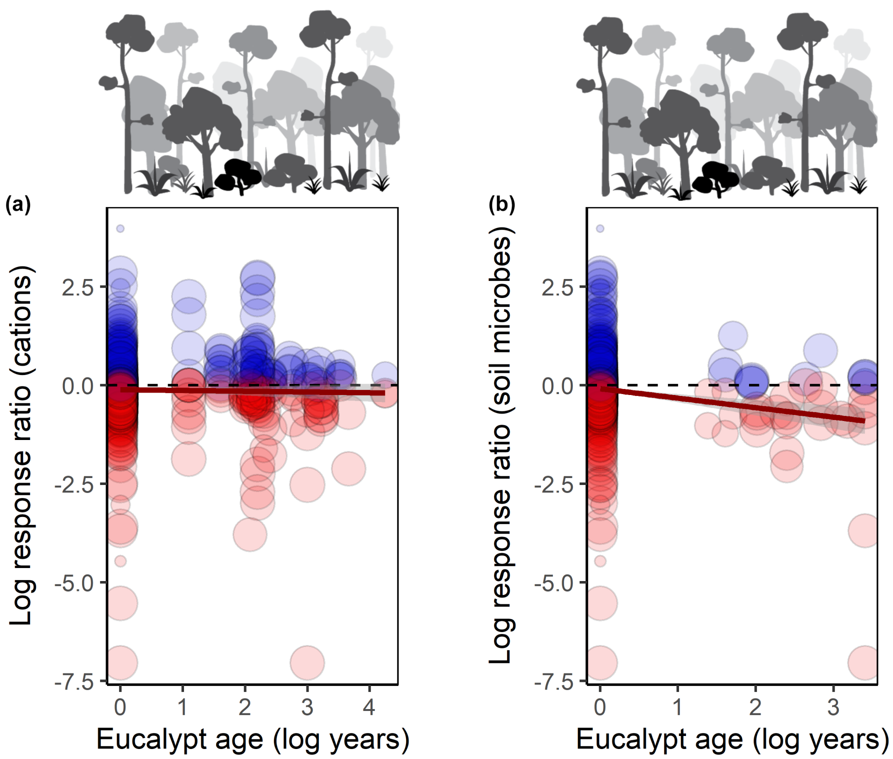

FIGURE 3 Bubble plot showing the model-predicted relationship between eucalypt plantation age (natural logarithm of years) and the natural logarithmic response ratio (lnRR) of (a) soil cation effects and (b) soil microbe effects, in comparison to native vegetation (colours indicate negative or positive effect sizes; point size is proportional to relative weight in the model; and the line represents the modelled relationship ±95% confidence interval in grey)

