MR. STUART JAMES MACDONALD (Orcid ID : 0000-0001-8979-9303)

Article type   : Research article

Martin Hermy

Coordinating Editor: Prof. Martin Hermy

Title: Stable states in soil chemistry persist in eucalypt woodland restorations

Running Head: Recalcitrance in woodland restoration   AVS-RA-02205 / 27th June 18

Authors: Stuart Macdonald (ORCID ID. 0000-0001-8979-9303/corresponding author)[1], Tanya

Bailey[1,2], Mark Hunt[1,2], Neil Davidson[3] and Greg Jordan[1]

[1]School of Natural Sciences, University of Tasmania, Hobart, Tasmania, Australia

[2] Australian Research Council, Centre for Forest Value, Hobart, Tasmania, Australia

[3] Greening Australia, Hobart, Tasmania, Australia

Correspondence

1. Stuart Macdonald, School of Natural Sciences, University of Tasmania, Hobart, Tasmania,

Australia

Email: stuart.macdonald@utas.edu.au

Abstract

Aim: To assess whether restoration of dry eucalypt dominated plant communities on ex-pasture

sites is constrained by soil characteristics.

Location: Central Tasmania, Australia.

Methods: We use nutrient status to test recovery trajectories of soils within eucalypt woodland

restorations established on ex-pasture sites. *Eucalyptus* trees within these sites have been successful

established but understorey plant communities have had negligible recovery. Soils from restoration

sites, aged from 3 to 22 years, were contrasted with those from two reference ecotypes: established

pastures and native eucalypt woodlands presumed to be similar to that originally replaced by the

pastures. We hypothesised that (1) total soil carbon to nitrogen ratios (C:N) would be substantially

higher in forest soils than in pasture soils; (2) soil nutrient levels would be lower in forest sites than

within pasture sites; and (3) if restoration soils were recovering they should fit between these

continuums according to age of planting.

Results: Woodland and pasture reference soils were highly constrained in soil C:N and conformed to expectations. However, ex-pasture restoration sites retained the characteristically low C:N and high nutrient levels of pasture soils, in particular total nitrogen. They also failed to demonstrate a transformational effect with age of planting.

Conclusions: This suggests that both restoration interventions and natural processes had not sufficiently disrupted existing below ground systems within the given time frame. Such an intractable stable state within the soil system highlights the need within restoration practice for an increased emphasis on soil ecological transformation. Improving and implementing practices aimed at driving soil change may assist a timelier reassembly of complex native ecosystems. This study also shows that soil C:N ratios may provide a cheap and simple means of identifying soil constraints on restoration.

Introduction

Experience worldwide has demonstrated that when aiming to restore native plant communities, historical legacies can create enduring limitations on restoration success so that sites often remain distinct from their target ecosystems (Cramer, Hobbs, & Standish, 2008; Matzek, Warren, & Fisher, 2016). Such legacies are prevalent in ecosystems previously cleared of natural vegetation and developed for agriculture (Flinn & Vellend, 2005). Significant ecological, chemical and physical changes that occur include loss of original soil biodiversity and function, increased fertility levels and soil structural changes (Brussaard, 1997; Marrs, 1993). The persistence of exotic plant communities with their unique suites of soil biota can reinforce the stability of these soil changes (Kulmatiski, Beard, & Stark, 2006). These environmental conditions can be major factors contributing to stable alternate states which present barriers to the re-establishment of native plants (Hamman & Hawkes, 2013; K.N. Suding, Gross, & Houseman, 2004).

Such barriers can be explained by adaptations of plants to their soil environment; many wild plants have evolved in infertile environments and have nutrient acquisition and use strategies that contrast markedly with agricultural and exotic species adapted to fertile soil conditions (Chapin, 1980). Accordingly, less productive woodland systems have soils characterised by high total carbon to nitrogen (C:N) ratios, low rates of litter turnover, low nitrification, fungi-dominated nutrient cycles, high abundance of arthropods, and highly conserved nutrient cycles (Chapman, Langley, Hart, & Koch, 2006; Wardle et al., 2004). Conversion to non-native pasture precipitates the evolution of a distinctly different soil system typified by low C:N, high-turnover high-quality litter, high nitrate availability, bacteria -based nutrient cycling, earthworms, and extravagant nutrient cycles (Chapman et al., 2006; Wardle et al., 2004).

Successful re-establishment of natural forest ecosystems on old-field pasture sites should therefore be paralleled by a positive shift in soil C:N, reduced soil nutrient availability and reversion from bacterial to fungal dominated food webs (Holtkamp et al., 2008; Kardol & Wardle, 2010). Such a re-

ordering necessarily involves the interruption of existing soil ecological networks and the building of new ones. Plants have often been considered as key drivers in soil change (Angers & Caron, 1998; Binkley, 1995), however plant soil interactions and recovery dynamics can be unpredictable (Eviner & Hawkes, 2008; Wallington, Hobbs, & Moore, 2005). In many instances, some plant species tend to be followers rather than facilitators of ecosystem change, therefore changes in soil community structure may actually precede plant community transformation and be a pre-requisite for the above ground change (Morriën et al., 2017; Wubs, van der Putten, Bosch, & Bezemer, 2016). This underlies a potential for recalcitrance in ecological restorations, where the re-establishment of above ground ecological communities is retarded by delays to belowground recovery.

We propose that soil nutrient analysis, in particular carbon and nitrogen stocks, may provide a useful means to track soil transformation, thus providing an indicator of restoration progress. The relative consistency of soil C:N within biomes and divergence between them is influenced by the elemental composition of plant litter, a dominant original source of soil C and N, and the microbial community which can be a dominant pathway through which carbon enters the soil organic matter pool (Cleveland & Liptzin, 2007; Godbold et al., 2006). We therefore investigated the progress of soil transformation in restoration plantings by studying changes in a range of nutrient characteristics. The study area was formerly native eucalypt woodland but throughout the 19th and 20th centuries much of this region was cleared and converted to cattle and sheep pastures dominated by exotic pasture species. Within our study system, post-agricultural restoration has resulted in moderately successful establishment of *Eucalyptus* tree species (Close, Davidson, Churchill, & Corkrey, 2010), but both active planting and natural recruitment have failed to establish a native forest understorey. To assess whether nutrient status is also recalcitrant we compared soil characteristics within three land management classes, unmanaged remnant native forest (forest), managed non-native pastures (pasture) and attempted forest restoration on old pasture sites (restoration). We hypothesized (1)

that forest soils would exhibit substantially higher C:N and lower nutrient levels than pasture soils, and, critically, that (2) restoration sites would be intermediate between pasture and forest and rank on this continuum according to age of planting restoration soils (i.e. C:N should be inversely related to time since establishment of the intervention). Support for hypothesis two would indicate that conditions were not recalcitrant. In contrast, failure of the restoration sites to show this transitional pattern would indicate that the pre-existing pasture-soil ecology is highly resilient, the established eucalypt plantings have failed to drive below ground change and that a stable state persists.

