

Above and below-ground disturbance responses in Mountain Ash forests

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December 2020

A thesis submitted for the degree of Doctor of Philosophy at The Australian National University.

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Candidate's declaration

This thesis by compilation contains no material that has been accepted for the award of any other degree or diploma in any university. The research, analysis and writing in the thesis are substantially (>90%) my own work. To the best of my knowledge, it contains no material previously published or written by another person, except where due reference is made in the text.

A handwritten signature in black ink, appearing to be 'EJB' with a long horizontal stroke extending to the right.

Elle Jane Bowd
21 December 2020

Acknowledgements

I would like to acknowledge the traditional owners of the Central Highlands region in Victoria, the land where I conducted my research. I pay my respects to their elders, past, present and emerging.

I would like to extend my upmost gratitude to my supervisors, David Lindenmayer, Sam Banks, Tom May and Andrew Bissett. You have been fundamental throughout my PhD. Thank you for your time, expertise, extensive feedback, and support over the last three and a half years.

Special mention to my chair and mentor, David Lindenmayer, you have been monumental in my development as an ecologist. Thank you for your consistent encouragement, unwavering support, timely and comprehensive feedback and enthusiasm in my work- your passion for the natural world has been a constant source of inspiration.

Special thanks to all the other legends I worked with over the course of my PhD including: Lachie McBurney, Wade Blanchard, Tabitha Boyer, Claire Shepperd, John Stein, and Andrew Higgins, and all Fenner PhD students, including James, George, Yan and Depi. You all made my journey so much more enjoyable.

To my friend and colleague, Dave Blair, I know you are still with us all, standing tall with the forests you loved. You are dearly missed, and your legacy will live on.

To the amazing volunteers who became friends, and the friends who became volunteers, hammering in countless soil cores, despite sweaty and challenging vegetation, soils and... rocks: Lan, Alana, Sam, Dave, James, Adam, Irene, Ange, Pat, Dougie, Jess, Lauren, Thea and Ash. I couldn't have done this without you all.

To my partner, Adam, thank you for your love, unwavering support, keeping me grounded, and belief in my capabilities even during times of serious doubt.

Finally, to my dear friends, mum and family, thank you for your love, guidance, support and belief in me, while far away, it always felt like you were with me. You have always been my wings.

To my late father, thank you for your unwavering support and encouragement throughout this period. You are dearly missed, and this is for you.

Abstract

Above and below-ground biological communities and abiotic properties form interactions and feedbacks that underpin critical ecological functions across all terrestrial ecosystems. Despite this, disturbance ecology has traditionally focused on understanding disturbance responses above-ground, with little consideration of those below-ground, or of the interactions between them. New methods such as DNA and RNA meta-barcoding provide an exciting opportunity to quantify below-ground biodiversity and broaden our understanding of the ecological impacts of disturbances. This thesis takes advantage of these new approaches to describe how soil properties, microbial and plant communities, and their respective multi-trophic interactions are influenced by wildfires, and clearcut and salvage logging. My research is based on 81 sites across a multi-decadal chronosequence (differing in disturbance histories) in the Mountain Ash forests of the Victorian Central Highlands in south-eastern Australian.

My findings in **Chapter 1** revealed differences in the responses of plant communities to clearcut logging and multiples fires. Specifically, I found that resprouting plant species are more sensitive to mechanical disturbances such as clearcut and salvage logging than the impacts of wildfires alone. Further, multiple wildfires resulted in declines in the abundance of some onsite-seeder plant species, which may indicate they are maladapted to short-fire-return intervals.

Chapter 2 details my research findings of multi-decadal disturbance impacts on forest soils. Specifically, it describes declines in key soil nutrients including nitrate and available phosphorus for up to at least eight decades post-wildfire and three decades post-clearcut logging, relative to long-undisturbed forest. These adverse impacts on soil measures were more pronounced in the topsoil and were exacerbated with compounding disturbance.

Chapter 3 highlights how highly-functional, yet poorly described, fungal communities, and their respective functional groups are impacted by disturbances. This chapter provides evidence of changes in the composition of fungal communities for up to 34 years post-disturbance. It also shows that clearcut logging reduces symbiotrophic fungi and salvage logging increases pathotrophic fungi.

Chapter 4 describes the highly-diverse, yet highly-cryptic soil microbiome of the Mountain Ash forests for the first time. It also provides evidence that disturbances can reduce the diversity of individual microbial communities (bacteria, archaea, fungi) and total microbial diversity, especially in the topsoil. This chapter also identifies key edaphic and environmental drivers of the composition of individual microbial communities post-

disturbance.

Finally, **Chapter 5** integrates all previous chapters by disentangling the complex relationships between disturbances and plant-soil-microbial interactions. Specifically, this chapter provides evidence wildfires, logging and post-fire (salvage) logging can simultaneously impact plant and microbial communities, and abiotic soil properties both directly and indirectly through plant-soil-microbial interactions. Further, it also describes over 68 direct and indirect disturbance impacts, including those mediated by plant-soil-microbial interactions. These findings highlight the extent of which disturbance impacts can penetrate whole-forest ecosystems.

My research concludes that multiple fires and logging can have extensive adverse impacts below-ground, which may have widespread functional implications in forests. This suggests that traditional above-ground-focused approaches to land management may be underestimating disturbance impacts in forests. Further, my research highlights the need for a multifaceted approach to management that considers whole forest ecosystems including below-ground ecological components, and their interactions above-ground.

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Preface

This thesis ‘by compilation’ is structured as a series of linked papers that have been published in or submitted to peer reviewed journals at the time of submission. Below I have described the five papers that constitute this thesis, detailing the respective authors, relative contributions and published status. Each paper is representative of a thesis chapter, which have been written as stand-alone pieces of work. Therefore, there is unavoidable repetition between chapters, specifically in methods and background information. Further, the structure and formatting of each chapter may differ depending on the requirements of each respective journal.

CHAPTER 1: Logging and fire regimes alter plant communities

Authors: E. J. Bowd, D. B. Lindenmayer, S. C. Banks, and D. P. Blair.

Contributions: Study concept EB (70%), DL, SB; Data collection EB (100%); Authorship of original manuscript EB (95%), DL, DB, SB; Statistical analysis EB (100%); Edits and revision EB (95%), DL, SB, DB.

Current status of paper: Published, 7 February 2018.

Journal: Ecological Applications

Citation: Bowd, E.J., Lindenmayer, D.B., Banks, S.C., Blair, D.P. 2018. Logging and fire regimes alter plant communities. Ecological Applications 28(3): 826-841.

CHAPTER 2: Long-term impacts of wildfire and logging on forest soils

Authors: E. J. Bowd, S. C. Banks, C.L. Strong and D. B. Lindenmayer.

Contributions: Study concept EB (90%), DL, SB; Data collection EB (100%); Authorship of original manuscript EB (90%), DL, SB, CS; Statistical analysis EB (100%); Edits and revision EB (95%), DL, SB, CS.

Current status of paper: Published, 21 January 2019

Journal: Nature Geoscience

Citation: Bowd, E.J., Banks, S.C., Strong, C.L., Lindenmayer, D.B., 2019. Long-term impacts of wildfire and logging on forest soils. Nature Geoscience 12: 113-118.

CHAPTER 3: Fire and logging regimes alter functional communities of fungi

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Contributions: Study concept EB (90%), DL, SB, AB, TM ; Data collection EB (100%); Authorship of original manuscript EB (90%), DL, AB, TM, SB; Statistical/ Data analysis EB (85%), AB

Current status of paper: Under revision, December 2020.

Journal: Ecosystems

CHAPTER 4: Wildfires and logging alter a forest soil microbiome

Authors: E. J. Bowd, S. C. Banks, A. Bissett, T. W. May, D. B. Lindenmayer

Contributions: Study concept EB (90%), DL, SB, AB, TM; Data collection EB (100%); Authorship of original manuscript EB (90%), DL, AB, TM, SB; Statistical/ Data analysis EB (85%), AB

Current status of paper: Under revision, December 2020.

Journal: Molecular Ecology

CHAPTER 5: Direct and indirect disturbance impacts in forests

Authors: E. J. Bowd, S. C. Banks, A. Bissett, T. W. May, D. B. Lindenmayer

Contributions: Study concept EB (90%), DL, SB, AB, TM; Data collection EB (100%); Authorship of original manuscript EB (90%), DL, AB, TM, SB; Statistical/ Data analysis EB (85%), AB

Current status of paper: Under revision, December 2020

Journal: Ecology letters

Introduction

Forests are among the most productive and diverse ecosystems globally, fulfilling many critical ecosystem functions. They constitute large, high-quality water-catchments (Taylor, Blair, Keith, & Lindenmayer, 2019), store vast amounts of carbon crucial for climate change mitigation (Paustian et al., 2016), and support a substantial proportion of the earth's biodiversity (Watson et al., 2018). Now, in a period of rapid, global, environmental change, forest ecosystems face a myriad of compounding and interacting challenges (Watson et al., 2018). These include: changing climatic conditions (Seidl et al., 2017), biological invasions (Farris et al., 2015; Ricciardi, 2007), pathogenic attacks (Sturrock et al., 2011), anthropogenic disturbances (Maxwell, Fuller, Brooks, & Watson, 2016; Watson et al., 2018) and wildfires (Bradstock, Cohn, Gill, Bedward, & Lucas, 2009; Schoennagel et al., 2017; Seidl, Schelhaas, Rammer, & Verkerk, 2014). In recent years, disturbance patterns in forests have been characterized by an increase in the frequency and intensity of wildfires, largely driven by climatic changes and anthropogenic disturbances (Abatzoglou & Williams, 2016; Bowman et al., 2011; Cochrane & Laurance, 2008; Seidl, Schelhaas, et al., 2014; Taylor, McCarthy, & Lindenmayer, 2014). For instance, novel intensities and frequencies of wildfires have been reported in the conifer forests of the Pacific north-west of the USA (Odion et al., 2004; Thompson, Spies, & Ganio, 2007), Brazilian Amazonian rainforests (Cochrane & Laurance, 2008), European forests (Seidl, Schelhaas, et al., 2014), and the wet sclerophyll forests of south-eastern Australia (Lindenmayer, Hobbs, Likens, Krebs, & Banks, 2011; Taylor, McCarthy, & Lindenmayer, 2014; Zylstra, 2018).

Natural disturbances including wildfire are major drivers of the structure and function of forests worldwide, and influence both above and below-ground ecological patterns, processes and biological communities (Ashton, 1981; Bond, Woodward, & Midgley, 2005; Bowman et al., 2009; Fraver et al., 2017; Seidl, Rammer, & Spies, 2014). However, novel wildfire intensities and frequencies, coupled with anthropogenic disturbances, can shift ecosystems into functionally compromised states (Bowman et al. 2014; Lindenmayer et al. 2011). The impact of altered disturbance regimes on above-ground communities in forests has been previously characterized (Blair et al. 2016; Enright et al. 2015; Lindenmayer et al. 2019; Taboada et al. 2018). However, how edaphic soil environments and soil microbial communities are impacted remains comparatively poorly-understood (Barnes et al., 2017; Wardle et al., 2004).

Soil properties, microbial communities and above-ground biodiversity form multi-trophic interactions that mediate critical ecological functions throughout ecosystems (Bardgett & Van Der Putten, 2014; van der Putten et al., 2013; Wardle et al., 2004). These include plant productivity (Delgado-Baquerizo et al., 2017), biogeochemical cycles, decomposition and carbon storage (Cavicchioli et al., 2019; Delgado-Baquerizo et al., 2015; Maron et al., 2018). Despite this, the disturbance responses of below-ground ecological components and their respective multi-trophic interactions remain poorly-understood. This limits the understanding of the full extent of which disturbances impact forest ecosystems and impedes forest management.

Theories of disturbance ecology primarily focus on processes such as succession (effect of time since disturbance), and the frequency and origin of disturbances (Pulsford, Lindenmayer, & Driscoll, 2016). Using these metrics, in this thesis, I address knowledge gaps by quantifying the impact of wildfires (differing in frequency), and clearcut and post-fire salvage logging on soil edaphic properties, microbial and plant communities, and their respective interactions across a multi-decadal chronosequence in the Mountain Ash forests of the Victorian Central Highlands in south-eastern Australia.

The wet-sclerophyll Mountain Ash forests (*Eucalyptus regnans*) are some of the tallest forests in the world. They are well-known for storing vast amounts of carbon and water (Keith et al., 2014; Taylor et al., 2019). They also have exceptional biodiversity values, including those critically endangered (*Gymnobelideus leadbeateri*, Leadbeater's possum) and vulnerable (*Petauroides volans*, Greater glider) (Burns et al. 2015; Lindenmayer et al. 2013). These forests have co-evolved with the occurrence of high-severity wildfires every 75-150 years, which typically produces a new cohort of the dominant obligate seeder, *Eucalyptus regnans* (Ashton 1981; Lindenmayer et al. 2012; McCarthy, Malcolm Gill, and Lindenmayer 1999). However, in recent decades, the frequency of these fires has increased, with major fires occurring in 1926, 1932, 1939, 1983 and most recently in 2009 (Lindenmayer et al. 2011). Further, since the 1970s, these forests have been extensively clearcut and salvage (post-wildfire) logged for timber and pulpwood production (Flint & Fagg, 2007). Collectively, these disturbances have dominated the landscape in a mosaic of regrowth forest, with just 1.16% of long-undisturbed forests remaining (Lindenmayer et al. 2012).

Chapter 1 entitled, *Logging and fire regimes alter plant communities*, asks two questions 1. What is the effect of the number of fires on plant community composition and functional traits? 2. What is the effect of clearcut and salvage logging on plant communities

and functional traits and how does it differ from unlogged sites in similarly aged, burnt forest? In this study, I compared the impact of nine disturbance histories, differing in the number of wildfires, and clearcut and salvage logging events on plant communities and their respective functional traits across a multi-decadal chronosequence in Mountain Ash forests. While differing from other chapters focused on below-ground disturbance responses, this chapter provides important contextual information on above-ground disturbance responses, which can be influenced by below-ground processes.

Chapter 2 entitled *Long-term impacts of wildfire and logging on forest soils*, quantifies the impact of nine disturbance histories, differing in the frequency of wildfires, and clearcut and salvage logging events and their respective component disturbances (no. fires, clearcut and salvage logging) on 22 key soil measures across a multi-decadal chronosequence in Mountain Ash forests. Specifically, in this chapter, I compared measures of organic carbon, macronutrients, micronutrients, soil pH and other compositional properties across two depths of forest soils (0-10 cm and 20-30 cm) in disturbed sites, relative to long-undisturbed sites to gauge temporal disturbance impacts.

Chapter 3 entitled *Fire and logging regimes alter functional communities of fungi*, follows a similar structure to chapter one, but is focussed on fungal communities. This chapter asks two questions: 1. What is the effect of the number of fires on fungal community composition and functional groups of fungi? and, 2. What is the effect of clearcut and post-fire salvage logging on fungal community composition and functional groups of fungi? Here I compared the impacts of nine different disturbance histories and their respective component disturbances (no. fires, clearcut and salvage logging) on the richness and abundance of functional groups of fungi (symbiotrophic, saprotrophic and pathotrophic) and fungal community composition. These data were collected using DNA and RNA metabarcoding across two depths of forest soils and a multi-decadal chronosequence in Mountain Ash forests.

Chapter 4 entitled *Wildfires and logging alter a forest soil microbiome*, asks two important questions: 1. What is the impact of the number of fires and clearcut and salvage logging on the community composition and diversity of the Mountain Ash forest soil microbiome? and, 2. What are the key drivers of changes in the composition and diversity of microbial communities post-disturbance in these forests? Here, using DNA metabarcoding, I described the highly-diverse Mountain Ash forest soil microbiome for the first time. Further, I compared the impacts of different disturbance histories and their respective component disturbances (no. fires, clearcut and salvage logging) on the community composition and

diversity of individual microbial communities (fungi, archaea, bacteria) across two depths of forest soil (0-10 cm and 20-30 cm). In this chapter, I also identified key environmental and edaphic soil drivers of the composition of microbial communities post-disturbance.