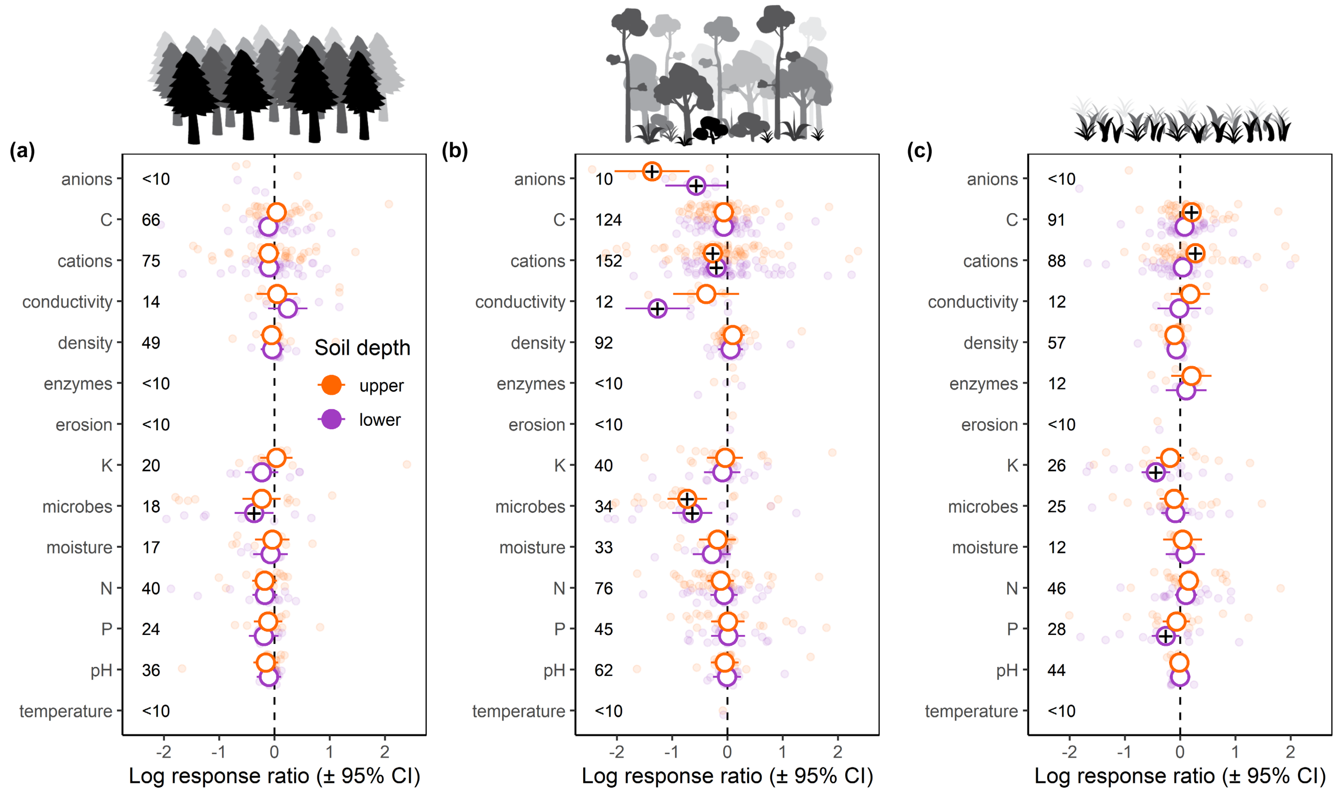

FIGURE 4 Effects of eucalypts on soil properties, partitioned among soil depths, relative to (a) silvicultural systems, (b) native vegetation and (c) agropastoral systems. Results significantly different from zero are indicated by a black plus sign. No properties were significantly different among soil depths. Background points represent raw effect sizes, and numbers along the vertical axis indicate sample sizes

vegetation (silvicultural and agropastoral systems). Conversely, the effect of eucalypts in reducing soil K was significant only relative to managed vegetation. Soil C was enhanced only relative to agropastoral systems, and this effect was stronger in older eucalypt plantations. Despite these effects, eucalypt species identity did not explain a substantial amount of variance in soil effects, indicating that these effects are, at most, weakly controlled by differences in species traits, such as root chemistry and leaf morphology (Senior et al., 2016; Zaiton et al., 2020). Although soil P was generally but not significantly reduced by eucalypts, these effects strengthened significantly with increasing eucalypt plantation age, as did the negative effects of eucalypts on cations and microbes. There was also some evidence that the effects of eucalypts on soil C were strongest in the topsoil. Overall, our findings provide robust empirical evidence that eucalypts in plantation settings exert a strong influence on a range of soil properties and functions globally.

We found strong evidence that eucalypts modify soil hydrology relative to native vegetation. It is well known that eucalypts exploit both ground water and moisture from the upper vadose zone (Engel et al., 2005; Madalcho et al., 2019), even under low water potentials (Thorburn & Walker, 1994). Despite the tendency of eucalypts to scavenge moisture from the uppermost soil layers and to intercept rainfall (Livesley et al., 2014), they also have the potential to enhance soil moisture by conducting water from deeper to surface layers (hydraulic lift; Brooksbank et al., 2011), increasing infiltration (Eldridge & Freudenberger, 2005), conducting rainfall via stem flow, and reducing evaporation through shading and wind buffering (Bosi et al., 2020). The net effects of eucalypts on soil moisture therefore depend on the balance of water-enhancing and water-reducing processes. Eucalypt stands had significantly lower soil moisture than native vegetation, suggesting that water-reducing processes (primarily water uptake) are stronger and/or water-enhancing processes (e.g., macropore creation, canopy shading) are weaker in eucalypt systems. The finding that eucalypt plantations did not differ significantly in their soil moisture compared with non-eucalypt silvicultural plantations is likely to reflect similarities in water use (Benyon & Doody, 2015; White et al., 2021) or land management, because harvesting machinery can lead to soil compaction and reduced infiltration (Greacen & Sands, 1980).

The soil nutrient results generally align with the broader narrative of nutrient depletion beneath eucalypts (Jagger & Pender, 2003; Madalcho et al., 2019; Zaiton et al., 2020). The great ability of eucalypts to retranslocate and conserve N, P and K during leaf senescence is likely to be driving the observed reductions in soil N and K (Killingbeck, 1996; Saur et al., 2000). Equally plausible is that the particular chemical composition of eucalypt litter, characterized by high concentrations of polyphenols and lignified compounds (del Moral & Muller, 1970), acts to inhibit nitrification and thus reduce soil nitrate (Castro-Díez et al., 2012). The latter explanation is supported by our finding that eucalypts reduce microbial activity relative to native vegetation, although this finding could also be explained by low-quality eucalypt litter (Bini et al., 2013), differences in canopy structure resulting in lower soil temperature and moisture (Kara et al., 2008; Wang et al., 2020), and other effects on soil moisture, such as high water uptake (White et al., 2021). We also found that eucalypt plantations had higher soil C relative to agropastoral systems, and this effect was strongest in more mature plantations. Soil C is known to decline initially with eucalypt plantings (Cook et al., 2016) and then to increase gradually with age, although residual litter from a previous land use can persist for several years and obscure this pattern (Epron et al., 2009; Paul et al., 2002). Eucalypts typically produce more litter than pastures (Paul et al., 2002; Sangha et al., 2006), particularly in more mature stands, resulting in higher C returned to the soil.