Methods

The survey area is within the Midlands of Tasmania, Australia, at 41.76 to 42.82°S and 147.61 to 146.77°E. Mean temperatures of the warmest month range from 15.5 to 18.7°C, mean temperatures of the coldest month are between 4.0 and 8.1°C, mean annual rainfall ranged between 452 and 639 mm (Bureau of Meteorology 2015) and elevation of the sites varied from 13 to 496m ASL.

Prior to European occupation of the region in the early 19th Century, vegetation throughout the region is believed to have consisted predominantly of eucalypt woodland types with small areas of treeless plains and wetlands (Fensham, 1989). This study employed 11 pasture sites, 12 forest sites and 11 restoration sites. Sites were selected so that each management class was represented across a broad geographical area (Fig. 1). The pasture sites were chosen as having been cleared, cultivated, fertilized and sown to pasture grasses followed by a minimum of 40 years of continuous grazing by sheep or cattle. These sites contained few or no native species. The restoration sites were pasture sites that had previously satisfied the above criteria prior to replanting with native species. Site preparation mirrored contemporary silvicultural techniques which use a combination of ploughing and herbicide treatment with the aim of removing competition and improving moisture retention (Close & Davidson, 2003). Although *Eucalyptus* species have established well at all of these sites and appear healthy, there has been little to no establishment of native forest understorey species. Instead, the understoreys remain dominated by exotic pasture grasses and weedy species. Time

since establishment ranged between 3 and 22 years. The forest sites had no history of land clearance, cultivation or fertilization and no or low intensity grazing. Each of the forest sites was eucalypt woodland with varying eucalypt species, abundant native plant recruitment and few exotic plant species.

At each site, a 25 x 25m plot was selected on the basis that it reasonably reflected the typical vegetation, soil and topographical characteristics of the site. A central pit was dug within each plot to a depth of approximately 40 cm and the soil profile photographed. Sub samples of soil were then collected at ten random points around the central pit at two depths: 0-10cm and 20-30 cm. For each depth sub samples were combined and mixed thoroughly in plastic bags to produce a single sample per depth per site. Samples were then air dried at approximately 20^0 C and sieved to <2mm.

Soil chemical analysis:

Total carbon and nitrogen analysis was conducted using a Perkin Elmer Series II CHNS/O elemental analyzer (Analytical Development Company, Adelaide, Australia; precision of standards ± 0.2% for both C and N). Colwell phosphorous (9B), organic carbon (Walkley-Black), nitrate and ammonium (7C2b), pH 1:5 soil/$CaCl_2$ solution (4B3) were measured at CSBP Laboratories, Western Australia, following the methods of Rayment and Lyons (2011) .

Data analysis:

For each of the measured soil parameters (total carbon, total nitrogen, total carbon to nitrogen ratio – henceforth "C:N" – , nitrate, pH, total N and Colwell P) a two-way factorial analysis of variance was conducted with land management classes (forest, pasture or restoration) and depth interval (0-10cm versus 20-30cm) as factors. Post Hoc comparisons among treatments were made using Tukey's HSD. Pearson correlations among soil parameters for each management class were tested. For restoration

sites this also included correlations with age of restoration. Data was log transformed where conditions of normality were not met. All tests were implemented using R (R development core team 2014).

Results

For each treatment at each depth, total soil C was tightly correlated with total N ($R^2 > 0.941$; $p < 0.001$; Fig. 2). However, C:N in both pasture and restoration soils were significantly different from those in forest soils ($p < 0.001$), but pasture and restoration soils were not significantly different ($p > 0.05$) (Fig. 3). C:N at 0-10cm and 20-30 was significantly different ($p < 0.01$). Interaction effects were not significant ($p > 0.05$). The differences were striking: mean C:N of forest soils was much higher (23.5 at 0-10cm depth and 18.2 at 20-30cm depth) than both restoration and pasture soils which both fell between 11.3 and 12.1. In spite of a 22 year age span, C:N in restoration soils did not differ with time since planting, relative to the pasture results (Fig. 4).

The patterns in C:N were similar to differences among site types in total nitrate, pH and available phosphorous, but not in total carbon, organic carbon or ammonium. Thus, forest was significantly ($p < 0.05$) lower than both restoration and pasture in % total N, NO_3, pH and Colwell P (Fig. 4), but there were no significant differences among management classes in % total C, NH_4 and % organic C ($p > 0.05$; Fig.5). As with C:N, there were no significant differences between restoration and pasture for any of the soil traits tested ($p > 0.05$). There was no significant correlation between age of plantings and any of these variables at either soil depth (Fig. 7).

Discussion

Our results point to a pasture-type stable state persisting within the restoration soils. The fact that our measured soil characteristics did not differ significantly between pasture and restoration across a wide range of restoration site ages suggests that the current soil system is highly resistant to change. The clearly divergent C:N of our pasture and forest reference sites (Fig. 3) was driven by differences in total N while total and organic C were not significantly different between management classes. These results both confirm our ecotype predictions and support the use of soil C:N as a proxy for below ground ecotype across these systems. Further validation is provided by the highly constrained nature of the relationship between C and N for all management classes and soil depths combined (R^2 = 0.804). This relationship between C and N approximated the global average of 0.75 (Cleveland & Liptzin, 2007) and within management class the relationships were even tighter (Fig. 2).

In addition to the lack of difference in soil C:N between restoration and pasture soils, these ratios did not, as hypothesised, rank along a continuum and increase toward forest soil values with age of planting (Fig. 4). This indicates that the restoration interventions and natural processes have failed to facilitate measurable below ground transformation within the time frames considered.

Total nitrogen, nitrate, pH and Colwell P levels were elevated in both restoration and pasture soils in comparison to forest soils (Fig. 5) and as with C:N levels in restoration sites, did not change with time (Fig. 7). This provides further evidence that a stable pasture-soil system remains entrenched despite the successful establishment of eucalypt over-storey. This raises some fundamental questions: what mechanisms are likely to be underpinning stability within the soil system; why the establishment of structurally significant species such as eucalypts has not driven below ground transformation; and what are the implications for the re-assembly of complex native plant communities?