Chapter 5 entitled *Direct and indirect disturbance impacts in forests*, uses structural equation modelling to compare the relative impacts of component disturbances (no. fires, clearcut and salvage logging) on above-ground plant communities and below-ground soil properties and microbial communities, across a multi-decadal chronosequence in Mountain Ash forests. This chapter also identifies direct and indirect, cascading disturbance impacts through multi-trophic interactions which mediate disturbance impacts throughout whole forest ecosystems.

Understanding above and below-ground disturbance responses, and the mechanisms which underpin them, is an integral part of preserving the functional integrity of forests. This knowledge provides for a multi-faceted approach to land-management, which traditionally has been biased toward above-ground biodiversity.

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Chapter 1

Logging and fire regimes alter plant communities

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Abstract

Disturbances are key drivers of plant community composition, structure and function. Plant functional traits, including life forms and reproductive strategies are critical to the resilience and resistance of plant communities in the event of disturbance. Climate change and increasing anthropogenic disturbance are altering natural disturbance regimes, globally. When these regimes shift beyond the adaptive resilience of plant functional traits, local populations and ecosystem functions can become compromised. We tested the influence of multiple disturbances, of varying intensity and frequency, on the composition and abundance of vascular plant communities and their respective functional traits (life forms and reproductive strategies) in the wet sclerophyll, Mountain Ash *Eucalyptus regnans* forests of south-eastern Australia. Specifically, we quantified the effect of the type and number of disturbances (including fires, clearcut logging and salvage logging) on plant community composition. We found that clearcut and salvage logging and the number of fires significantly influenced plant community composition and functional traits. Specifically, multiple fires resulted in lower populations of species that depend on on-site seeding for persistence. This includes the common tree species, *Eucalyptus regnans*, *Pomaderris aspera* and *Acacia dealbata*. In contrast, clearcut and salvage logged sites supported abundant on-site seeder species. However, species that depend on resprouting by surviving individuals, such as common and keystone ‘tree ferns’ *Dicksonia antarctica* and *Cyathea australis* declined significantly. Our data have important implications for understanding the relationship between altered disturbance regimes and plant communities and the respective effects on ecosystem function. In a period of rapid global environmental change, with disturbances predicted to increase and intensify, it is critical to address the impact of altered disturbance regimes on biodiversity.

Keywords: *disturbance regimes, wildfire, plant functional traits, post-disturbance, clearcut logging, species composition, Eucalyptus regnans*

Introduction

Disturbances are key drivers of the composition and function of ecosystems worldwide (Bowman *et al.*, 2009; Siedl *et al.*, 2014a; Fraver *et al.*, 2017). Fire is a major form of natural disturbance and it can influence many ecological patterns and processes including biogeochemical cycles, climate, plant composition, and functional diversity (Westerling and Bryant, 2008; Bowman *et al.*, 2009; Bowman *et al.*, 2011; Sitters *et al.*, 2016).

Species are adapted to specific fire and disturbance regimes that occur within ecosystems (Keeley, 2009; Siedl *et al.*, 2014a). When these regimes exhibit novel intensities and frequencies of disturbance events, or are altered beyond adaptive mechanisms, several key properties can be compromised including, (1) ‘resilience’ (the ability of an ecosystem to return to its original (pre-disturbance) state post-disturbance), and (2) ‘resistance’ (the ability of an ecosystem to maintain its original (pre-disturbance) state in the face of disturbance). Changes to these properties can fundamentally modify the environmental conditions required for habitat suitability and species persistence (Diaz and Cabido, 2001; Cochrane and Laurance, 2008; Bowman *et al.*, 2009; Siedl *et al.*, 2014b; Lindenmayer *et al.*, 2016).

In recent decades, large-scale, high severity fires and anthropogenic disturbances have increased across terrestrial ecosystems worldwide (Hooper *et al.*, 2005; Cochrane and Laurance, 2008; Bowman *et al.*, 2009; Siedl *et al.*, 2014a; Lindenmayer *et al.*, 2017). Key examples include, the impacts of novel fire regimes and logging that now characterise disturbance patterns in the Pacific north-western forests of the USA (Odion *et al.*, 2004; Thompson *et al.*, 2007), Amazonian rainforests (Cochrane and Laurance, 2008) and south-eastern Australian wet sclerophyll forests (Lindenmayer *et al.*, 2011; Taylor *et al.*, 2014). Changing climatic conditions are predicted to increase dry and hot conditions in many parts of the world, which would amplify and further alter these disturbance regimes (Siedl *et al.*, 2014a; Thom and Seidl, 2016). In a period of rapid global environmental change, it is critical to examine the impact of changing disturbance regimes on biodiversity (Bowman *et al.*, 2011).

Plant populations are influenced by climate (Levine and Rees, 2004; Westerling and Bryant, 2008), natural disturbance (Lloret and Zedler, 2009), human-accelerated environmental change (Likens, 1991; Ribeiro-neto *et al.*, 2016) or a combination of these (Lindenmayer *et al.*, 2011). Plant functional traits such as physiological adaptations and reproductive strategies are critical to plant species persistence under the prevailing disturbance regime (McIntyre and

Lavorel, 1999; Johnstone *et al.*, 2016). These structural and functional traits are an important ecological tool for determining how plant communities respond to disturbance and the respective effect on ecosystem function (Noble and Slatyer, 1980; McIntyre and Lavorel, 1999; Cornelissen *et al.*, 2003; Sitters *et al.*, 2016). They also can act as surrogates for physiological functional patterns that are often impractical to measure (McIntyre and Lavorel, 1999; Diaz and Cabido, 2001). Plant communities and natural disturbances such as fire interact and influence the dynamics of one another (Cochrane and Laurance, 2008). For example, post-disturbance, early seral environments can be more susceptible to high severity fire, which in turn, increases early successional, fire-prone vegetation and suppresses the return of mature composition and structure (Thompson *et al.*, 2007; Cochrane and Laurance, 2008; Taylor *et al.*, 2014). This can drive positive feedback loops leading to increased fire frequency and severity (Thompson *et al.*, 2007; Cochrane and Laurance, 2008). It has been proposed that additional disturbances such as clearcut logging (Thompson *et al.*, 2007; Cochrane and Laurance, 2008; Lindenmayer *et al.*, 2011) and altered climatic conditions (Westerling and Bryant, 2008; Bowman *et al.*, 2009) can intensify these positive feedback loops and shift ecosystems into functionally compromised states (Lindenmayer *et al.*, 2016).

Changes in natural disturbance regimes can alter plant population dynamics and trigger declines in common and keystone species (Walker, 1995; Diaz and Cabido, 2001; Brigham and Schwartz, 2003; Rodrigo *et al.*, 2004; Hooper *et al.*, 2005; Honnay and Jacquemyn, 2006; Ribeiro-neto *et al.*, 2016). The implications of these changes can extend beyond individual species and impact ecological function and resilience (Lawton, 1994; Walker, 1995; Ough and Murphy, 2004; Cochrane and Laurance, 2008). Determining the response of plant communities to changing disturbance regimes is therefore fundamental for environmental conservation, planning and management (Pickett and White, 1985; Stevens-Rumann and Morgan, 2016). While the effects of altered disturbance regimes are described for some ecosystems (Hessburg *et al.*, 2005; Donato *et al.*, 2009), relatively few studies have examined the synergistic effects of altered disturbance regimes on plant communities and their respective functional traits (Thuiller *et al.*, 2004; Bowman *et al.*, 2009; Osazuwa-Peters *et al.*, 2015).

We quantified the disturbance responses of vascular plant communities in south-eastern Australian wet sclerophyll, Mountain Ash *Eucalyptus regnans* F.Muell. forests. These forests provide an ideal system to address key questions about the response of plant communities to disturbance regimes as they have a well-characterised and diverse disturbance history and

have been subject to more than 30 years of long-term ecological monitoring (Lindenmayer, 2009). To examine plant community responses, we gathered data in forests that had last been burnt in 1850, 1939, 1983 and 2009 and also forests that had experienced clearcut logging in 1980-85 and 2009-10, and salvage logging in 2009-10. We quantified plant species richness, abundance and respective functional traits (life forms and reproductive strategies) in forests subject to these different kinds of disturbance. This enabled us to address two important questions:

1. What is the effect of the number of fires on plant community composition and functional traits?

Floristic variation within forests can be strongly influenced by fire (Ough and Ross, 1992; Rodrigo *et al.*, 2004; Bowman *et al.*, 2009). Fire regimes in *Eucalyptus regnans* forests are characterized by infrequent, high-intensity fires which historically had a return period of 75-150 years (McCarthy *et al.*, 1999). We hypothesized that following fire within this fire return period, plant communities would follow the pattern of gradual succession described by the Initial Floristic Composition model (Elger, 1954; McCarthy *et al.*, 1999). The model describes shifts in dominant plant communities that are consistent with the initial, natural succession of wet sclerophyll forests (Elger, 1954; Noble and Slater 1980; Ashton and Attiwill 1994; Pulsford *et al.*, 2016). This can be partially explained by the resilience and availability of dominant plant propagules that persist post-fire (Lindenmayer and Laurance, 2016). Additionally, following this model, we predicted species richness would increase with multiple fires (Elger, 1954). We made this prediction based on the post-disturbance influx of early successional and ruderal herbaceous species that are largely absent from mature forests (Cochrane and Laurance, 2008; Donato *et al.*, 2009; Blair *et al.*, 2016).

We also hypothesized that the composition of plant communities would differ between sites rarely burnt (only once since 1850), and frequently burnt within a period substantially less than the historical fire return period (e.g., 70 years). This was largely because multiple fires within a short period have the potential to alter ecosystem function (Burns *et al.*, 2015). For example, biological legacies such as logs and large dead trees can be lost after multiple fires, subsequently influencing plant spatial dynamics, as forecast from trait-based disturbance models (Noble and Slater, 1980; Franklin *et al.*, 2000; Mason *et al.*, 2016; Siedl *et al.*, 2014b). Additionally, fire intervals must be sufficient to allow species to develop reproductive propagules. For example, when fire intervals are less than 25 years, *Eucalyptus*

regnans fails to attain sexual maturity and is displaced by *Acacia* species (Adams and Attiwill 1984; Lindenmayer, 2009). Therefore, with successive fires in the last 70~ years, we predicted the decline of species which are dependent on on-site seeding (low seed dispersal ability), especially those without persistent soil seed banks or rapid maturation.

2. What is the effect of clearcut and salvage logging on plant communities and functional traits and how does it differ from unlogged sites in similarly aged, burnt forest?

Some authors have argued that clearcut logging imitates the post-disturbance environment of high-severity fire (Attiwill, 1994). However, empirical evidence suggests this is not the case (Cochrane and Laurance, 2008; Lindenmayer *et al.*, 2011; Blair *et al.*, 2016). We hypothesised that sites subject to clearcut logging would support different plant communities compared to similarly aged, unlogged/burnt sites. Specifically, we predicted a reduced occurrence of species which are sensitive to mechanical disturbance. These include species which possess resprouting functional traits, such as ‘tree ferns’, midstory ‘trees’ and ‘ground ferns’ that occur in this ecosystem. This is because logging machinery can uproot and cause physical damage to resprouting structures and subsequently expose them to the high intensity, slash-burn that occurs after clearcutting (McIntyre *et al.* 1999; Ough and Murphy, 2004; Blair *et al.*, 2016).

We also hypothesized that plant communities within salvage logged sites and sites subject to multiples fires and clearcut logging, would be the most different in comparison to similarly-aged clearcut and unlogged/burnt sites. This is largely because these sites have experienced two successive, different disturbances relative to sites subject only to fire. Moreover, in the event of salvage logging, burned areas are subject to clearcut logging at a time when natural regeneration is just beginning to occur and young plants are vulnerable to disturbance (Lindenmayer and Ough, 2006). Such intense disturbances within a relatively short time interval would likely result in the reduction of plant species with particular functional traits such as those with on-site seed and resprouting propagules (McIntyre and Lavorel, 1999; Siedl *et al.*, 2014b).

Our study addresses the ecological outcomes of changes in climate (fire) and anthropogenic (logging) disturbance regimes that are also characterizing many other forest ecosystems worldwide.

Methods

Site description

We conducted this study in the *Eucalyptus regnans* forests of the Victorian Central Highlands, 80-100 km north-east of Melbourne, in south-eastern Australia (Figure 1). These forests occur at altitudes ranging from 150 to 1100 m and experience consistent high rainfall, receiving on average between 600 and 2000 mm annually (Blair *et al.*, 2016; Keenan and Nitschke, 2016). The typical climate of the region is defined by cool summers and mild, humid winters, with occasional periods of snow (Mackey *et al.*, 2002; Burns *et al.*, 2015). However, periodic hot and dry summers and infrequent wildfires also occur and the frequencies of both have increased over time (CSIRO, 2010; Taylor *et al.*, 2014).

Eucalyptus regnans forests are characterized by tall eucalypt overstory trees, scattered understory trees, broad-leaved shrubs and a moist ground layer rich in fern species (Ough 2001; Burns *et al.*, 2015). The world's tallest flowering plant, *Eucalyptus regnans*, dominates these forests. *Eucalyptus obliqua* LHer. (Messmate), *Eucalyptus cypellocarpa* LAS. Johnson (Mountain Grey Gum), *Eucalyptus viminalis* Labill. (Manna Gum), *Eucalyptus nitens* Deane & Maiden (Shining Gum), and *Eucalyptus delegatensis* RT. Baker. (Alpine Ash) may also be present (Flint and Fagg, 2007; Burns *et al.*, 2015; Victorian State Government, 2014). *Acacia* species such as *Acacia dealbata* Link., *Acacia frigescens* J. H. Willis, and *Acacia obliquinervia* Tindale, Contr. dominate the midstory (Adams and Attiwill, 1984; Lindenmayer, 2009). Common understory species include; *Correa lawrenceana* Hook., *Prostanthera lasianthos* Labill., *Olearia argophylla* Labill., *Pomaderris aspera* Sieber., *Coprosma quadrifida* Labill., *Pimelea axiflora* F Muell., *Bedfordia arborescens* Hochr. and tree ferns *Dicksonia antarctica* Labill. and *Cyathea australis* R.Br. (Ough and Murphy 2004; Flint and Fagg 2007; Blair *et al.*, 2016).

The edaphic environment of *Eucalyptus regnans* forests is characterised by well-drained, deep and nutrient-rich soils that primarily consist of dermosols derived from Ordovician and Devonian sediments, extrusives, granitic rocks and alluvium (McKenzie *et al.*, 2004; Burns *et al.*, 2015).

Disturbance history

Approximately 157 000 ha of the Central Highlands support *Eucalyptus regnans* forests. Of this, 20% is in closed water catchments and National Parks and 80% in State forests, which consist of large areas designated for timber and pulp production (Langford, 1976; Burns *et al.* 2015). Large stand-replacing fires in *Eucalyptus regnans* forests have historically had an average return interval of 75-150 years (McCarthy *et al.*, 1999). However, over the past decadal, these forests have experienced major fires in 1926, 1932, 1939, 1983 and most recently in 2009 (Lindenmayer *et al.*, 2011; Turner *et al.*, 2011). In 1939, more than 70% of these forests were burnt and many were subsequently salvage logged until the 1960s (Lindenmayer and Franklin, 1997; Lindenmayer and Ough, 2006). Because *Eucalyptus regnans* is an obligate seeder, forests regenerating after large fires, such as those in 1939, have resulted in landscapes with relatively homogenous-aged regrowth (Figure 2). This dominant age cohort is now the primary resource for the logging industry (Florence, 1996; Lutze *et al.*, 1999). The 2009 fires burnt 78 300 ha of *Eucalyptus regnans* forest, with a large proportion of the burned area being the 70 year old forest which regenerated after the 1939 fires. The 70 year old dead trees resulting from this fire were generally too small to form hollows and the majority of older hollow-bearing trees that pre-dated the fires, were lost (Lindenmayer *et al.*, 2012; Burns *et al.*, 2015). The result has been young, dense, fire-prone regrowth with limited structural diversity (Figure 3.) (Lindenmayer *et al.*, 2009; Taylor *et al.*, 2014). Less common, low intensity fires are not severe enough to kill overstory trees, but trigger a new cohort of regeneration producing mixed-age heterogenous forests (Lindenmayer *et al.*, 1999; Burns *et al.*, 2015).