We found that eucalypts did not have a consistent effect on soil pH, contrary to our hypothesis and much empirical evidence (e.g., Leite et al., 2010; Rhoades & Binkley, 1996; Soumare et al., 2016). Soil acidity can arise from several sources, yet the evidence from the study by Jobbágy and Jackson (2003) suggests a dominant effect of cation redistribution, whereby base cations are largely relocated from the main rooting zone to the surface, via absorption and subsequent litter fall, leading to higher acidity with increasing depth. However, we found no strong evidence that pH was reduced by eucalypts on average nor that cation effects were stratified by soil depth. There are several possible explanations for our results: (1) sources of acidity tend to be similar across agrosilvicultural systems and native vegetation; (2) variation in soil pH is controlled predominantly by other factors, such as climate (Hong et al., 2019); and/or (3) ecophysiological processes governing plant effects on pH are highly variable among ecosystems.

There are several important caveats to consider when interpreting the results of our study. First, as with most meta-analyses, our findings represent average effects that are underlaid by a large amount of variation (e.g., Figure 2). Consequently, our results do not preclude neutral or opposite effects in certain ecosystem conditions. Second, there was some evidence of publication bias in particular data subsets, which could inflate the significance of certain results. It is also worth noting that a surprisingly large number of studies did not measure replicate communities (e.g., eucalypt plantation, native Cerrado savanna, managed pasture), although mean values were produced from pseudoreplicates located within the same community. However, we still found clear and unambiguous effects of eucalypts on soil properties, despite the fact that our analyses encompassed a large number of studies, often poorly replicated, from markedly different environmental contexts, years, seasonal conditions and eucalypt species. Determining the extent to which climate, soil type and other environmental factors control variation in the effects of eucalypts on soil is a worthy topic of further investigation.

4.1 | Implications for land management

Our findings have immediate practical implications, allowing managers to predict the likely outcomes arising from land-use transitions. For example, when converting natural vegetation to a eucalypt plantation, there is likely to be a reduction in soil N, moisture, cations and microbial functioning, with the last two strengthening as plantation age increases. In the case of a eucalypt plantation replacing a different plantation (e.g., *Pinus*), few changes are likely to occur beyond reductions in soil N and K. When pastures or croplands are converted to eucalypt plantations, there is likely to be an increase in soil C, particularly as plantations become more mature, which aligns with the general model of afforestation (Paul et al., 2002). The implications of increasing soil C might have benefits for carbon abatement programmes. However, it is important to note that our analysis considered only soil effects, and positive effects of eucalypt afforestation on soil C are likely to trade off against negative effects on biodiversity and other ecosystem properties (Phifer et al., 2017; Saccol et al., 2017).

4.2 | Conclusions

Our study provides new evidence of the effects of eucalypts on soils at the global scale, relative to both natural and managed ecosystems. Overall, our synthesis suggests a multitude of negative outcomes for soils and microbial functioning when eucalypt soils are compared with soils from native (non-eucalypt) plant communities, implying that eucalypt plantations would be a poor substitute for native ecosystems and their ecological processes. Nevertheless, our synthesis indicates that eucalypts might have a role in increasing soil carbon in managed landscapes. Several past studies have recommended that degraded agricultural lands or wastelands be converted to eucalypt plantations (e.g., Jagger & Pender, 2003; Liang et al., 2016), thereby balancing socio-economic benefits (reviewed by Jaleta et al., 2016 and Madalcho et al., 2019) and environmental outcomes, which in this context would be largely positive. Our findings generally support this recommendation. Another recent study indicates that there might also be a role for eucalypts as an intermediate phase in the reforestation of agricultural land, providing rapid canopy cover, enhanced soil C and a source of revenue while intercropped native plants can regenerate (Brancalion et al., 2020). Altogether, our results provide a basis for reconciling such trade-offs across different ecosystems world-wide, allowing policy-makers and land managers to assess the net environmental and economic benefits of eucalypts and avoid potentially detrimental effects on ecological functioning.

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AUTHOR CONTRIBUTIONS

D.J.E. conceived the study. M.M.-C. led the design of the extraction protocol with support from D.J.E., J.A. and Z.A.X. All authors contributed equally to data extraction. Data curation was conducted by

G.M.C., M.M.-C., J.A. and Z.A.X. Data analysis was led by M.M.-C. with support from J.A. and Z.A.X. Data presentation was led by M.M.-C. and Z.A.X., with support from B.W. The first draft of the manuscript was led by M.M.-C. with support from D.J.E., J.A. and B.W., and all authors contributed to edits therein.

DATA AVAILABILITY STATEMENT

All data and code are available on the Open Science Framework at https://osf.io/2x53b/.

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BIOSKETCH

Our research team (the Eucanerds) assembled during a coronavirus disease 2019 lockdown, owing to a shared interest in broad-scale patterns of terrestrial ecosystem functioning and a desire to stay connected and collaborative in a rapidly digitalizing world.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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