Stability Mechanisms

Multiple factors influence the stability of a soil system. Within microbial communities, resistance and resilience are particularly governed by soil physiochemical structure which relate to soil history and disturbance regime (Griffiths & Philippot, 2013; Lauber, Strickland, Bradford, & Fierer, 2008). An additional legacy from long term grazing is the entrenchment of exotic pasture grasses and annual weedy species. The persistence of these species contributes to a recalcitrant state via plant soil feedbacks, in particular the elemental stability of the soil organic matter pool (Putten et al., 2013; Katharine N Suding, 2011). For example, grasses and other fast growing annual species sustain a characteristic nitrifying system via their relatively high litter quality and direct rhizosphere influence (Van Der Krift & Berendse, 2001). Within this low C:N, higher pH and high total N environment, primary decomposers within the established below ground community are able to mineralize sufficient N for their own requirements and leach sufficient excess mineral N which in turn sustains the nitrifying community. Such conditions across all our restoration sites are likely to ensure a competitive advantage to this exotic plant/microbe community. As a significant contributor to soil organic matter (Miltner, Bombach, Schmidt-Brücken, & Kästner, 2012), microbe communities also strongly influence soil C:N via the stoichiometry of elemental pools within their living biomass, detritus and stable metabolites (Clemmensen et al., 2013; Lovett, Weathers, & Arthur, 2002; Manzoni, Trofymow, Jackson, & Porporato, 2010; Miltner et al., 2012; Prescott, 2010; Six, Frey, Thiet, & Batten, 2006). Alternate soil biota that can drive ecosystem changes may lack dispersal vectors or confront niche limitations (Harris, 2009). Where dispersal is not a limitation, soil community composition may be controlled along nutrient gradients (Nilsson et al. 2005). For example a low C:N soil environment is likely to present a C limitation for prospective forest microbe recruits (Gallardo & Schlesinger, 1992). In our restoration sites this competitive disadvantage is exacerbated because eucalypts adapt to high nutrient conditions by de-coupling or reducing C allocation to mycorrhizal symbionts (Högberg, Bååth, Nordgren, Arnebrant, & Högberg, 2003; Treseder, 2004; Zheng, Hu, Guo, Anderson, & Powell, 2017).

Eucalypts fail to drive changes in restoration soils

There is a common understanding that eucalypts are keystone species with a disproportionally large contribution to ecosystem function (Manning, Fischer, & Lindenmayer, 2006). However, the lack of soil transformation found in this study imply that eucalypts have had limited influence on soil succession. This suggests the eucalypts in this system are more adaptors to pasture soil conditions rather than drivers of change.

Adaptability to diverse soil conditions is a hallmark of many eucalypt species, as evidenced by their adoption world-wide as a plantation species (Turnbull, 1999). Additionally, the prevalence of eucalypts as paddock trees throughout rural Australian environments suggests a tolerance to higher fertility levels and nitrifying systems. While these environments have been found to increase eucalypt vulnerability to environmental stresses (Close et al., 2010; Davidson et al., 2007; Philippot, Raaijmakers, Lemanceau, & van der Putten, 2013) and reduce natural recruitment (Dorrough & Moxham, 2005), within our study sites active planting has resulted in eucalypt populations seemingly well-adapted to pasture fertility levels.

The absence of native understorey species in our restoration sites suggests that soil recalcitrance presents significant barriers to both active establishment and natural recruitment, as described in other systems by Hamman and Hawkes (2013). Most native plant species have obligate microbial associations which assist resource acquisition and provide biological defence (Berendsen, Pieterse, & Bakker, 2012). Resource limitation is an important driver in mycorrhizae formation (Johnson, Wilson, Bowker, Wilson, & Miller, 2010), therefore high nutrient concentrations and the probable absence of forest microbial communities may compromise formation of these associations. This is likely to result in establishment failure for native species less amenable to these conditions. In short, the unchallenged persistence of exotic plant and below ground communities within this relatively high pH and nitrifying environment is likely to be the major barrier to understory recruitment.

Intervention

Despite early enthusiasm for overcoming obstacles to ecological restorations (Bradshaw, 1983), diversity within post agricultural forests world-wide is constrained by long term changes to soil properties which may persist for centuries (Dupouey, Dambrine, Laffite, & Moares, 2002; Flinn & Vellend, 2005). Recalcitrance within restoration plantings must therefore be countered by active interventions that accelerate and direct successional processes.

While pre-planting preparation on our study sites focused on the removal of competitive pasture species through cultivation and herbicide treatment, surviving soil seed banks and natural seed dispersal may have contributed to the recovery and persistence of pasture and exotic annual species amenable to the relatively fertile conditions. Fertility reduction has long been recognized as an integral step in the re-establishment of many natural environments (Gough & Marrs, 1990; Marrs, 1985). In preparation for native direct seeding, Gibson-Roy et al. (2010) found that 'scalping' or removal of surface soil, in combination with herbicide, was effective for initial weed suppression, removal of the exotic seed bed and also provided an immediate reduction in fertility. In contrast, biomass removal through fire or harvesting achieves a gradual depletion of soil nutrients over time (Bakker & Berendse, 1999). Top soil removal can also diminish pre-existing microbial communities effectively reducing competition and improving the efficacy of soil inoculations which in turn can steer plant community development (Carbajo, Den Braber, Van Der Putten, & De Deyn, 2011; Wubs et al., 2016).

While potentially only practical on a smaller scale, the addition of high C:N amendments such as sawdust or wood chips has been shown to effect long term reductions in nitrate and P availability, improve soil biophysical condition and reduce exotic plant biomass (Prober, Stol, Piper, Gupta, & Cunningham, 2014; Sollenberger, Kadlec, O'Shaughnessy, & Egerton‐Warburton, 2016). Direct manipulation of soil C:N through such additions also favours forest type fungal communities by rebalancing energy and biomass availability and changing abiotic soil factors (van der Heijden 2012,

Boberg 2009, Harris 2009). These and similar disruptive interventions that directly target soil processes are needed to provide sufficient disturbance, undermine resilience of the pasture-soil system and assist transformation to a high C:N, low nutrient soil state.

Similarly, the facilitating role of 'eco engineer' plant species offer opportunities where species specific effects can directly influence soil properties through marked differences in the production and chemistry of plant litter (Lovett et al. 2002). The influence of plant metabolites on decomposition has significant consequences for nutrient competition between plants and microbes, nutrient recycling and retention (Hattenschwiler and Vitousek 2000). Such plant feedback mechanisms can provide a desired shift in the plant/microbe loop resulting in significant root zone modifications such as increases in C:N, inhibition of nitrification and modification of pH (Gunina, Smith, Godbold, Jones, & Kuzyakov, 2017; Lodhi, 1978; Osanai et al., 2012; Quideau et al., 2001; You, Dalal, & Huang, 2016). Robust, more easily established sub-dominants such as native grasses, shrubs and bracken can effectively reduce soil compaction, improve water infiltration and may also act as a nutrient sink effectively reducing soil nutrient availability (McGlone, Wilmshurst, & Leach, 2005). Such species can also assist in the competitive exclusion of exotic weeds, additionally the role of particular species as nurse plants has long been recognised (Went, 1942).

We suggest that interventions may need to be applied in a sequential manner whereby initial transformations create a protective niche for the later introduction of sensitive native species (Gallegos, Hensen, Saavedra, & Schleuning, 2015; Yates, Hobbs, & Atkins, 2000). This may be particularly important where obligate associations are involved (Kardol and Wardle 2010).