In the early 1960s, clearcut logging replaced the less intensive, selection logging as the primary silvicultural system in Victorian wet sclerophyll forests (Florence 1996; Lindenmayer *et al.*, 2011; Turner *et al.*, 2011). Clearcutting is a practice where all trees are cut within a block of between 15-40 ha (Lutze *et al.*, 1999; Flint and Fagg, 2007; Lindenmayer *et al.*, 2011). The remaining debris or slash within a 'cutblock' is then burnt at high intensity and the cut over area is then aerially seeded with the dominant eucalypt species (Lutze *et al.*, 1999; Flint and Fagg, 2007; Lindenmayer *et al.*, 2011). Salvage logging is a form of clearcut logging that occurs usually within three years following high severity fire (Lindenmayer and Ough, 2006; Blair *et al.*, 2016). This practice emulates standard clearcut logging methods, with the exception that there is no slash burn if the regeneration from the initial wildfire is adequate (Blair *et al.*, 2016). In addition, in salvage logging, harvesting

occurs after fire, whereas in conventional clearcutting the sequence is reversed. That is, the forest is logged and then subsequently burned.

Study design

The design of our study was based on the diversity of disturbance histories and the respective availability of replicate sites. We selected nine disturbance types in total: five types experienced fire only and the remaining four types were clearcut or salvage logged. Fire only sites consisted of forests, long-undisturbed (unburnt since 1850), burnt once (1939 fire), twice (1939/1983 and 1939/2009) and three times (1939/1983/2009). Logged sites were those burnt in 1939 and clearcut in 1980-85 or, 2009-10 and salvage logged in 2009-10 after a second fire in 2009. In addition, sites which experienced multiple fires and clearcut logging were those burnt in 1939/1983 and clearcut in 2009-10. All sites were replicated 10 times with the exception of forests long-undisturbed (1850), burnt twice (1939/2009), and three times (1939/1983/2009) (Table 1). All fires were of high severity. However, given the ‘patchy’ nature of fire events, all sites were inspected prior to sampling to ensure consistent age structure, accounting for the potential variability in disturbance severity within each site type. In this study we define ‘twice burnt’ sites as those that had experienced two fires relative to our long-undisturbed sites. This differs from the North American use of ‘twice burnt’ that refers to a repeat fire early in succession which can produce dramatic ecological effects (Fontaine *et al.*, 2009).

Sites were characterised by a southerly aspect and were positioned away from ridges and gullies, which can provide a lot of the variation in disturbance regimes and recovery (Keeton *et al.*, 2004).

We sampled all 81 sites during the Australian summer of December 2016 – March 2017. Using 1 ha long-term monitoring and newly established plots, we measured quadrats of 25 m x 25 m at least 20 m away from the roadside to account for edge effects (Dupuch and Fortin, 2013). In each 625 m² quadrat we estimated the projective foliage cover (%) of each vascular plant species using the survey protocol and sample configurations developed by the Australian Department of the Environment, Land, Water and Planning (Victorian State Government, 2004). Projective foliage cover was used as a measure of species abundance, and is hereafter referred to as ‘abundance’.

Defining functional traits

We assigned all species into one of eleven life forms and one of nine reproductive categories (Appendix S1: table S1). These categorisations allowed us to examine potential trends in the occurrence and abundance of functional traits as per trait-based disturbance models (Noble and Slatyer, 1980; Blair *et al.*, 2016; Norman *et al.*, 2016; Sitters *et al.*, 2016). We assigned these categorisations based on field observation and literature reviews (Walsh and Entwisle, 1994, 1996, 1997; Costermans, 2009; Wood *et al.*, 2010; Bull and Stolfo, 2014). Life forms were: (1) ‘eucalypts’ (overstory), (2) ‘*Acacia*,’ (3) ‘trees’ (midstory), (4) ‘shrubs’, (5) ‘tree ferns’, (6) ‘ground ferns’, (7) ‘climbers’, (8) ‘graminoids’, (9) ‘epiphytes’, (10) ‘herbs’ and (11) ‘exotic’ (Blair *et al.*, 2016). ‘Tree ferns’ and ‘ground ferns’ were categorised into separate groups as tree ferns are structurally a midstory tree, differing in size and function from other fern species and midstory ‘trees’ (Blair *et al.*, 2016). Additionally, we separated ‘eucalypts’ and ‘*Acacia*’ species from other lifeform groups. This was because eucalypts (trees belonging to the *Eucalyptus* genus) are the dominant overstory species within these forests, whereas *Acacia* species dominate the midstory and have different ecological roles, such as nitrogen fixation (Blair *et al.*, 2016). In determining reproductive strategy groups, each species was characterised by their respective temporal dynamics (persistent (long-lived) or transitory (species which thrive in post-disturbance environments but do not usually persist beyond several years, otherwise known as ruderal species)) and reproductive mechanisms (wind-dispersed seed, sprout, on-site seed, on-site seed and sprout). These groups were: (1) ‘transitory, wind-dispersed seed’, (2) ‘transitory, on-site seed’, (3) ‘transitory, sprout’, (4) ‘persistent, wind-dispersed seed’, (5) ‘persistent, on-site seed’, (6) ‘persistent’, (7) ‘persistent, seed and sprout’, (8) ‘persistent, sprout’ and (9) ‘exotic’. ‘Persistent’ species were separated from other groups because they are not limited to one reproductive strategy (May and Attiwill, 2003; Blair *et al.*, 2016). Exotic species are not specifically a lifeform or reproductive strategy. However, as they are relatively uncommon, and primarily are transitory, herbaceous species such as, *Cirsium vulgare* (Savi.) we grouped them into a separate category.

Statistical analysis

We evaluated the influence of the number of fires and the effect of clearcut and salvage logging on the composition and abundance of plant communities and respective functional traits (reproductive strategies and life forms) using multivariate permutational analysis of variance (PERMANOVA) based on the Bray-Curtis resemblance matrix of square-root

transformed abundance data (Bray and Curtis, 1957; Anderson, 2001; Anderson *et al.*, 2013). PERMANOVA is routine testing of the simultaneous response of one or more variables to one or more factors in an analysis of variance (ANOVA) based on resemblances between measures using permutation methods (Anderson, 2001). All data for each analysis were square-root transformed to minimise the contributions of common taxa with consistently high abundance values (within each group) in relation to those rarer species with consistently lower abundance values (Clarke and Warwick, 2001). Significant terms were investigated using *posteriori* pair-wise comparisons with the PERMANOVA *t* statistic (Anderson *et al.*, 2013). A maximum of 999 permutations were used to obtain *p* values in each dataset. Analysis of similarity percentages (SIMPER) allowed us to identify species and functional groups which were responsible for 70% of the dissimilarity between the number of fires and similarly aged logged and unlogged/burnt sites respectively, as confirmed by the PERMANOVA (Clarke and Warwick, 2001).

In determining the effect of the number of fires on the abundance and composition of plant communities and respective functional traits, pairwise tests within each analysis were between fire only sites: '1850F' (0 fire), '39F' (1 fire), '39/83F' (2 fires), '39/09F' (2 fires), and '39/83/09F' (3 fires). When determining the effect of similarly aged logged and unlogged/burnt sites within each analysis, pairwise comparisons were made between sites last burnt in 2009 ('39/09F'; '39/83/09F') and those clearcut/salvage logged in 2009-10 ('09CC'; '09SL'; '83F/09CC') and between sites last burnt in 1983 ('39/83F') and clearcut in 1980-85 ('80CC').

Additionally, a non-parametric Kruskal-Wallis H test was used to determine differences in species richness between different number of fires, and between similarly aged clearcut and unlogged/burnt sites, respectively.

Application of PERMANOVA, and SIMPER were conducted in the PRIMER program version 5 and 7 (Primer-E Ltd. Plymouth, UK) (Clarke, 1993; Clarke and Gorley, 2015). The Kruskal-Wallis H test was employed using IBM SPSS Statistical software (IBM Corp. SPSS, Armonk, NY).

Results

Species richness

We identified 121 species across 81 sites within nine disturbance types (Appendix S1: table S1). The most species-rich reproductive functional groups were: ‘persistent’ (31 species total) and ‘persistent, sprout’ (28 species total); and the most species-rich life forms were: ‘herb’ (31 species total) and ‘shrub’ (28 species total) (Appendix S1: table S2). Mean species richness differed between the nine disturbance types ($p < 0.05$). Sites burnt twice (‘39/09F’) had the highest mean species richness (28 ± 3.6 species/site; mean $\pm$ standard deviation, SD), followed by clearcut (‘09CC’) sites (27 ± 8.0). Long-undisturbed (‘1850F’) sites supported the lowest number of species (15 ± 5.2) (Figure 4).

What is the effect of the number of fires on the abundance and composition of plant communities?

The number of fires that occurred at each site influenced plant composition and abundance (*Pseudo F*=4.57; $p=0.001$). With the exception of pairwise tests between sites burnt once (‘39F’) and twice (‘39/83F’)(Average dissimilarity (Av.dis.) = 58.02; $t=1.20$; $p=0.189$), the composition and abundance of plant species within all fire only sites were significantly different from one another ($p < 0.05$). Similarly aged sites burnt twice (‘39/09F’) and three times (‘39/83/09F’) respectively, were significantly different from one another ($p < 0.05$). In addition, sites that were both burnt twice, (‘39/09F’) and (‘39/83F’) also were significantly different from one another ($p < 0.05$)(Table 2).

Twenty-two species explained 70% of the dissimilarity in plant composition and abundance between fire only sites (Appendix S1: table S3). Of these species, *Olearia argophylla*, *Pomaderris aspera*, *Dicksonia antarctica*, *Eucalyptus regnans*, *Bedfordia arborescens*, *Polystichum proliferum* R. Br., *Cyathea australis*, *Tetrarrhena juncea* R. Br., *Blechnum watsii* Tindale. and *Correa lawrenceana* consistently contributed the most to these differences. The mean abundance of common species *Eucalyptus regnans*, *Dicksonia antarctica* and *Blechnum watsii* decreased in sites burnt twice (‘39/83F’; ‘39/09F’), and three times (‘39/83/09F’), relative to sites burnt once (‘39F’). In contrast, *Pomaderris aspera*, *Olearia argophylla*, *Polystichum proliferum* and *Bedfordia arborescens* increased across this comparison. Furthermore, in sites burnt three times (‘39/83/09F’), the mean abundance of ‘persistent, on-site-seed’ species such as *Pomaderris aspera* and *Acacia dealbata* decreased,

whereas ‘persistent, resprout’ species such as *Olearia argophylla* and *Bedfordia arborescens* increased in comparison to those burnt once (‘39F’)(Table 3).

How does the number of fires influence plant functional traits?

Reproductive strategies

The composition and abundance of reproductive functional groups differed with the number of fires that occurred at each site (*Pseudo F*=4.25; *p*=0.001). However, pairwise tests between sites burnt once (‘39F’) and twice (‘39/83F’) and between long-undisturbed (‘1850F’) sites and sites burnt once (‘39F’) and twice (‘39/83F’ and ‘39/09F’) indicated the composition and abundance of these functional groups were not significantly different from one another (*p*>0.05) (Table 4). ‘Persistent, on-site seed’, ‘persistent, on-site seed and sprout’, ‘persistent’, ‘persistent, sprout’ and ‘persistent, wind-dispersed’ functional groups explained 70% of the differences between sites (Appendix S1: table S4). ‘1850F’ sites supported the highest mean abundance of ‘persistent, sprout’ and a low mean abundance of ‘persistent, on-site seed’ species. Sites burnt three times (‘39/83/09F’) had the lowest mean abundance of ‘persistent, on-site seed’ species, ‘persistent’ and ‘persistent, on-site seed and sprout’ species. In contrast, sites burnt twice (‘39/83F’) had the highest mean abundance of ‘persistent, on-site seed’ and ‘persistent on-site seed and sprout’ species (Figure 5).

Life forms

The composition and abundance of life forms differed with the number of fires that occurred at each site (*Pseudo F*=2.91; *p*=0.001). However, the composition and abundance of life forms in long-undisturbed (‘1850F’) sites did not significantly differ from other fire only sites (*p*>0.05). Furthermore, sites burnt once (‘39F’) and twice (‘39/83F’) were also not significantly different from one another (Table 5). ‘Tree’, ‘Acacia’, ‘ground fern’, ‘eucalypt’, ‘graminoid’, ‘shrub’ and ‘tree fern’ species explained 70% of the dissimilarity between sites (Appendix S1: table S5). Long-undisturbed (‘1850F’) sites had the lowest mean abundance of life forms: ‘Acacia’ and ‘shrub’ species, but had a high mean abundance of ‘ground ferns’ and ‘trees’. Sites burnt once (‘39F’) and twice (‘39/83F’) had the greatest mean abundance of ‘tree ferns’, ‘Acacia’ and ‘eucalypt’ life forms. In contrast, sites burnt three times (‘39/83/09F’) had a low mean abundance of ‘eucalypt’, ‘Acacia’ and ‘graminoid’ species. ‘Herb’ and ‘graminoid’ species were the most abundant in sites burnt twice (‘39/09F’) (Figure 6). ‘Epiphytes’ were the most abundant in long-undisturbed (‘1850F’) sites.

What is the effect of clearcut logging in comparison to similarly aged unlogged/burnt forest?

Plant species composition and abundance differed between similarly aged unlogged/burnt and logged sites (*Pseudo F*= 6.59; *p*=0.001) (Table 6). Salvage logged ('09SL') and sites burnt three times ('39/83/09F') were the most different from one another (Av.dis.=82.03; *t*=3.93; *p*=0.002). This trend was followed in pairwise tests between clearcut sites ('09CC') and sites burnt three times ('39/83/09F')(Av. dis. = 86.57; *t*=3.50; *p*=0.001); and sites burnt twice and clearcut ('83F/09CC') and sites burnt three times ('39/83/09F')(Av. dis. =83.70; *t*= 3.35; *p*=0.001). Similarly aged sites burnt twice ('39/83F') and clearcut ('80CC') had the lowest dissimilarity and *t* value of all pairwise tests but also differed significantly in species composition and abundance (Av. dis.=61.57; *t*=1.68; *p*=0.003).

Twenty-nine species explained 70% of the dissimilarity in plant composition and abundance between similarly aged logged and unlogged/burnt sites (Appendix S1: table S6). Of these species, *Pomaderris aspera*, *Eucalyptus regnans*, *Acacia dealbata*, *Olearia argophylla*, *Tetrarrhena juncea*, *Acacia obliquinervia*, *Polystichum proliferum*, *Bedfordia arborescens*, *Pteridium esculatum* and *Dicksonia antarctica* contributed the most to dissimilarity between site types. *Acacia dealbata* and *Acacia obliquinervia* were more abundant in logged sites, whereas 'persistent, resprout' species such as *Cyathea australis*, *Dicksonia antarctica*, *Olearia argophylla* and *Bedfordia arborescens* declined in comparison to similarly aged unlogged/burnt sites. Furthermore, salvage logged ('09SL') sites supported no common 'persistent, resprout' species: *Dicksonia antarctica*, *Polystichum proliferum* and *Olearia argophylla*, (Table 7).

How does clearcut logging influence plant functional traits?

Reproductive strategies

The mean abundance of reproductive functional groups differed between similarly aged unlogged/burnt and logged sites (*Pseudo F*=8.48; *p*=0.001). However, similarly aged logged sites ('83F/09CC'; '09CC'; '09SL') and, logged and unlogged/burnt sites ('80CC'; 39/83F') were not significantly different from one another (*p*>0.05) (Table 8). 'Persistent, sprout' and 'persistent, on-site seed' species were the highest contributors of dissimilarity across pairwise tests between similarly aged logged and unlogged/burnt sites (Appendix S1: table S7).