Conclusion

While it has been noted that soil transformation processes can occur naturally after the cessation of agriculture (Maharning, Mills, & Adl, 2009), both here and in many other systems throughout the world the challenges of re-establishing native plant communities within ex-agricultural landscapes persist (Flinn & Vellend, 2005). In deference to their iconic status and role as key stone species, there has been a concerted effort within our study region to prioritise the establishment of eucalypts. The apparent success of putting trees back into the landscape has not been mirrored in regard to outcomes for native biodiversity or soil function. This highlights the importance of a soil ecological focus and the need for active and calculated interventions which short cut natural time lines toward a desired trajectory (Callaham, Rhoades, & Heneghan, 2008; Heneghan et al., 2008). In this study nutrient levels provide a strong and practical signature of soil change indicating that these restoration sites remain trapped in an alternate state.

References

Angers, D. A., & Caron, J. (1998). Plant-induced changes in soil structure: processes and feedbacks *Biogeochemistry, 42*, 55-72.

Bakker, J. P., & Berendse, F. (1999). Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends in Ecology & Evolution, 14*(2), 63-68.

Berendsen, R. L., Pieterse, C. M., & Bakker, P. A. (2012). The rhizosphere microbiome and plant health. *Trends in plant science, 17*(8), 478-486.

Binkley, D. (1995). *The Influence ofTree Species on Forest Soils: Processes and Patterns.* Paper presented at the Proceedings of the trees and soil workshop.

Bradshaw, A. (1983). The reconstruction of ecosystems. *Journal of Applied Ecology, 20*(1), 1-17.

Brussaard, L. (1997). Biodiversity and ecosystem functioning in soil. *Ambio*, 563-570.

Callaham, M. A., Rhoades, C. C., & Heneghan, L. (2008). A striking profile: soil ecological knowledge in restoration management and science. *Restoration ecology, 16*(4), 604-607.

Carbajo, V., Den Braber, B., Van Der Putten, W. H., & De Deyn, G. B. (2011). Enhancement of late successional plants on ex-arable land by soil inoculations. *PloS one, 6*(7), e21943.

Chapin, F. S. (1980). The mineral nutrition of wild plants. *Annual review of ecology and systematics*, 233-260.

Chapman, S. K., Langley, J. A., Hart, S. C., & Koch, G. W. (2006). Plants actively control nitrogen cycling: uncorking the microbial bottleneck. *New Phytologist, 169*(1), 27-34.

Clemmensen, K., Bahr, A., Ovaskainen, O., Dahlberg, A., Ekblad, A., Wallander, H., . . . Lindahl, B. (2013). Roots and associated fungi drive long-term carbon sequestration in boreal forest. *Science, 339*(6127), 1615-1618.

Cleveland, C. C., & Liptzin, D. (2007). C: N: P stoichiometry in soil: is there a "Redfield ratio" for the microbial biomass? *Biogeochemistry, 85*(3), 235-252.

Close, D. C., & Davidson, N. J. (2003). Revegetation to combat tree decline in the Midlands and Derwent Valley Lowlands of Tasmania: practices for improved plant establishment. *Ecological Management & Restoration, 4*(1), 29-36.

Close, D. C., Davidson, N. J., Churchill, K. C., & Corkrey, R. (2010). Establishment of native Eucalyptus pauciflora and exotic Eucalyptus nitens on former grazing land. *New forests, 40*(2), 143-152.

Cramer, V. A., Hobbs, R. J., & Standish, R. J. (2008). What's new about old fields? Land abandonment and ecosystem assembly. *Trends in Ecology & Evolution, 23*(2), 104-112.

Davidson, N. J., Close, D. C., Battaglia, M., Churchill, K., Ottenschlaeger, M., Watson, T., & Bruce, J. (2007). Eucalypt health and agricultural land management within bushland remnants in the Midlands of Tasmania, Australia. *Biological Conservation, 139*(3), 439-446.

Dorrough, J., & Moxham, C. (2005). Eucalypt establishment in agricultural landscapes and implications for landscape-scale restoration. *Biological Conservation, 123*(1), 55-66.

Dupouey, J.-L., Dambrine, E., Laffite, J.-D., & Moares, C. (2002). Irreversible impact of past land use on forest soils and biodiversity. *Ecology, 83*(11), 2978-2984.

Eviner, V. T., & Hawkes, C. V. (2008). Embracing variability in the application of plant–soil interactions to the restoration of communities and ecosystems. *Restoration ecology, 16*(4), 713-729.

Fensham, R. (1989). The pre-European vegetation of the Midlands, Tasmania: a floristic and historical analysis of vegetation patterns. *Journal of Biogeography*, 29-45.

Flinn, K. M., & Vellend, M. (2005). Recovery of forest plant communities in post‐agricultural landscapes. *Frontiers in Ecology and the Environment, 3*(5), 243-250.

Gallardo, A., & Schlesinger, W. H. (1992). Carbon and nitrogen limitations of soil microbial biomass in desert ecosystems. *Biogeochemistry, 18*(1), 1-17.

Gallegos, S. C., Hensen, I., Saavedra, F., & Schleuning, M. (2015). Bracken fern facilitates tree seedling recruitment in tropical fire-degraded habitats. *Forest ecology and management, 337*, 135-143.

Gibson‐Roy, P., Moore, G., & Delpratt, J. (2010). Testing methods for reducing weed loads in preparation for reconstructing species‐rich native grassland by direct seeding. *Ecological Management & Restoration, 11*(2), 135-139.

Godbold, D. L., Hoosbeek, M. R., Lukac, M., Cotrufo, M. F., Janssens, I. A., Ceulemans, R., . . . De Angelis, P. (2006). Mycorrhizal hyphal turnover as a dominant process for carbon input into soil organic matter. *Plant and soil, 281*(1-2), 15-24.

Gough, M., & Marrs, R. (1990). A comparison of soil fertility between semi-natural and agricultural plant communities: Implications for the creations of species-rich grassland on abondoned agricultural land. *Biological Conservation, 51*(2), 83-96.

Griffiths, B. S., & Philippot, L. (2013). Insights into the resistance and resilience of the soil microbial community. *FEMS microbiology reviews, 37*(2), 112-129.

Gunina, A., Smith, A. R., Godbold, D. L., Jones, D. L., & Kuzyakov, Y. (2017). Response of soil microbial community to afforestation with pure and mixed species. *Plant and soil, 412*(1-2), 357-368.

Hamman, S. T., & Hawkes, C. V. (2013). Biogeochemical and Microbial Legacies of Non‐Native Grasses Can Affect Restoration Success. *Restoration ecology, 21*(1), 58-66.

Harris, J. (2009). Soil microbial communities and restoration ecology: facilitators or followers? *Science, 325*(5940), 573-574.

Heneghan, L., Miller, S. P., Baer, S., Callaham, M. A., Montgomery, J., Pavao‐Zuckerman, M., . . . Richardson, S. (2008). Integrating soil ecological knowledge into restoration management. *Restoration ecology, 16*(4), 608-617.

Högberg, M. N., Bååth, E., Nordgren, A., Arnebrant, K., & Högberg, P. (2003). Contrasting effects of nitrogen availability on plant carbon supply to mycorrhizal fungi and saprotrophs–a hypothesis based on field observations in boreal forest. *New Phytologist, 160*(1), 225-238.

Holtkamp, R., Kardol, P., van der Wal, A., Dekker, S. C., van der Putten, W. H., & de Ruiter, P. C. (2008). Soil food web structure during ecosystem development after land abandonment. *Applied Soil Ecology, 39*(1), 23-34.

Johnson, N. C., Wilson, G. W., Bowker, M. A., Wilson, J. A., & Miller, R. M. (2010). Resource limitation is a driver of local adaptation in mycorrhizal symbioses. *Proceedings of the National Academy of Sciences, 107*(5), 2093-2098.

Kardol, P., & Wardle, D. A. (2010). How understanding aboveground–belowground linkages can assist restoration ecology. *Trends in Ecology & Evolution, 25*(11), 670-679.

Kulmatiski, A., Beard, K. H., & Stark, J. M. (2006). Soil history as a primary control on plant invasion in abandoned agricultural fields. *Journal of Applied Ecology, 43*(5), 868-876.

Lauber, C. L., Strickland, M. S., Bradford, M. A., & Fierer, N. (2008). The influence of soil properties on the structure of bacterial and fungal communities across land-use types. *Soil Biology and Biochemistry, 40*(9), 2407-2415.

Lodhi, M. (1978). Comparative inhibition of nitrifiers and nitrification in a forest community as a result of the allelopathic nature of various tree species. *American Journal of Botany*, 1135-1137.

Lovett, G. M., Weathers, K. C., & Arthur, M. A. (2002). Control of Nitrogen Loss from Forested Watersheds by Soil Carbon: Nitrogen Ratio andTree Species Composition. *Ecosystems, 5*(7), 0712-0718.

Maharning, A. R., Mills, A. A., & Adl, S. M. (2009). Soil community changes during secondary succession to naturalized grasslands. *Applied Soil Ecology, 41*(2), 137-147.

Manning, A. D., Fischer, J., & Lindenmayer, D. B. (2006). Scattered trees are keystone structures–implications for conservation. *Biological Conservation, 132*(3), 311-321.

Manzoni, S., Trofymow, J. A., Jackson, R. B., & Porporato, A. (2010). Stoichiometric controls on carbon, nitrogen, and phosphorus dynamics in decomposing litter. *Ecological Monographs, 80*(1), 89-106.

Marrs, R. (1985). Techniques for reducing soil fertility for nature conservation purposes: a review in relation to research at Roper's Heath, Suffolk, England. *Biological Conservation, 34*(4), 307-332.

Marrs, R. (1993). Soil fertility and nature conservation in Europe: theoretical considerations and practical management solutions. *Advances in ecological research, 24*, 241-300.

Matzek, V., Warren, S., & Fisher, C. (2016). Incomplete recovery of ecosystem processes after two decades of riparian forest restoration. *Restoration ecology, 24*(5), 637-645.

McGlone, M. S., Wilmshurst, J. M., & Leach, H. M. (2005). An ecological and historical review of bracken (Pteridium esculentum) in New Zealand, and its cultural significance. *New Zealand Journal of Ecology, 29*(2), 165-184.

Miltner, A., Bombach, P., Schmidt-Brücken, B., & Kästner, M. (2012). SOM genesis: microbial biomass as a significant source. *Biogeochemistry, 111*(1-3), 41-55.

Morriën, E., Hannula, S. E., Snoek, L. B., Helmsing, N. R., Zweers, H., de Hollander, M., . . . Dimmers, W. (2017). Soil networks become more connected and take up more carbon as nature restoration progresses. *Nature Communications, 8*, 14349.

Osanai, Y., Flittner, A., Janes, J. K., Theobald, P., Pendall, E., Newton, P. C., & Hovenden, M. J. (2012). Decomposition and nitrogen transformation rates in a temperate grassland vary among co-occurring plant species. *Plant and soil, 350*(1-2), 365-378.

Philippot, L., Raaijmakers, J. M., Lemanceau, P., & van der Putten, W. H. (2013). Going back to the roots: the microbial ecology of the rhizosphere. *Nature Reviews Microbiology, 11*(11), 789-799.

Prescott, C. E. (2010). Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils? *Biogeochemistry, 101*(1-3), 133-149.

Prober, S. M., Stol, J., Piper, M., Gupta, V., & Cunningham, S. A. (2014). Enhancing soil biophysical condition for climate-resilient restoration in mesic woodlands. *Ecological Engineering, 71*, 246-255.

Putten, W. H., Bardgett, R. D., Bever, J. D., Bezemer, T. M., Casper, B. B., Fukami, T., . . . Schweitzer, J. A. (2013). Plant–soil feedbacks: the past, the present and future challenges. *Journal of Ecology, 101*(2), 265-276.

Quideau, S., Chadwick, O., Trumbore, S. E., Johnson-Maynard, J., Graham, R., & Anderson, M. (2001). Vegetation control on soil organic matter dynamics. *Organic Geochemistry, 32*(2), 247-252.

R Development Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, V., Austria.

Rayment, G., Lyons, D. (2011). *Soil Chemical Methods - Australasia*. Melbourne: CSIRO Publishing.

Six, J., Frey, S., Thiet, R., & Batten, K. (2006). Bacterial and fungal contributions to carbon sequestration in agroecosystems. *Soil Science Society of America Journal, 70*(2), 555-569.

Sollenberger, D., Kadlec, C., O'Shaughnessy, J., & Egerton‐Warburton, L. (2016). Environmental filtering mediates grassland community assembly following restoration with soil carbon additions. *Restoration ecology, 24*(5), 626-636.

Suding, K. N. (2011). Toward an era of restoration in ecology: successes, failures, and opportunities ahead. *Annual Review of Ecology, Evolution, and Systematics, 42*(1), 465.

Suding, K. N., Gross, K. L., & Houseman, G. R. (2004). Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution, 19*(1), 46-53.

Treseder, K. K. (2004). A meta‐analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO2 in field studies. *New Phytologist, 164*(2), 347-355.

Turnbull, J. W. (1999). Eucalypt plantations *Planted Forests: Contributions to the Quest for Sustainable Societies* (pp. 37-52): Springer.

Van Der Krift, T. A., & Berendse, F. (2001). The effect of plant species on soil nitrogen mineralization. *Journal of Ecology, 89*(4), 555-561.

Wallington, T. J., Hobbs, R. J., & Moore, S. A. (2005). Implications of current ecological thinking for biodiversity conservation: a review of the salient issues. *Ecology and Society, 10*(1), 16.