'Persistent, resprout' species declined and 'persistent, on-site seed species' increased in sites

logged in 2009 ('83F09CC'; '09SL'; '09CC'), relative to unlogged sites burnt in 2009 ('39/09F'; '39/83/09') (Figure 7/8).

Life forms

The composition and abundance of life forms differed significantly between similarly aged logged and unlogged/burnt sites (*Pseudo F*= 7.88; $p=0.001$). However, similarly aged logged sites ('83F/09CC'; '09CC') were not significantly different from one another ($p>0.05$). 'Acacia', 'ground fern', 'tree fern', 'tree', 'eucalypt', 'shrub' and 'graminoid' life forms contributed to 70% of the dissimilarity between sites (Appendix S1: table S8). 'Acacia' species were more abundant in clearcut and salvage logged sites in comparison to similarly aged unlogged/burnt sites. With the exception of sites clearcut in 1980-85('80CC'), sites clearcut in 2009('09CC'; '09SL'; '83F/09CC') supported a lower mean abundance of 'tree ferns' and 'ground ferns' than similarly aged unlogged/burnt forest. Salvage logged sites had the highest abundance of 'herb' and 'eucalypt' life forms. Sites logged in 2009-10('09CC') had the greatest abundance of *Acacia* species and the least of eucalypt species in comparison to other sites (Figure, 9).

Discussion

The relationship between disturbance and the composition of plant communities is often dynamic and complex (McIntyre and Lavorel, 1999; Pulsford *et al.*, 2016). Many plant species are highly tolerant of disturbance and are adapted to specific disturbance intensities and frequencies owing their resilience to functional traits such as physiological adaptations and reproductive strategies (McIntyre and Lavorel, 1999, Diaz and Cabido, 2001; Johnstone *et al.*, 2016). However, when the frequency, type or severity of disturbance shifts outside the capacity of the functional traits of local species, plant community composition and structure can be altered (Thompson *et al.*, 2007; Cochrane and Laurance, 2008; Blair *et al.*, 2016; Stevens-Rumman and Morgan, 2016). We found that clearcut and salvage logging and the respective number of fires influenced plant community composition, abundance and functional traits in the south-eastern Australian, *Eucalyptus regnans* forests. Specifically, species which produce and regenerate from on-site seed decreased with multiple fires and increased with clearcut and salvage logging (in 2009-10). Whereas species which resprout declined significantly in sites subject to clearcut and salvage logging (in 2009-10). Our

research has important implications for understanding the relationship between altered disturbance regimes and plant communities and the associated effects on ecosystem function.

All sites, apart from those long-undisturbed, were burnt in 1939. Therefore, 1939 regrowth acted as a comparative control in our analysis, whereas long-undisturbed forest acted as a reference and contributed to our understanding of succession in *Eucalyptus regnans* forests. Furthermore, in the analysis of clearcut and salvaged logged sites, similarly aged sites were compared to one another to account for successional effects (Kayes *et al.*, 2010). One constraint of this study is it did not examine the difference between low and high fire severities, which could potentially explain some of the variation in plant community composition within sites (Blair *et al.*, 2016).

The number of fires and plant community composition

We have demonstrated that the number of fires influenced the composition and abundance of plant communities and their respective functional traits. Consistent with our predictions, plant community composition and abundance in long-undisturbed sites was the most similar to sites burnt once in 1939, and followed the pattern of gradual succession described by the Initial Floristic Composition Model (Elger, 1954). Furthermore, following the model, species richness was the lowest in long-undisturbed sites and highest in sites burnt twice in 1939 and 2009. This can be explained by an increase in disturbance-adapted graminoid and herbaceous species, and the ground fern *Pteridium esculatum* post-disturbance in response to an influx in available resources and reduced competition (Kayes *et al.*, 2010; Blair *et al.*, 2016).

In contrast, the composition and abundance of plant communities in eight year old forest forests burnt twice and three times differed from other sites and from one another. This indicates that whilst succession (time since the most recent fire) is a major factor in determining plant community composition, the number of fires is also a key contributor, especially in the event of multiple fires. Similarly, North American forests (Thompson *et al.*, 2007; Stevens-Rumann and Morgan, 2016) and Amazonian forests (Cochrane and Laurance, 2009) have experienced changes in vegetation community structure and abundance after successive fires. These changes in vegetation communities can alter fire regimes and the risk of high severity fire in a variety of ways (Thompson *et al.*, 2007; Cochrane and Laurance, 2008; Stevens-Rumann and Morgan, 2016).

Consistent with our prediction at the outset of this investigation, the composition and abundance of plant functional traits, particularly reproductive strategies were influenced by

the number of fires. The most obvious trends were in eight year old forests burnt twice and three times respectively, where we observed declines in dominant on-site seeder species, *Eucalyptus regnans* and resprouting ‘tree ferns’, *Cyathea australis*, *Dicksonia antarctica*. However, sites burnt three times, had a higher abundance of other resprouting species including, *Olearia argophylla*, *Bedfordia arborescens* and *Polyschitum proliferum* relative to other sites. This reflects the resilience of resprouting reproductive propagules to fire, as found in North American forests (Donato *et al.* 2009; Lindenmayer and Laurance, 2016). In contrast, sites burnt three times had the lowest mean abundance of on-site seeder species, which translated to a decline in common species, *Eucalyptus regnans*, *Pomaderris aspera* and *Acacia dealbata*, and an absence in *Correa lawrenceana*. On-site seeder species are particularly sensitive to fire return intervals shorter than their maturation ages and this can result in local extinction (Adams and Attiwill 1984; Bowman *et al.*, 2014; Smith *et al.*, 2014). Furthermore, this group of species is vulnerable to recruitment failure and loss of pollinators and dispersers after disturbance (Smith *et al.*, 2014). It is therefore possible that these species declined and were absent as a result of fire return intervals or dispersal failure. However, as this study did not examine the temporal dynamics within each site, or pre-disturbance conditions, it is possible that these species did not previously occupy these sites. It is also possible that nearby populations of these species could re-colonise these sites if conditions are appropriate. Furthermore, in the short-term, it is unlikely that declines in these species would pose serious ecological threats in isolated sites, and may enhance landscape-scale diversity. However, in the long term, the decline of these species lends concern for ecological function, especially in the event of future fire and disturbance.

Plant functional traits, particularly in dominant and common species, confer ecosystem resilience and resistance (Walker, 1995; Diaz and Cabido, 2001; Johnstone *et al.*, 2016). Declines in these species can have flow on consequences if their functional roles are lost or reduced (Lawton, 1994; Walker, 1995; Ough and Murphy, 2004; Cochrane and Laurance, 2008). As an example, the decline and absence of species such as *Acacia* species can have impacts on ecosystem function. *Acacia* species are known for their ability to fix nitrogen, which is particularly important post disturbance (May and Attiwill, 2003; Ma *et al.*, 2015). Furthermore, declines in common tree species, *Eucalyptus regnans*, *Pomaderris aspera* and *Acacia* species can result in a shift in forest structure and dominance, leading to potentially devastating effects on ecosystem function (Elger, 1954; Cochrane and Laurance, 2008; Lindenmayer *et al.*, 2011). These effects include changes to the availability of food and

complex habitat for biodiversity. For example, mature *Eucalyptus* species develop hollows from ~120+ years of age which provide for hollow-dependent mammals such as the Critically Endangered Leadbeater's possum (*Gymnobelideus leadbeateri*) and the vulnerable Greater glider (*Petauroides volans*) in *Eucalyptus regnans* forests (Lindenmayer *et al.*, 2013).

Clearcut logging and plant community composition

Our study provides evidence that clearcut logging does not mimic the post-disturbance environment of high severity fire. Forest clearcut, salvage logged in 2009-10 and similarly aged, unlogged, sites burnt twice and three times consistently differed from one another. In sites clearcut and salvaged logged in 2009-10, common and keystone resprouting species including *Cyathea australis*, *Dicksonia antarctica*, *Olearia argophylla* and *Bedfordia arborescens* declined significantly, whereas on-site seeder species such as *Acacia dealbata* increased (Figure 8). Resprouting species possess resprouting organs (lignotubers, rhizomes, non-woody tubers, etc.) which, whilst being resilient to fire, are sensitive to the mechanical disturbances associated with clearcut logging (Keith *et al.*, 2007; Ough and Murphy, 2004; Blair *et al.*, 2016). Furthermore, earth-moving machinery used in clearcutting operations can compact soil, displace soil seed banks and kill, damage and expose resprouting organs (Rab, 1996; Wienk, 2004; Ough and Murphy 2004; Parro *et al.*, 2015). Our findings are consistent with previous research which has identified declines in resprouting species such as 'tree ferns' following logging (Mueck and Peacock, 1992; Hickey, 1994; Ough, 2001; Ough and Murphy, 2004; Blair *et al.* 2016). Ough and Murphy (2004) found only 16% of 2391 tree ferns remained alive one year after clearcutting in Australian wet sclerophyll forests, with only 5% remaining upright. Resprouting species, such as tree ferns and broad-leaf shrubs, cast shadows on the forest floor, which influence the microclimate (Wood *et al.*, 2010; Taylor *et al.*, 2014). Furthermore, tree ferns including *Dicksonia antarctica* and *Cyathea australis*, provide substrates for epiphytic species, including rare and vulnerable plant taxa (Ough and Murphy, 2004). Changes in the abundance of these species will increase light and the temperatures experienced by the understory, favoring some species over others (Wienk *et al.*, 2004; Penman *et al.*, 2008).

The high mean abundance of *Eucalyptus regnans* in most clearcut and salvage logged sites (in 2009) is most likely to be a result of post-logging aerial seeding (VicForests, 2016). However, inconsistent with predictions we made at the outset of this investigation, the relative mean abundance of *Eucalyptus regnans* was much lower than expected in some recently clearcut sites which were dominated by *Acacia* species. We suspect re-seeding

attempts have failed in some of these sites. If eucalypt stocking rates are not achieved after the initial slash-burn post-logging, ‘cut-blocks’ can be mechanically re-disturbed and re-sewn to ensure a homogenous stand for future timber harvesting (VicForests, 2014).

The impacts of clearcut and salvage logging on biological legacies can explain the patterns we observed in plant communities (Lindenmayer *et al.*, 2008). All natural disturbances leave behind biological legacies. In the case of plant species, these biological legacies can include live and dead trees, and seeds which facilitate regeneration post-disturbance (Franklin *et al.*, 2000; Lindenmayer *et al.*, 2017). These enhance the recovery and resilience of forest ecosystems (Siedl *et al.*, 2014b). For example, biological legacies provide structural complexity which generates regeneration niches for shade-tolerant species (Keith *et al.*, 2007; Siedl *et al.*, 2014b). However, in the event of clearcut and salvage logging, few of these legacies remain (Lindenmayer *et al.*, 2008; Fraver *et al.*, 2017). Despite a long history of use in forested ecosystems, there is much debate surrounding clearcut and salvage logging practices (Lindenmayer and Ough, 2006; Lindenmayer *et al.*, 2008; Thompson *et al.*, 2007; Blair *et al.*, 2016; Parro *et al.*, 2015; Thorn *et al.*, 2017). Salvage logging in some ecosystems has had positive (Boucher *et al.*, 2014) or negative effects (Lindenmayer and Ough, 2006; Lindenmayer *et al.*, 2008; Thorn *et al.*, 2017) on long-term forest recovery. In our study, plant composition and abundance differed the most in sites salvage logged and those burnt twice and clearcut in comparison to similarly aged unlogged/burnt sites. These similarly aged logged sites were characterized by a low mean abundance of resprouting species relative to all other disturbance types. Furthermore, salvage logged sites contained no records of common species: *Polystichum proliferum*, *Olearia argophylla* and *Dicksonia antarctica*. The lack of biological legacies and subsequent exposure, and physical damage caused by logging machinery are thought to have played a major role in the absence of these integral species (Wienk *et al.*, 2004; Ough and Murphy, 2004). The intensity and lasting impact of these disturbances on microclimatic conditions suggests that it is unlikely that these species will re-occupy these sites in the near future (Ough and Murphy, 2004). Similarly, in North American forests, salvage logging has altered plant species composition (Thompson *et al.*, 2007; Parro *et al.*, 2015). Such shifts, especially in common and keystone species, may reduce ecosystem resistance and resilience, and can trigger ecosystem collapse and positive feedback loops (Ough and Murphy, 2004; Lindenmayer *et al.*, 2011; Belote *et al.*, 2012, Lindenmayer *et al.*, 2016).

Previous research in *Eucalyptus regnans* forests predicted species composition to rapidly return to that of pre-disturbance conditions after logging and fire (Attiwill, 1994; Ashton and Martin, 1996). However, we found that after 8 years, some common and keystone species had still not returned post-clearcut logging. We assume that these plant communities will take many years to recover. Sites clearcut and salvage logged in 2009-10 were dominated by *Acacia* and *Eucalyptus* species and had an understory consisting of species life forms that are more characteristic of drier environments including, ‘graminoids’, ‘herbs’ and ‘shrubs’ such as *Cassinia aculeata* Labill. Species and life forms that are more characteristic of wet-forest including ‘tree ferns’ and broad leaved shrubs and trees were consistently absent or had low populations following these disturbances, indicating a shift favoring drier and disturbance-tolerant species (Mueck and Peacock, 1992; Ough and Murphy 2004; Blair *et al.*, 2016). These changes in plant community composition could potentially influence the flammability and likelihood of high severity fire during a fire. Therefore, our findings provide evidence of ‘landscape trap’ theory, whereby successive fires, anthropogenic disturbance and climate change drive positive feedback loops between vegetation composition, structure and ecosystem function (Lindenmayer *et al.*, 2011; Hughes *et al.*, 2013). The already changing and intensifying disturbance regimes in North American forests and Amazonian forests could eventually produce similar positive feedback loops (Thompson *et al.*, 2007; Cochrane and Laurance, 2009; Bowman *et al.*, 2011; Lindenmayer *et al.*, 2011).

Implications for forest management and conservation

Our findings have important implications for forest management globally. We have found that plant community composition and abundance and their respective functional traits can be altered by clearcut and salvage logging and multiple fires within a 26-70 year interval. Similar changes in plant communities have occurred in other ecosystems around the world that have been affected by fire and clearcut logging (Thompson *et al.*, 2007; Cochrane and Laurance, 2008; Lindenmayer *et al.*, 2009). However, disturbance may sometimes enhance diversity in other landscapes that are subject to multiple disturbances if one disturbance type is not dominant, and historic landscape dynamics are considered (Hessburg, *et al.*, 2005; Donato *et al.*, 2009; Fontaine *et al.*, 2009).

Anthropogenic disturbances and climate change are driving large-scale changes to fire and disturbance regimes, globally (Brotons *et al.*, 2013; Hughes *et al.*, 2013; Siedl *et al.*, 2014b). As such, many ecosystems are thought to be at risk of substantial change or collapse (Sato

and Lindenmayer, 2017). The greatest challenge in addressing altered disturbance regimes is incorporating them into global governance and management (Hughes *et al.*, 2013). Given the changes in plant community composition as a result of altered disturbance regimes in south-eastern Australian *Eucalyptus regnans* forests, our results suggest land managers take a precautionary approach to ecological management and conservation. Furthermore, in a period of rapid, global environmental change, with disturbances predicted to increase and intensify, it is critical we mitigate the negative impacts of altered disturbance regimes on biodiversity (Hughes *et al.*, 2013). Our data indicates major interventions are needed in policy and land management practices to manage the threats associated with altered disturbance regimes (Bowman *et al.*, 2011; Siedl *et al.*, 2014b). These include conserving large areas of intact forest (>1000 ha) and reducing the rates of clearcut logging, particularly in sensitive locations and areas already subjected to prior disturbance (Lindenmayer *et al.*, 2011; Blair *et al.*, 2016). These patches provide invaluable refugia for biodiversity and are fundamental in providing source populations for the recolonization of disturbed sites (Lindenmayer *et al.*, 2011). Furthermore, we urge land managers to reconsider salvage logging operations to retain crucial biological legacies and plant functional traits, which will allow for the natural recovery of post-fire environments. Moreover, there is a need to incorporate the abundance and diversity of plant functional traits into ecosystem assessments and future empirical studies.

Acknowledgements

We thank the volunteers who assisted in data collection. Supporting funding was provided by The Australian National University and the Paddy Pallin Foundation. We thank editor Dr. Bradford Wilcox and the two anonymous reviewers for their comments, which improved the manuscript.

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Tables

Table 1. The disturbance history and number of replicate sites of each of the nine disturbance types. F= fire, CC= Clearcut, SL= Salvage logged.

	1850 Fire	1939 Fire	1983 Fire	2009 Fire	1980-85 Clearcut	2009-10 Clearcut	2009-10 Salvage	Number of sites
'1850F'	✓							4
'39F'		✓						10
'39/83F'		✓	✓					10
'39/09F'		✓		✓				11
'39/83/09F'		✓	✓	✓				6
'80CC'		✓			✓			10
'09CC'		✓				✓		10
'09SL'		✓		✓			✓	10
'83F/09CC'		✓	✓			✓		10

Table 2. Main and pairwise tests of multivariate permutational analysis of variance (PERMANOVA) of plant composition and abundance between fire only sites. Numbers in brackets in the first column specify the number of fires.

	Average dissimilarity (%)	T statistic	P value
1850F (0) vs 39/83/09F (3)	66.09	2.10	0.009
1850F (0) vs 39/09 F (2)	76.45	2.12	0.002
1850F (0) vs. 39F (1)	65.08	1.43	0.035
1850F (0) vs. 39/83F (2)	67.17	1.65	0.006
39F (1) vs. 39/83/09F (3)	65.94	2.49	0.002
39/83F (2) vs. 39/83/09F (3)	68.12	2.74	0.001
39/83F (2) vs. 39/09F (2)	70.4	2.45	0.001
39/83F (2) vs. 39F (1)	58.02	1.20	0.189
39/09F (2) vs. 39F (1)	71.82	2.51	0.001
39/09F (2) vs. 39/83/09F (3)	62.69	2.18	0.001

PERMANOVA: Pseudo F=4.57; p=0.001.

Table 3. Mean abundance of species which consistently contributed to dissimilarity between fire only sites. Numbers in brackets in the top row specify the number of fires.

	1850(0)	39F(1)	39/83F(2)	39/09F(2)	39/83/09F(3)
<i>Eucalyptus regnans</i>	13.4	20.13	14.63	9.07	5.88
<i>Olearia argophylla</i>	5.31	2.35	1.93	9.66	11.04
<i>Pomaderris aspera</i>	0.00	2.68	12.6	13.78	0.97
<i>Dicksonia antarctica</i>	10.94	11.23	10.14	2.66	5.8
<i>Blechnum wattsi</i>	16.06	6.63	6.28	0.02	0.00
<i>Tettrarrhena juncea</i>	7.82	8.33	3.91	8.92	0.1
<i>Cyathea australis</i>	0.19	6.32	12.58	1.63	2.74
<i>Polystichum proliferum</i>	0.00	1.03	1.25	0.02	0.00
<i>Bedfordia arborescens</i>	0.00	0.3	1.08	4.65	9.83
<i>Correa lawrenceana</i>	1.56	5.65	14.38	0.44	0.00

Table 4. Main, and pairwise tests of multivariate permutational analysis of variance (PERMANOVA) of the composition and abundance of reproductive strategies between fire only sites. Numbers in brackets specify the number of fires.

	Average dissimilarity (%)	T statistic	P value
39/09F (2) vs. 39/83/09F (3)	33.59	2.28	0.004
39/09F (2) vs. 39/83F (2)	33.28	2.20	0.001
39/09F (2) vs. 1850F (0)	34.34	1.52	0.065
39/09F (2) vs. 39F (1)	33.46	2.10	0.002
39/83/09F (3) vs. 39/83F (2)	38.43	3.26	0.001
39/83/09F (3) vs. 1850F (0)	32.50	1.69	0.03
39/83/09F (3) vs. 39F (1)	35.46	2.75	0.001
39/83F (2) vs. 1850F (0)	32.10	1.47	0.07
39/83F (2) vs. 39F (1)	27.32	1.24	0.178
1850F (0) vs. 39F (1)	32.71	1.44	0.086
PERMANOVA: Pseudo F= 4.25; p=0.001			

Table 5. Main and pairwise tests of multivariate permutational analysis of variance (PERMANOVA) of the composition and abundance of life forms between fire only sites. Numbers in brackets specify the number of fires.

	Average dissimilarity (%)	T statistic	P value
39/09F (2) vs. 39/83/09F (3)	34.74	1.89	0.004
39/09F (2) vs. 39/83F (2)	37.61	2.07	0.001
39/09F (2) vs. 1850F (0)	41.73	1.46	0.063
39/09F (2) vs. 39F (1)	38.35	2.0	0.001
39/83/09F (3) vs. 39/83F (2)	36	2.55	0.001
39/83/09 (3) vs. 1850F (0)	35.81	1.35	0.106
39/83/09 (3) vs. 39F (1)	33.16	1.95	0.001
39/83F (2) vs. 1850F (0)	36.42	1.08	0.32
39/83F (2) vs. 39F (1)	31.45	1.02	0.377
1850F (0) vs. 39F (1)	37.24	1.03	0.372

PERMANOVA: *Pseudo F*=2.91; p=0.001

Table 6. Main and pairwise tests of multivariate permutational analysis of variance (PERMANOVA) of vascular plant composition and abundance between similarly aged logged and unlogged/burnt sites using.

	Average dissimilarity (%)	T statistic	P value
39/83F vs. 80CC	61.57	1.68	0.003
39/09F vs. 09CC	73.677	2.39	0.001
39/09F vs. 39/83/09F	62.70	2.18	0.003
83F/09CC. vs. 39/09F	74.45	2.49	0.001
83F/09CC vs. 39/83/09F	83.70	3.35	0.001
83F/09CC vs. 09CC	70.16	1.94	0.001
83F/09CC vs. 09SL	68.28	2.26	0.001
09CC vs. 39/83/09F	86.57	3.5	0.001
09SL vs. 39/83/09F	82.03	3.93	0.002
09SL vs. 39/09F	69.44	2.55	0.001
09SL vs. 09CC	65.77	2.03	0.001

PERMANONA: *Pseudo F*= 6.59; p=0.001

Table 7. Mean abundance of species which consistently contributed to dissimilarity between similarly aged unlogged/burnt and logged sites.

	39/83F	80CC	39/09F	39/83/09F	09CC	83F/09CC	09SL
<i>Eucalyptus regnans</i>	14.6	12.4	9.1	5.9	3.3	16.9	32.0
<i>Pomaderris aspera</i>	12.6	1.9	13.8	1.0	8.6	22.8	2.5
<i>Acacia dealbata</i>	3.6	12.7	1.5	0.0	25.0	8.8	10.3
<i>Tetrarrhena juncea</i>	3.9	2.0	8.9	0.1	17.1	10.2	7.7
<i>Polystichum proliferum</i>	5.5	13.5	2.4	9.1	0.3	0.0	0.0
<i>Dicksonia antarctica</i>	10.1	7.7	2.7	5.8	0.2	0.7	0.0
<i>Olearia argophylla</i>	1.9	1.4	9.7	11.0	0.1	0.1	0.0
<i>Bedfordia arborescens</i>	1.08	0.0	4.6	9.83	0.0	0.0	0.13
<i>Acacia obliquinervia</i>	0.15	1.73	0.00	0.00	17.34	0.00	11.98
<i>Pteridium esculatum</i>	0.21	0.27	11.2	0.3	0.8	0.08	6.53

Table 8. Main and pairwise tests of multivariate permutational analysis of variance (PERMANOVA) of the composition and abundance of reproductive functional groups between similarly aged logged and unlogged/burnt sites.

	Average dissimilarity (%)	T statistic	P value
39/09F vs. 09CC	41.63	2.74	0.001
39/09F vs. 39/83/09F	33.58	2.28	0.004
39/09F vs. 83F/09CC	40.43	3.5	0.001
39/09F vs. 09SL	35.5	3.05	0.001
09CC vs. 39/83/09F	58.94	4.33	0.001
09CC vs. 83F/09CC	29.0	1.00	0.424
09CC vs. 09SL	29.44	1.25	0.155
39/83/09 vs. 83F/09CC	57.05	5.53	0.001
83F/09CC vs. 09SL	49.03	1.27	0.199
80CC vs. 39/83F	29.03	1.04	0.338
39/83/09F vs. 09SL	25.20	5.05	0.001

PERMANOVA: Pseudo F= 8.48; p=0.001

Table 9. Main and pairwise tests of multivariate permutational analysis of variance (PERMANOVA) of lifeform composition and abundance between similarly aged logged and unlogged/burnt sites.

	Average dissimilarity (%)	T statistic	P value
39/83F vs. 80CC	39	2.42	0.002
39/09F vs. 09CC	51.35	3.18	0.001
39/09F vs. 39/83/09F	34.74	1.89	0.002
09CC vs. 39/83/09F	57.21	3.82	0.001
83F/09CC vs. 39/83/09F	55.99	3.59	0.001
83F/09CC vs. 09SL	41.80	1.78	0.015
83F/09CC vs. 09CC	42.55	1.60	0.051
83F/09CC vs. 39/09F	47.48	2.60	0.001
09SL vs. 39/09F	47.88	3.15	0.001
09SL vs. 39/83/09F	54.91	4.14	0.001
09SL vs. 09CC	45.50	2.37	0.001
PERMANOVA: <i>Pseudo F</i> = 7.88; p=0.001			

Figures

Figure 1. Location of study sites within the south-eastern, Victorian Central Highlands in Australia, with respect to National Parks and reserves and State forest.

Figure 2. *Eucalyptus reganans* forest: 1939 fire regrowth (photographer: David Blair).

Figure 3. *Eucalyptus regnans* forest: 2009 fire and salvage logging regrowth.

Figure 4. Mean species richness across nine disturbance types, with standard errors.

Figure 5. Mean abundance of reproductive functional groups across fire only sites, with standard errors. Wind-disp. =wind-dispersed.

Figure 6. Mean abundance of life forms across fire only sites, with standard errors. G. fern= ground fern

Figure 7. Mean abundance of the most common functional groups across logged and unlogged/burnt sites, with standard errors. Open shapes indicate unlogged/burnt sites, and closed shapes indicate logged sites.

Figure 8. Mean abundance of persistent, on-site seed and persistent, sprout functional groups across similarly aged logged and unlogged/burnt sites, with standard error bars.

Figure 9. Mean abundance of life forms across similarly aged logged and unlogged/burnt sites, with standard error bars. Open shapes indicate unlogged/burnt sites, and closed shapes indicate logged sites, the 'x' is salvage logged sites. G. fern= Ground fern.

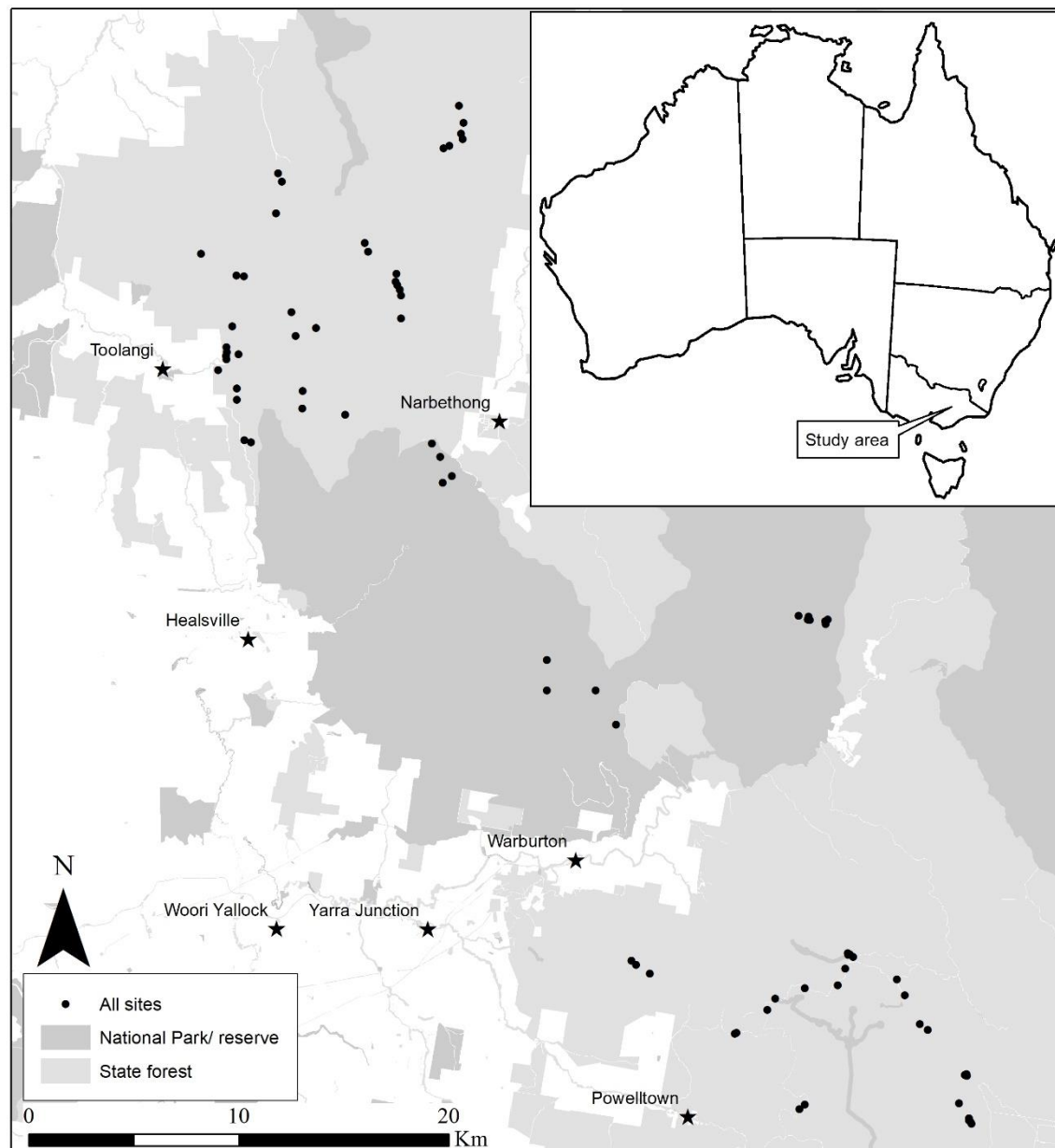


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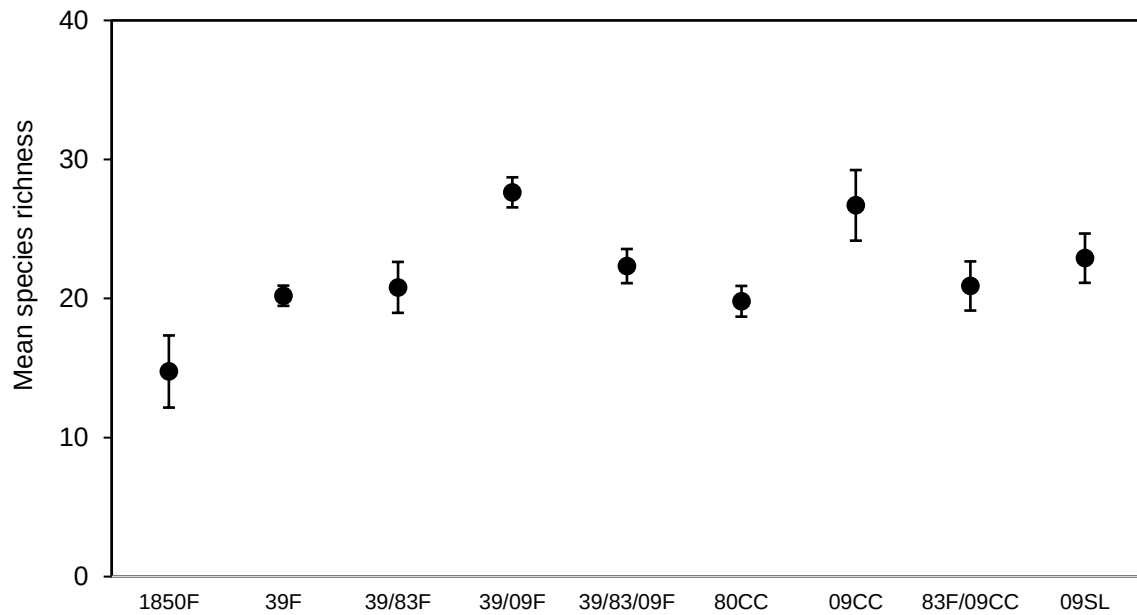


Figure 4. Mean species richness across nine disturbance types, with standard errors.