Wardle, D. A., Bardgett, R. D., Klironomos, J. N., Setälä, H., Van Der Putten, W. H., & Wall, D. H. (2004). Ecological linkages between aboveground and belowground biota. *Science, 304*(5677), 1629-1633.

Went, F. (1942). The Dependence of Certain Annual Plants on Shrubs in Southern Californi Deserts. *Bulletin of the Torrey Botanical Club, 69*(2), 100-114.

Wubs, E. J., van der Putten, W. H., Bosch, M., & Bezemer, T. M. (2016). Soil inoculation steers restoration of terrestrial ecosystems. *Nature plants, 2*, 16107.

Yates, C. J., Hobbs, R. J., & Atkins, L. (2000). Establishment of perennial shrub and tree species in

degraded Eucalyptus salmonophloia (salmon gum) remnant woodlands: effects of

restoration treatments. *Restoration ecology, 8*(2), 135-143.

You, F., Dalal, R. C., & Huang, L. (2016). Biochemical properties of highly mineralised and infertile soil

modified by acacia and spinifex plants in northwest Queensland, Australia. *Soil Research,

54*(3), 265-275.

Zheng, Y., Hu, H.-W., Guo, L.-D., Anderson, I. C., & Powell, J. R. (2017). Dryland forest management
alters fungal community composition and decouples assembly of root-and soil-associated
fungal communities. *Soil Biology and Biochemistry, 109*, 14-22.

Appendix S1. Environmental description for each site.
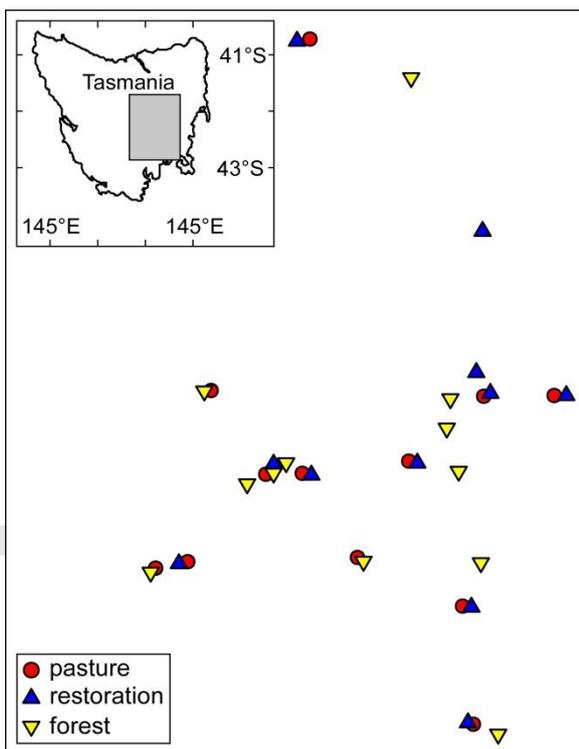
Figure 1. Distribution of each sample plot by land management class throughout the Midlands of
Tasmania.
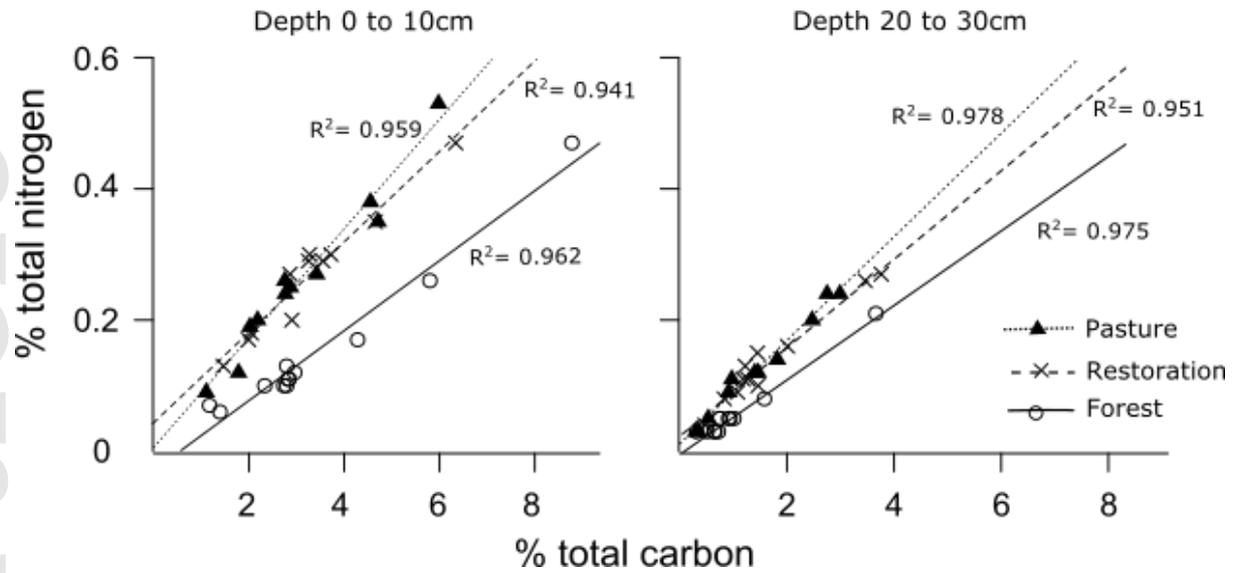
Figure 2. Associations between total soil carbon and total soil nitrogen in pasture, restoration and forest soils at two depths (0-10cm and 20-30cm). Note the tightly constrained elemental ratios (high R^2 values).
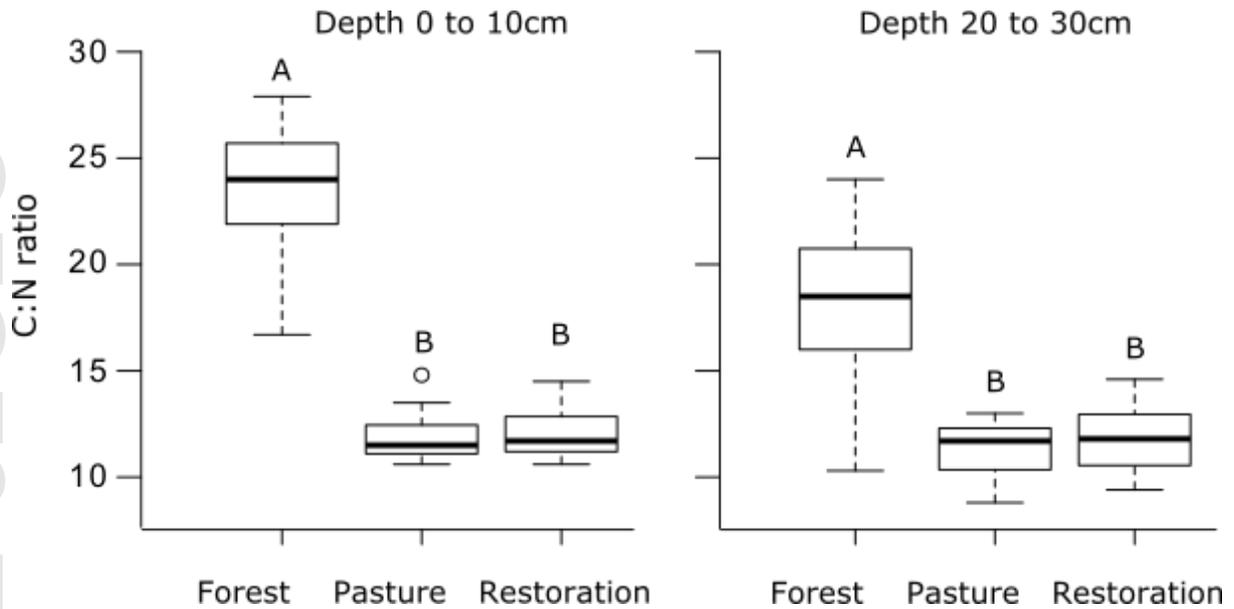
Figure 3. Total soil nitrogen and carbon expressed as C:N in forest, pasture and restoration soils at two depths (0-10cm and 20-30cm). Within depths, columns with different capital letters were significantly different (*p* < 0.001).
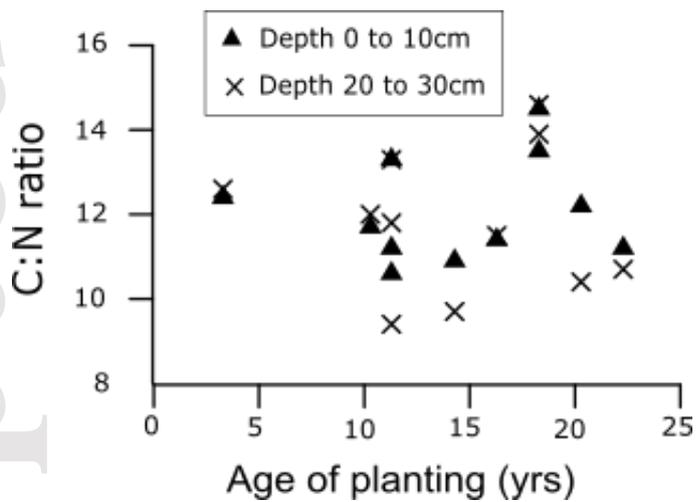

Figure 4. C:N versus age of restoration planting at two soil depths. There was no significant correlation between C:N and age of restoration at either depth (0-10 cm, *R*=-0.091, *p*=0.69; 20-30cm, *R*=0.108, *p*=0.87).
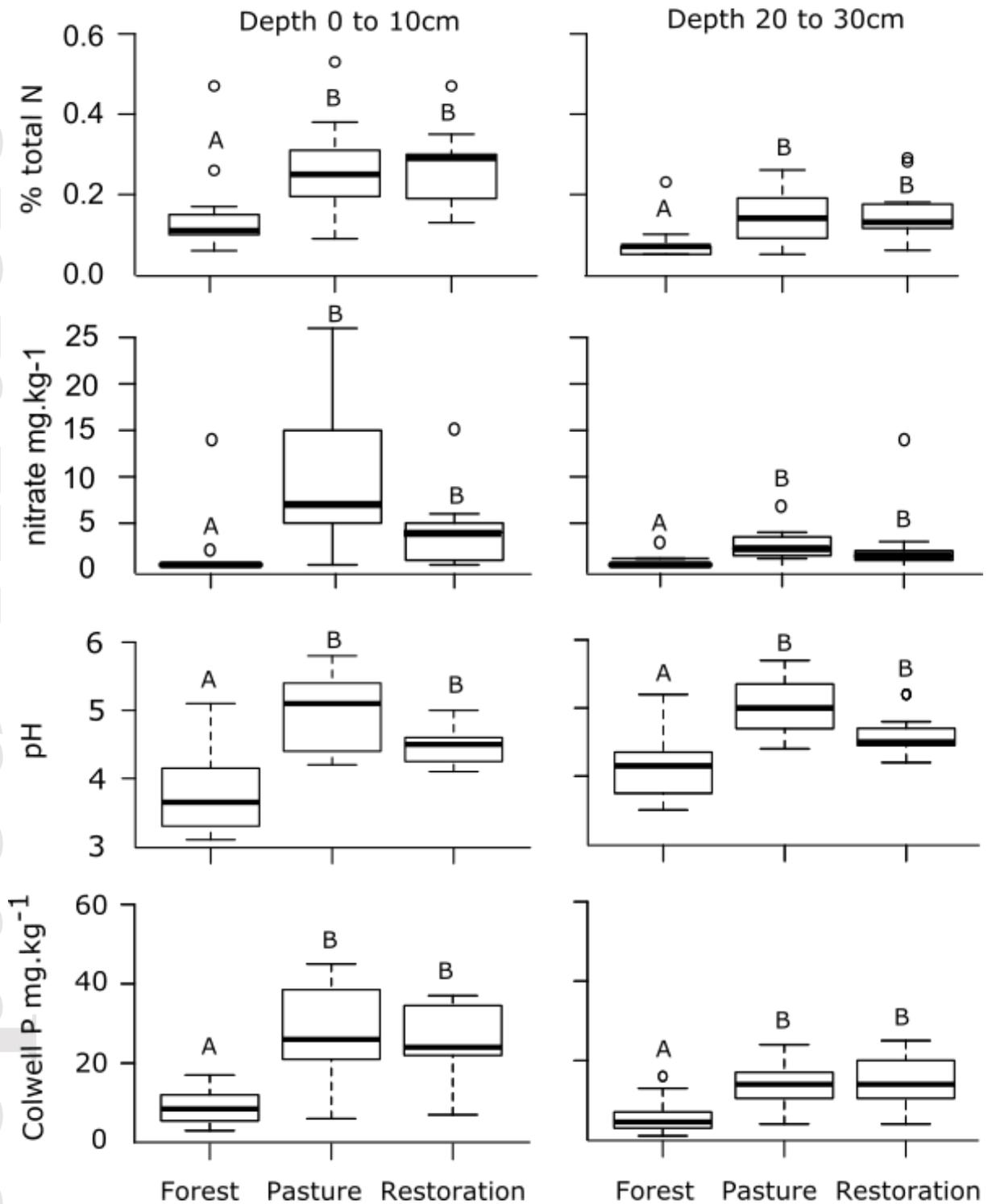
Figure 5. Percentage total N, nitrate, pH and Colwell *p* values for each management class at two soil depths. Different capital letters within each variable denote significant difference (*p*>0.05). Note nitrate, total N and nitrate data was log transformed for statistical analysis.