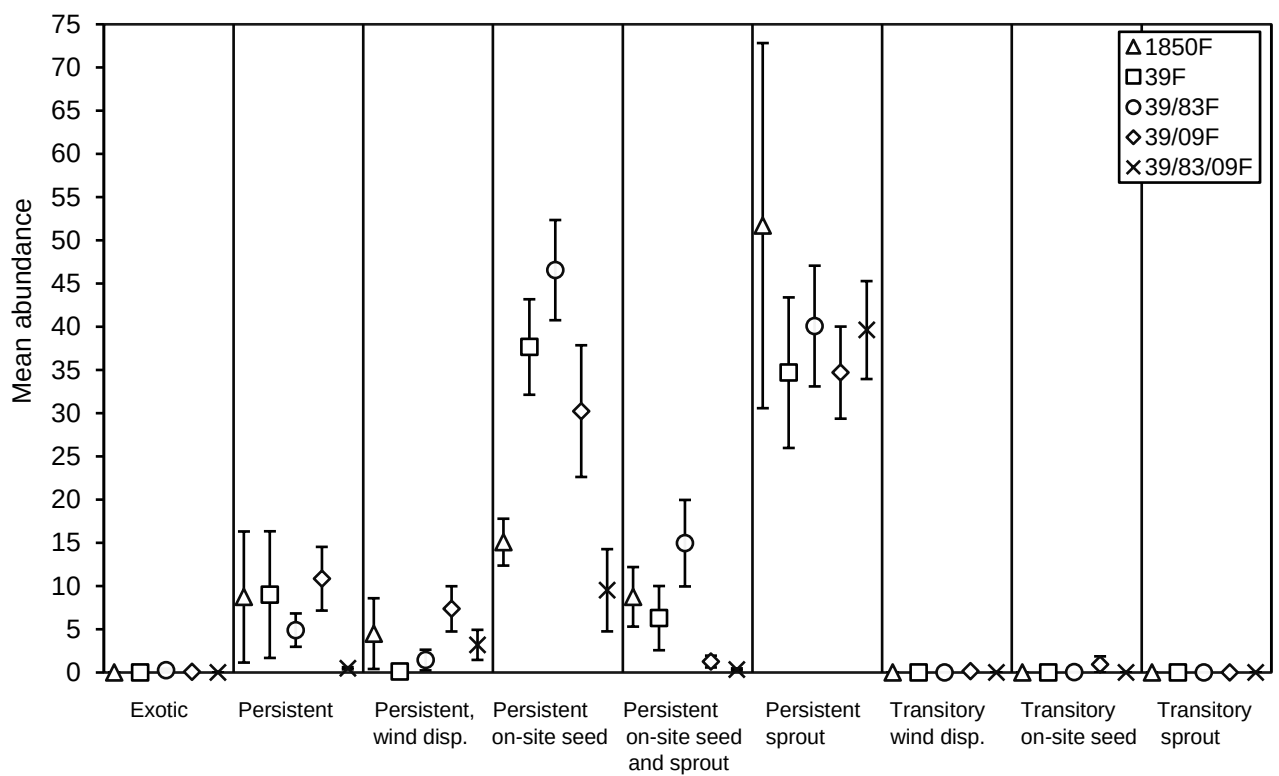


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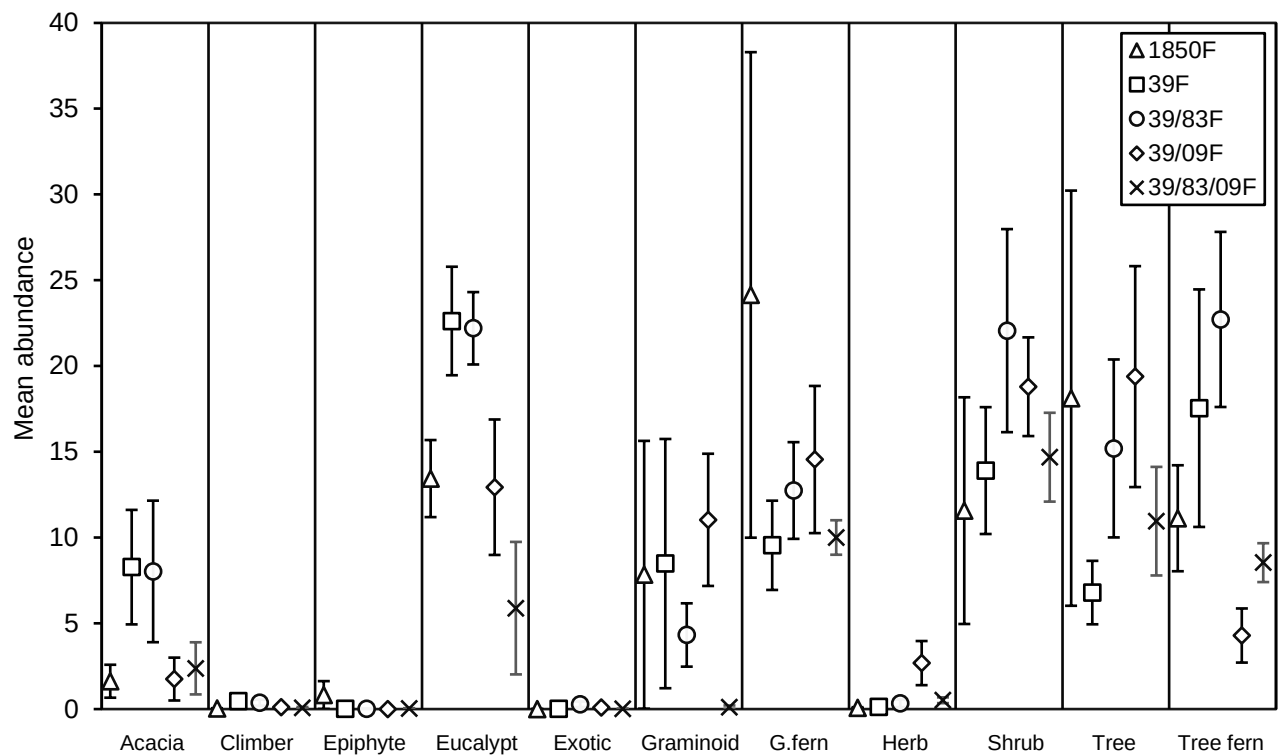


Figure 6. Mean abundance of life forms across fire only sites, with standard errors. G. fern= ground fern.

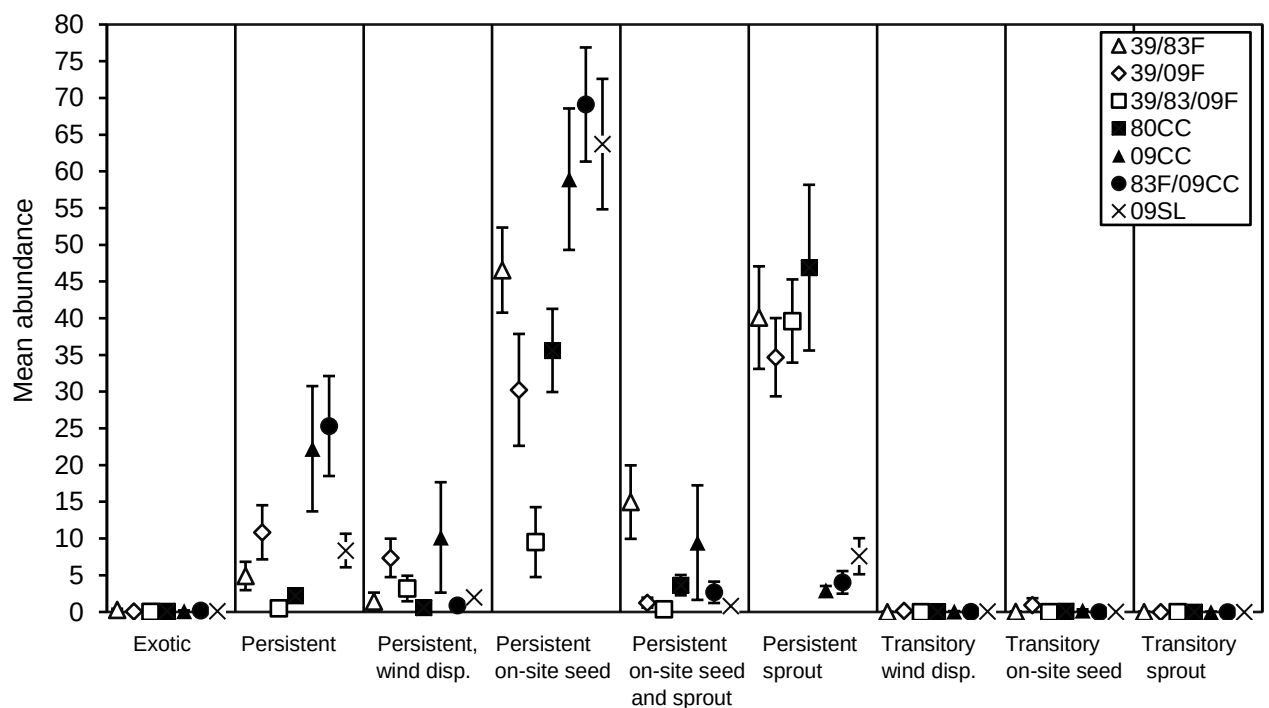


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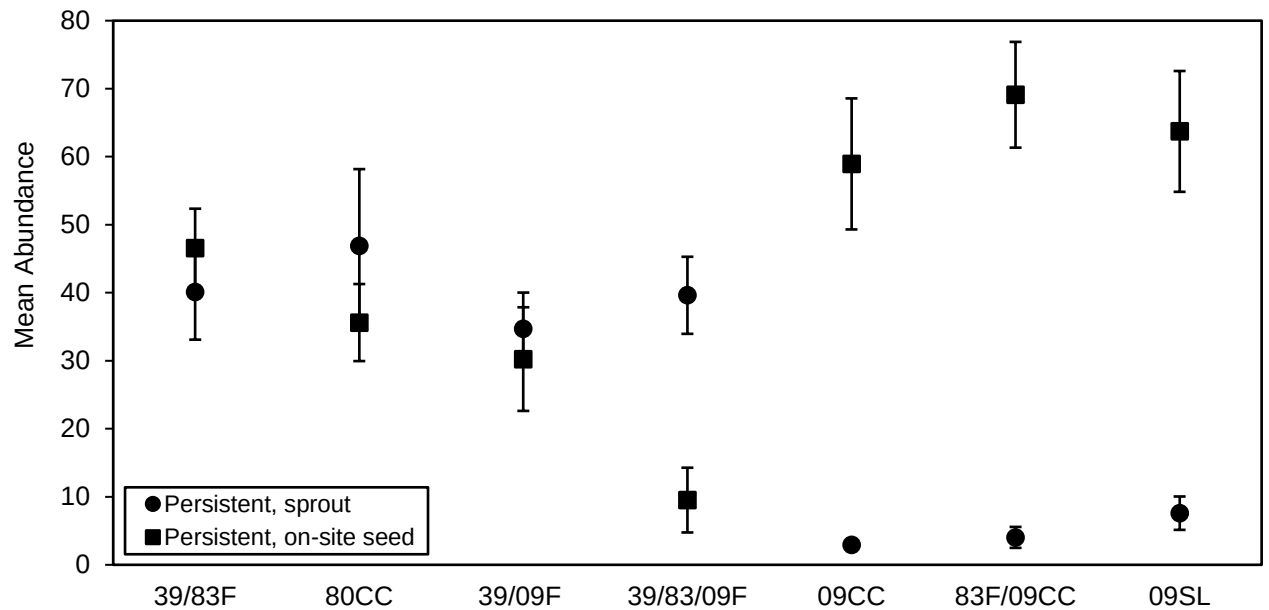


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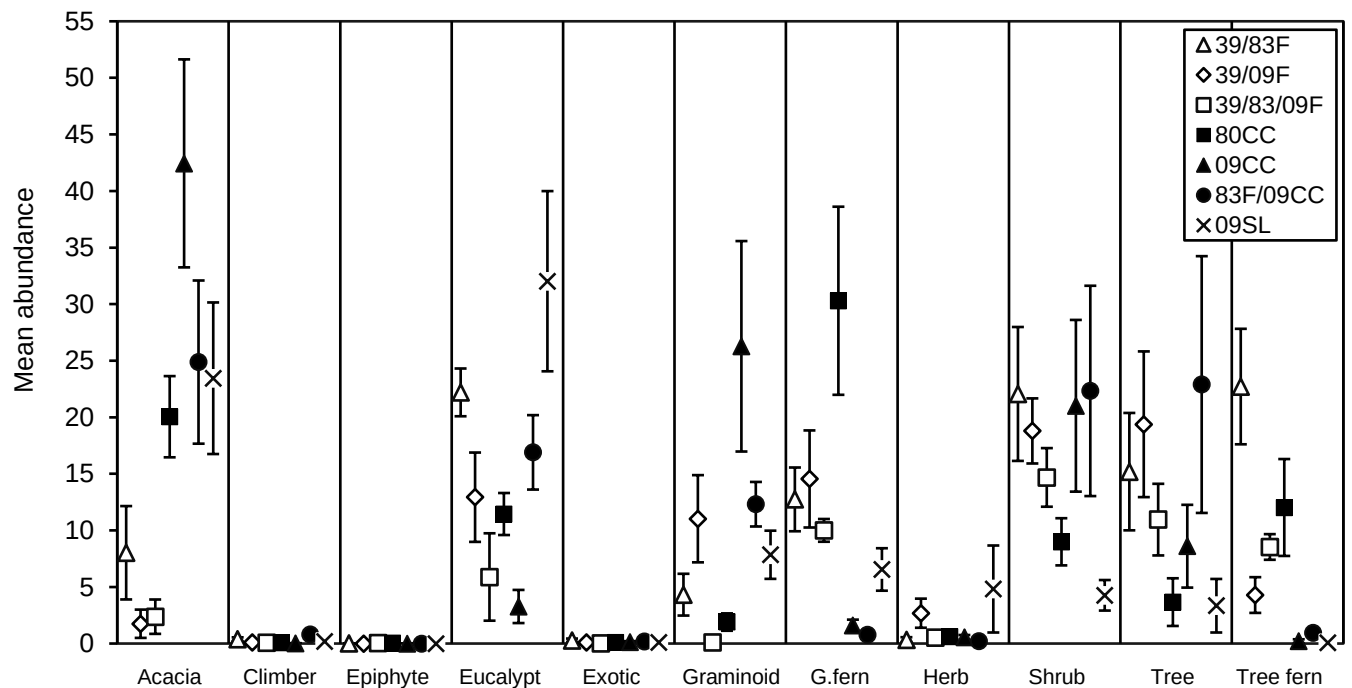


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Chapter 2

Long-term impacts of wildfire and logging on forest soils

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Abstract

Soils are a fundamental component of terrestrial ecosystems, and play key roles in biogeochemical cycles and the ecology of microbial, plant and animal communities. Global increases in the intensity and frequency of ecological disturbances are driving major changes in the structure and function of forest ecosystems, yet little is known about the long-term impacts of disturbance on soils. Here we show that natural disturbance (fire) and human disturbances (clearcut logging and post-fire salvage logging) can significantly alter the composition of forest soils for far longer than previously recognized. Using extensive sampling across a multi-century chronosequence in some of the tallest and most carbon-dense forests worldwide (southern Australian, mountain ash (*Eucalyptus regnans*) forests), we provide compelling evidence that disturbance impacts on soils are evident up to least eight decades after disturbance, and potentially much longer. Relative to long-undisturbed forest (167 years old), sites subject to multiple fires, clearcut logging or salvage logging were characterized by soils with significantly lower values of a range of ecologically important measures at multiple depths, including available phosphorus and nitrate. Disturbance impacts on soils were most pronounced on sites subject to compounding perturbations, such as multiple fires and clearcut logging. Long-lasting impacts of disturbance on soil can have major ecological and functional implications.

Natural disturbances such as fire are major drivers of the structure and function of terrestrial ecosystems worldwide, and influence key biotic and abiotic patterns and processes^{1–4}. Climate change and increases in human disturbances, such as logging, have altered natural fire regimes, resulting in an increase in large-scale fires across terrestrial ecosystems over the past few decades^{1,5,6}. These compounding disturbances are driving significant changes in the structure and function of ecosystems^{7,8}.

While the effects of natural and human disturbances are well characterized for biotic communities, little is known about their long-term impacts on the abiotic components of soil environments, despite their importance for ecosystem function^{9–11}. Soils play key roles in (1) the demography, interspecific interactions and community structure of plant and microbial communities, (2) biogeochemical cycles, (3) biomass production and environmental filtering and buffering, and (4) climate change mitigation through the sequestration of carbon and other greenhouse gases^{12–17}. Limited knowledge about the impacts of disturbances on soils hinders the ability to predict the long-term responses of ecosystems to increasing natural and human disturbance^{10,16,18,19}. In a period of rapid, global environmental and climatic change during which disturbances such as fire and anthropogenic land use changes are predicted to increase and intensify, it is critical to quantify their respective impacts on soils to facilitate management and planning^{3,20,21}.

Here, we quantify the impact of natural disturbance (fire) and human disturbances (clearcut and post-fire salvage logging) on soil measures across a multi-century chronosequence in the mountain ash forests of southeastern Australia. Typical fire regimes in these forests are characterized by infrequent, high-intensity fires that have historically occurred every 75–150 years²². However, the frequency of these fires has increased and some areas have experienced multiple high-severity fires over the past century, including those in 1926, 1932, 1939, 1983 and most recently in 2009⁸. Fires in 1939, 1983 and 2009 burned large areas of mountain ash forest (> 150,000 ha in 1939, 17,250 ha in 1983 and 53,500 ha in 2009²³). In addition, these forests have been subject to clearcut logging since the 1970s and post-fire salvage logging since the late 1930s^{8,24}. Climatic changes within southeastern Australia are predicted to increase the prevalence of hot and dry conditions over the next few decades²⁵. These predictions, coupled with the increasing coverage of high-severity- fire-prone logging regrowth (aged 7–35 years) will potentially increase the frequency of high-intensity stand-replacing fires in these forests^{20,21,25,26}.

From 729 soil cores collected across 81 sites, we used generalized linear models to investigate the influence of nine disturbance history categories varying in stand age (8, 34, 78 and 167 years), fire frequency (0, 1, 2 and 3 fires in recorded history since 1850), clearcut and salvage logging events and environmental variables on measures of organic carbon, macro soil nutrients (ammonium nitrogen (ammonium), nitrate nitrogen (nitrate), available phosphorus, available potassium, sulfur), micronutrients (boron (hot CaCl_2), diethylene triamine pentaacetic acid (DTPA) iron, DTPA manganese, DTPA copper, DTPA zinc), exchangeable cations (exc.) (exc. aluminium, exc. calcium, exc. magnesium, exc. Potassium and exc. sodium), soil chemistry ($\text{pH}(\text{CaCl}_2)$, electrical conductivity (conductivity)), sand/silt/clay (%) and soil moisture (% dry mass) (gravimetric moisture content) from two depths of forest soil (0–10 cm and 20–30 cm)²⁷.

Multi-decadal disturbance impacts on forest soils

We discovered that fire, clearcut logging and salvage logging significantly influenced soil measures in the 0–10 cm and 20–30 cm layers of soil. Significant effects were evident up to at least eight decades post-fire and three decades post-clearcut logging ($P < 0.001$ to $P = 0.05$) (Supplementary Tables 3 and 4). For instance, nitrate and available phosphorus were significantly lower across the chronosequence at sites burnt and/or logged and aged 78, 34 and 8 years old, relative to long-undisturbed sites ($P < 0.001$ to $P = 0.05$) (Fig. 1, Supplementary Fig. 1 and Supplementary Table 3 and 4).

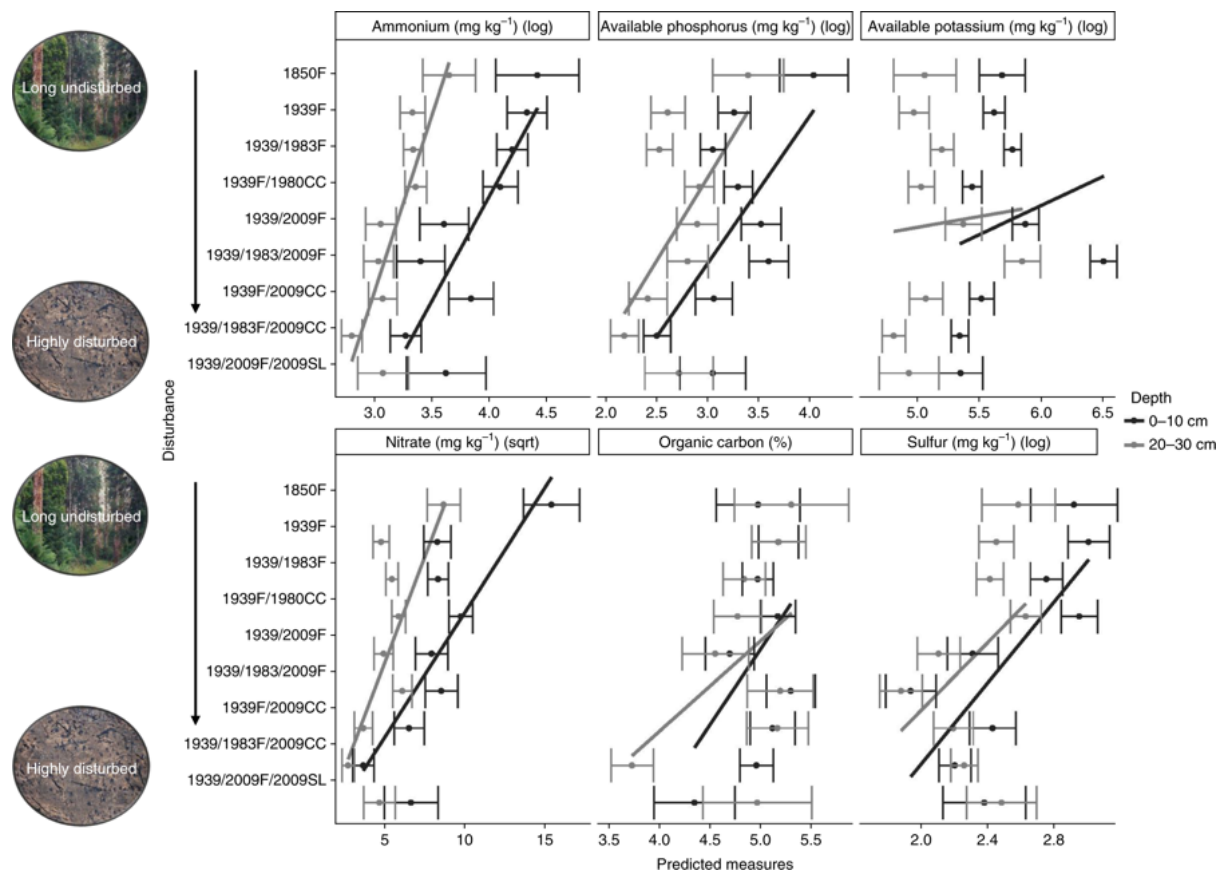


Figure 1. Disturbance histories influence soil measures along a multi-century chronosequence. Predicted values of vital soil measures (± standard error) in relation to disturbance history category, with trend lines. Predictions are shown for a single parent rock type (type 3: Supplementary Table 2), Australian soil classification type (dermosol) and the mean elevation, slope and abundance of dominant plant life forms for each respective disturbance history category. See Supplementary Tables 3 and 4 for a complete list of the influence of all environmental factors. The y axis lists disturbance history categories with the year of occurrence of each disturbance event (F = fire, CC = clearcut, SL = salvage logged). Credit: photographs taken by Esther Beaton and David Lindenmayer.

Relative to sites burnt once, forest stands burnt twice in recorded history (since 1850) were characterized by significantly lower levels of ammonium, nitrate, organic carbon, available phosphorus, sulfur, DTPA iron, boron and exchangeable aluminium cations in the 0–10 cm layer of soil ($P < 0.001$ to $P = 0.02$), and ammonium, organic carbon, available phosphorus, exchangeable potassium and aluminum cations, and soil moisture in the lower layer of soil (20–30 cm depth) ($P < 0.001$ to $P = 0.04$) (Fig. 2 and Supplementary Tables 5 and 6). In contrast, soil pH(CaCl₂) was significantly higher in the 0–10 cm layer of soil, relative to sites burnt once ($P = 0.01$) (Supplementary Table 5).

In forest stands burnt three times, ammonium, sulfur, exchangeable aluminium cations and DTPA iron were significantly lower in the top 0–10 cm of soil, relative to sites subject to one fire ($P < 0.001$ to $P = 0.05$) (Fig. 2 and Supplementary Tables 5 and 6). In contrast, available potassium and pH(CaCl₂) were significantly higher in the 0–10 cm of soil ($P < 0.001$) and exchangeable cations were significantly higher in the 0–10 cm and 20–30 cm layers of soil, relative to sites burnt once ($P < 0.001$ to $P = 0.02$) (Fig. 2 and Supplementary Tables 5 and 6).

Sites subject to compounding disturbances, such as multiple fires and clearcut logging or post-fire salvage logging, consistently had the lowest values of soil measures across the chronosequence, relative to long-undisturbed sites ($P < 0.05$) (Fig. 1 and Supplementary Tables 3 and 4). Specifically, clearcut logging resulted in significantly lower levels of ammonium, nitrate, available phosphorus, available potassium, DTPA zinc, DTPA copper, boron and exchangeable cations in the 0–10 cm of soil ($P < 0.001$ to $P = 0.04$), and available potassium, ammonium, organic carbon, available phosphorus, exchangeable cations and soil moisture in the lower 20–30 cm layer of soil, relative to unlogged forest ($P < 0.001$ to $P = 0.04$) (Supplementary Tables 5 and 6). Furthermore, clearcut logged sites had a significantly higher sand content in the 0–10 cm of soil, compared to unlogged sites ($P = 0.01$). Salvage logged sites had significantly lower ammonium, DTPA iron, boron and exchangeable cations in the 0–10 cm layer of soil ($P < 0.001$ to $P = 0.04$), and exchangeable sodium and boron in the 20–30 cm layer of soil, relative to unlogged forest ($P < 0.001$) (Fig. 2 and Supplementary Table 5 and 6) (see Supplementary Information for further details).

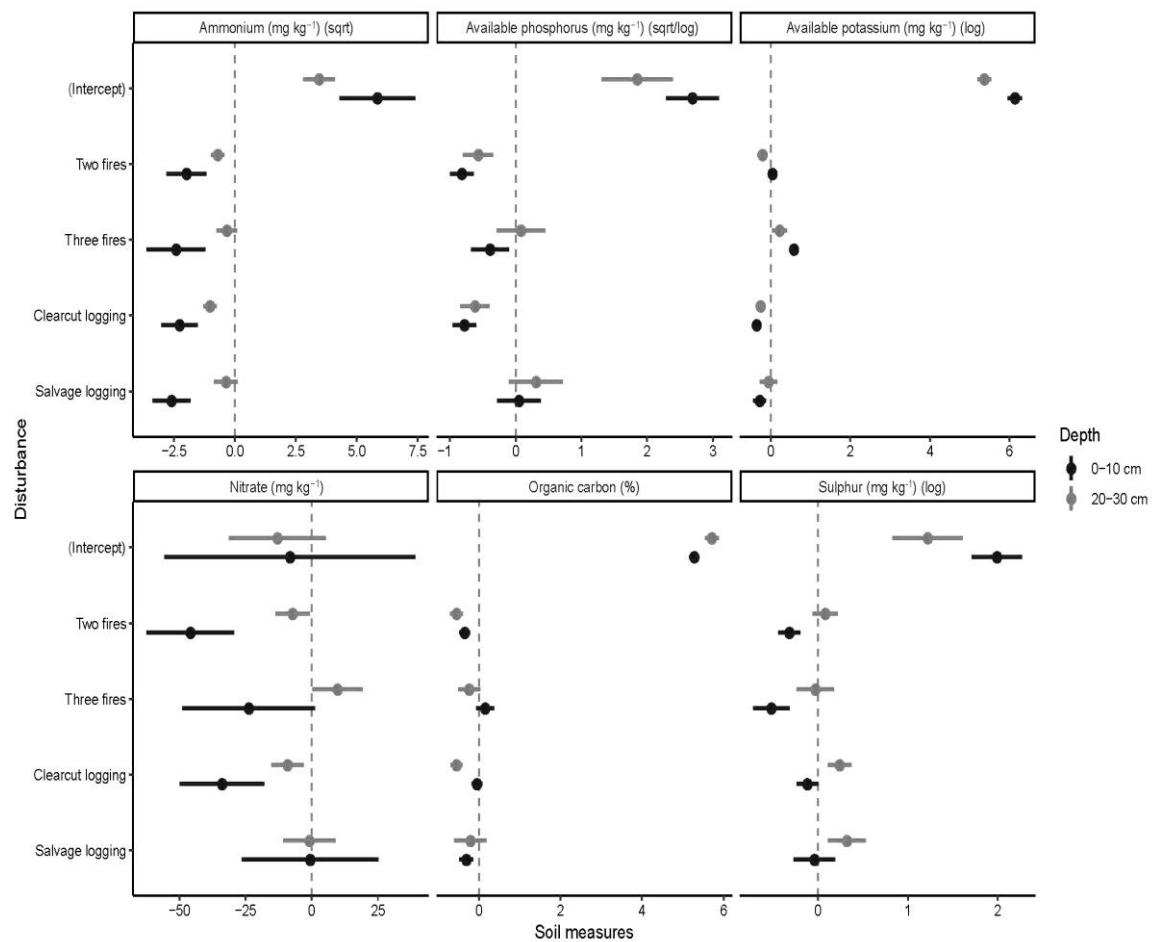


Figure 2 The pervasive impacts of multiple fires and logging on soil measures. Coefficients from generalized linear models of each soil measure with respect to disturbance type, parent rock and Australian soil classification, elevation, slope and the abundance of dominant plant life forms (parent rock type, Australian soil classification, elevation, slope and the abundance of dominant plant life forms not displayed here). Model factors = number of fires, clearcut and salvage logging, parent rock and Australian soil classification; covariates = elevation, slope and the abundance of dominant plant life forms. Note that available phosphorus levels in the 0–10 cm were log-transformed, and in the 20–30 cm were square-root transformed. A complete list of the influence of the factors and covariates generated using these models is provided in Supplementary Tables 5 and 6.