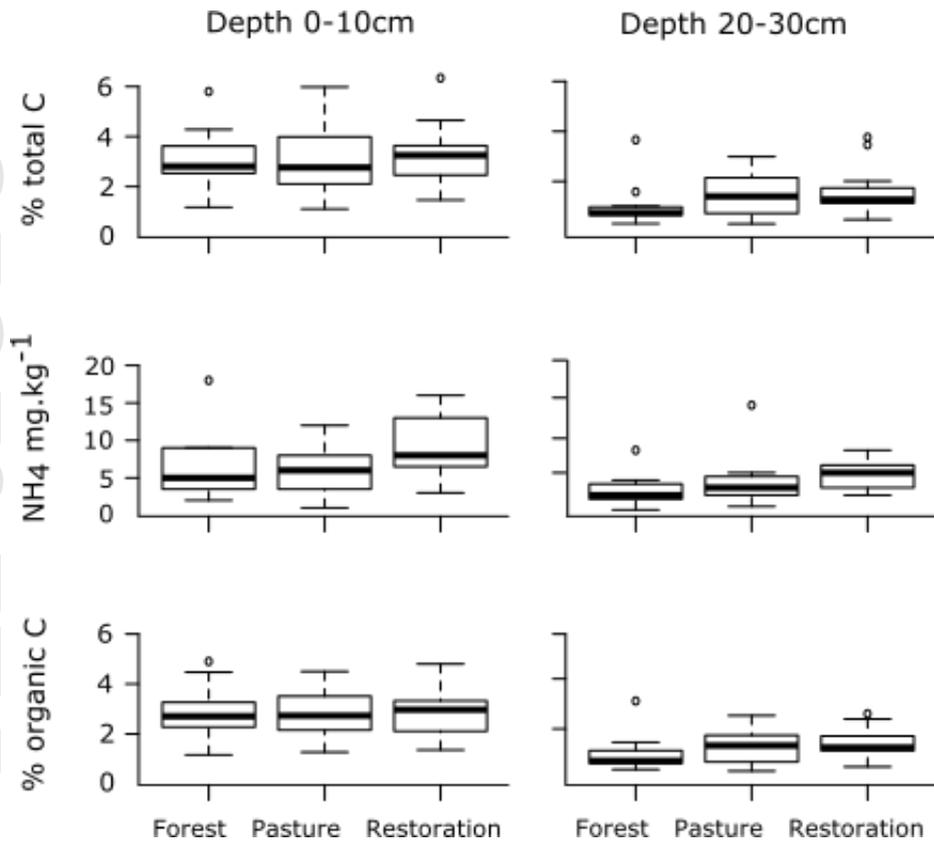
Figure 6. Percentage total C, NH$_4$ and % organic C for management classes at two soil depths. There were no significant differences at either depth interval. Total C and NH$_4$ data was log transformed for statistical analysis.
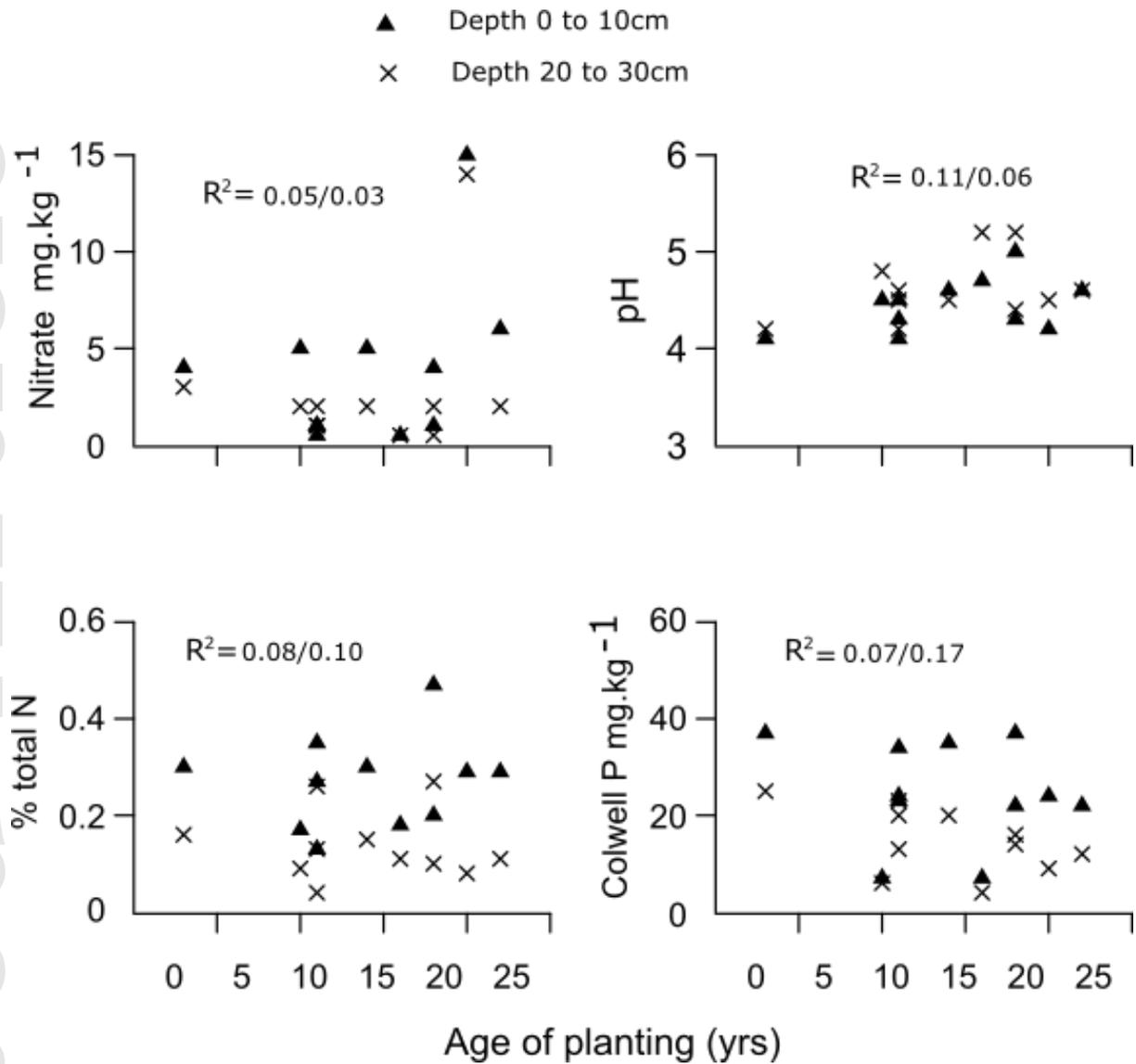
Figure 7. Soil chemical traits versus time since planting for restoration sites at two soil depths. There were no significant correlations at either depth (*p*>0.05). Adjusted R^2 values are given for each depth (0-10cm/20-30cm).