Historical impacts on soil measures

By analysing a subset of our data with identical stand age (8 years) but with different prior disturbance histories, we demonstrate that fire and clearcut logging significantly influence key soil measures even when controlling for age/successional effects. Sites clearcut in 2009 were characterized by significantly lower concentrations of nitrate, available phosphorus and available potassium in the top 0–10 cm layer of soil ($P < 0.001$ to $P = 0.03$), and ammonium, organic carbon, available phosphorus and available potassium in the 20–30 cm of soil, relative to similarly aged unlogged sites ($P < 0.001$ to $P = 0.04$). Sites burnt twice (last in 2009) resulted in significantly lower levels of available phosphorus and sulfur in the 0–10 cm of soil ($P = 0.02$ to $P = 0.03$) and of ammonium, organic carbon and available potassium in the 20–30 cm of soil, relative to similarly aged sites burnt once ($P < 0.001$ to $P = 0.02$). Sites burnt three times (last in 2009) had significantly lower levels of sulfur in the 0–10 cm of soil ($P < 0.01$), and higher levels of available potassium, relative to similarly aged sites burnt once ($P < 0.001$) (Fig. 3 and Supplementary Table 7).

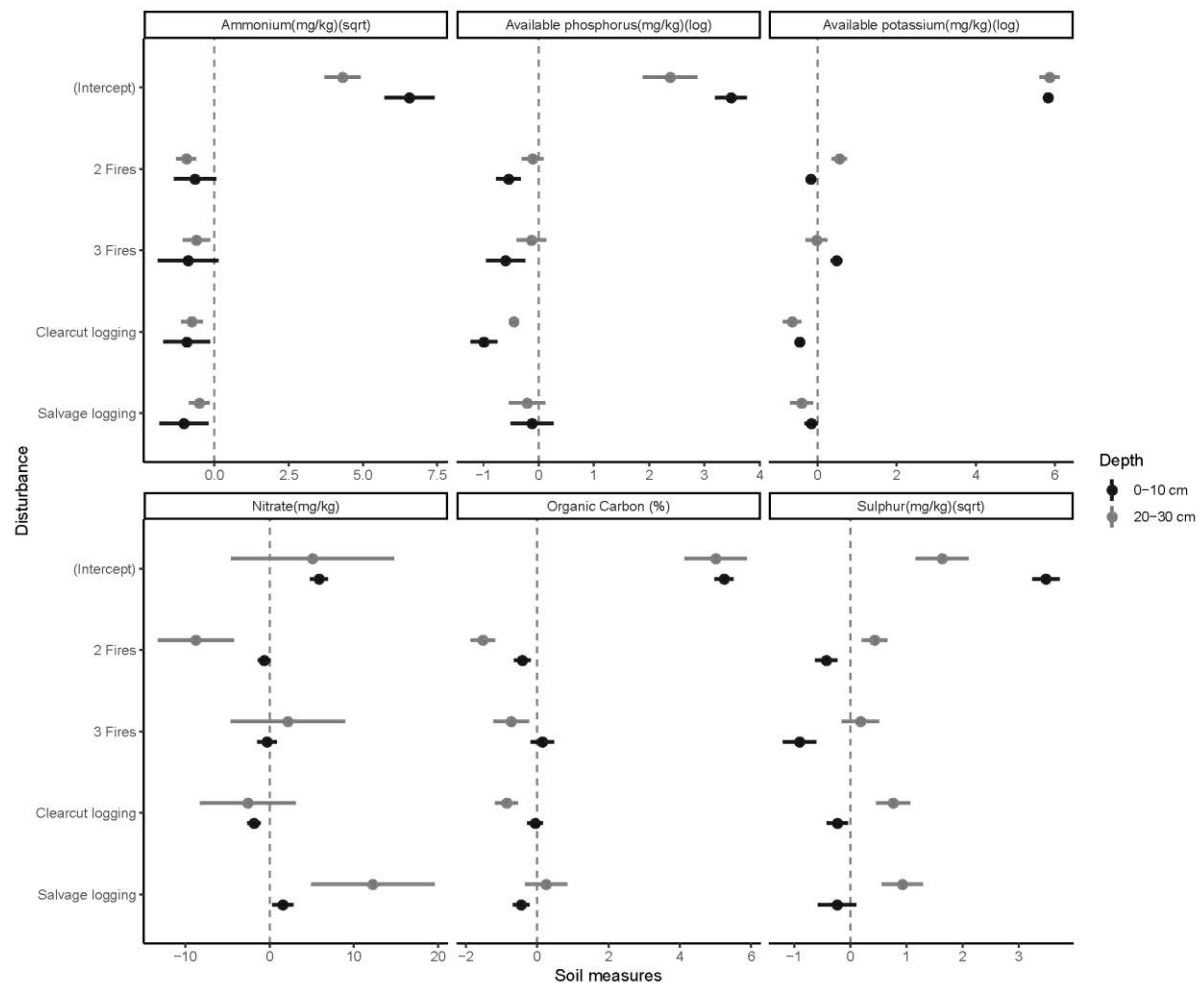


Figure 3. The impact of fire and logging in similarly aged forests on soil measures. Coefficients from generalized linear models of each soil measure in similarly aged sites (last disturbed in 2009) with respect to disturbance type, parent rock and Australian soil classification, elevation, slope and the abundance of dominant plant life forms. Model factors = number of fires, clearcut and salvage logging, parent rock and Australian soil classification; covariates = elevation, slope and the abundance of dominant plant life forms. Note that nitrate levels in 0–10 cm were square-root transformed. A complete list of the influence of the factors and covariates generated using these models is provided in Supplementary Table 7.

Implications of long-term impacts on forest soils

We discovered that both natural and human disturbances can have long-term effects on forest soils. Soil temperatures can exceed 500 °C during high-intensity fires and result in the loss of soil nutrients, organic carbon and organic matter through volatilization and postfire erosion, which can reduce soil fertility^{10,18,28,29}. Consistent with other studies, we found multiple fires resulted in lower levels of soil measures, across both soil depths, relative to long-undisturbed forests¹⁰. In contrast to our discoveries, the impacts of a single fire on forest soils have been previously found to be short-term, and can result in an increase in plant productivity, decomposition and microbial activity^{10,18,28}. However, we found that a single fire event can result in significantly lower levels of key measures, such as nitrate nitrogen and available phosphorus, that persist for at least eight decades post-fire, relative to long-undisturbed sites. These long-lasting impacts also were seen in the 20–30 cm soil layer, which indicates that these post-fire effects may not only be attributed to changes in key soil measures, but probably indicate post-fire erosion and nutrient leaching, and reflect changes in biological processes and composition^{28–30}.

Logging impacts observed in this study were highly significant in both the short and mid term (8 and 34 years), and result from the high-intensity combination of physical disturbance (clearing of forest with machinery) and post-logging ‘slash’ burning (of remaining vegetation)³¹. These disturbances can expose the forest floor¹⁸, compact the soil³², volatilize soil nutrients²⁸ and redistribute organic matter^{28,33}, resulting in the release of large amounts of CO₂ into the atmosphere (Fig. 4)³³. These impacts can alter plant–soil–microbial dynamics and subsequently decomposition rates and carbon storage, and result in the leaching of dissolved organic carbon and nitrogen, and the depletion of base cations, reducing overall site productivity^{3,18,28,34}. Given the long-lasting impacts of fire, we suggest that the logging-related depletion of key soil measures may act as a precursor for longer-term, and potentially severe changes in soil composition³³. Multi-decadal logging impacts occur in other large-tree, slow turnover forests, such as boreal forests (which experience losses in soil carbon and nitrogen), and can take up to a century to recover^{3,9,18,19,28,33,35}. The long-lasting impacts of both fire and clearcut logging in mountain ash ecosystems indicate that the abiotic soil environments of this (and possibly other) forest ecosystems may be maladapted to frequent, high-intensity disturbances that exceed natural disturbance return intervals^{3,28}. Therefore, predicted changes to global disturbance patterns, such as increasing fire intensity and

frequency, could result in severe declines in key soil measures in the long term, with major ecological and functional implications³.

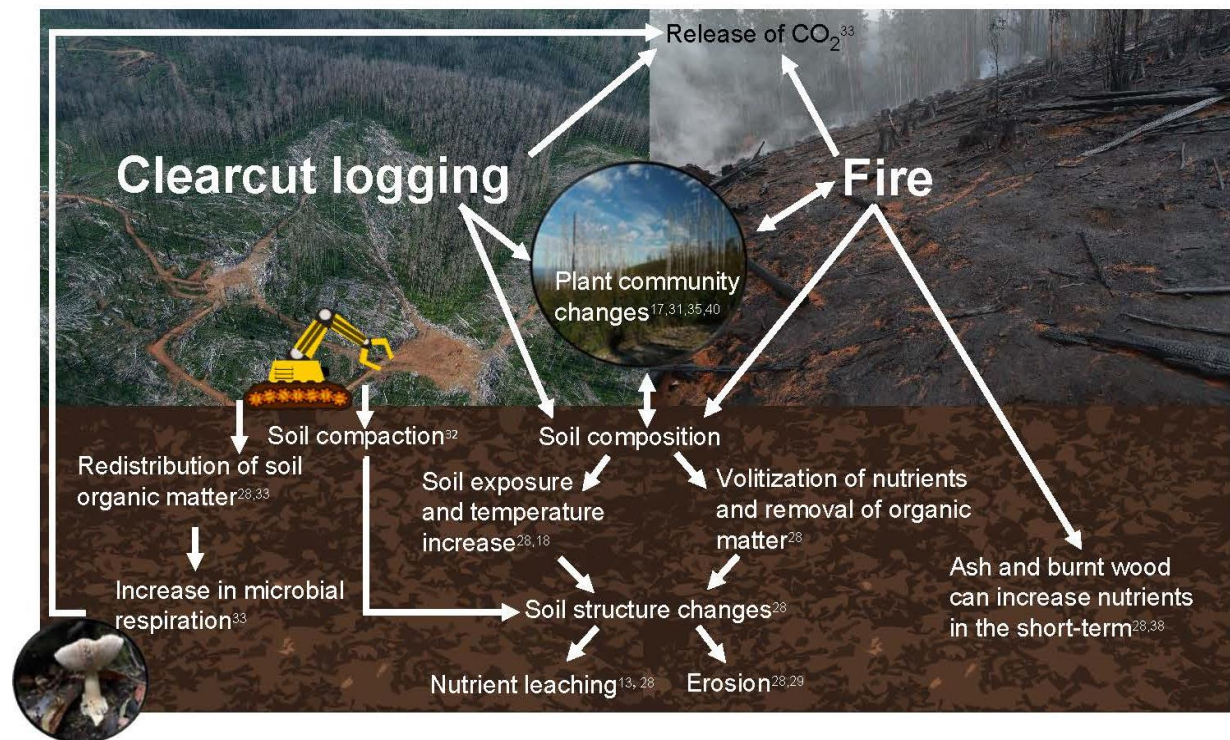


Figure 4. Post-disturbance processes and pathways that influence and impact abiotic soil environments. White arrows indicate influential relationships and flow-on effects associated with disturbance in soil environments. For example, fire and clearcut logging can alter the structural integrity of soils, which can impede the water and nutrient holding capacity of soils and subsequently result in nutrient leaching and erosion, potentially impacting plant productivity. Credit: images provided by Elle Bowd, David Lindenmayer and David Blair.

In mountain ash forests and other slow-turnover forests, vegetation rapidly regenerates after stand-replacing disturbances^{36,37}. This growth is supported by an increase in light and the availability of phosphorus and nitrogen from surface ash deposits³⁸. Further inputs of these key nutrients are a product of self-thinning and litterfall³⁹, microbial activity⁴⁰ and above-ground biological fixation from species such as Acacias, which can dominate post-disturbance regrowth and offset losses in nitrogen within nine years post-disturbance⁴¹. Despite these biochemical inputs, our results demonstrate that significantly lower concentrations of key nutrients such as nitrate and available phosphorus are still evident up to eight decades post-fire and three decades post logging, with the lowest measures found in highly disturbed forests subject to compounding disturbances. We did not measure the uptake rate of nutrients in the surrounding vegetation, which may explain some deficits within the soil in some ecosystems⁴². However, when controlling for successional stage, we found unlogged sites burnt in 2009 consistently had higher estimates of key soil measures relative to similarly aged sites logged in 2009. This comparison indicates that disturbance intensity and frequency is a major factor in determining the composition of forest soils, regardless of stand age and nutrient uptake (Fig. 3).

Recommendations for forest management

We have empirically demonstrated long-term natural and human disturbance impacts on forest soils. Climate change and human disturbances are projected to increase large stand-replacing fires globally^{3,43,44}. This will probably result in substantial long-term losses of crucial soil measures, which can effect ecosystem function and forest productivity and growth over the medium to long term^{18,45–47}. To maintain vital soil nutrient pools and preserve the key functions that soils have in ecosystems, such as carbon sequestration and the regulation of plant and microbial community productivity, land managers should consider the impacts of current and future disturbances on soils in ecosystem assessments and land-use management and planning. Specifically, perturbations such as fire (outside the historical fire return interval of 75–150 years²²) and clearcut and post-fire salvage logging should be limited wherever possible, especially in areas previously subject to these disturbances. Aboveground ecosystem legacies that occur in highly fertile, long-undisturbed sites, such as large old trees, are diminishing globally, and can take over a century to recover from the impacts of disturbance⁴⁸. Our findings suggest that below-ground abiotic soil environments may take a similar amount of time to recover.

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Acknowledgments

The authors thank the Victorian Department of Environment, Land, Water and Planning and Parks Victoria for granting access to restricted sites, volunteers who assisted in data collection, A. Bissett for methodological advice, W. Blanchard for statistical advice, and the following groups for funding: the Paddy Pallin Foundation, Centre of Biodiversity Analysis, the Ecological Society.

Supplementary methods

Site description

We conducted our study in the high altitude and high rainfall *Eucalyptus regnans* (mountain ash) forests of the Victorian Central Highlands located in southeastern Australia^{49,50}. These forests typically experience cool summers and mild, humid winters, with occasional periods of snow^{23,51}. However, periodic dry and hot summers and large infrequent fires also occur, and the frequencies of both have increased over time^{21,25,26}. *Eucalyptus regnans* forests are wet-sclerophyll forests defined by tall eucalypt overstorey trees, scattered mid-storey trees, broad-leaved shrubs and a moist ground layer rich in fern species^{49,52}. Under natural historical fire-return intervals of between 75 and 150 years, the vegetation of these forests has co-evolved to cope with the impacts of fire, rapidly regenerating from seed or resprouting organs or structures^{22,49}. In 1939, more than 70% of these forests were burnt and many were subsequently salvage logged until the 1960s, which has dominated the landscape with relatively homogeneous regrowth^{53,54}. This dominant age cohort is now the primary resource for the logging industry²⁴. The 2009 fires burnt 53,500 ha of *Eucalyptus regnans* forest, with a large proportion being regrowth from the 1939 fires²³. This has resulted in an abundant young, dense, fire-prone regrowth landscape with limited structural diversity²⁶.

Since the 1970s, clearcut logging has been the primary silvicultural system in Victorian wet sclerophyll forests^{8,24}. Clearcutting is a practice where all trees are cut within a block of between 15 and 40 ha; the remaining debris or ‘slash’ is then burned at high intensity and high severity, and subsequently aerially seeded with *Eucalyptus regnans* seed^{38,55}. Salvage logging is a type of clearcut logging that occurs usually within three years following a high-severity natural fire⁵⁴. This practice follows standard clearcut logging methods, with the exception that there is no slash burn if the regeneration from the initial wildfire is adequate⁴⁹.

Experimental design

The design of our study was based on the diversity of disturbance histories and the respective availability of replicate sites. We selected nine disturbance history categories in total: five categories experienced fire-only, and the remaining four categories were clearcut or salvage logged. Fire-only sites consisted of forests, long-undisturbed (unburnt since 1850), burnt once (1939 fire), twice (1939/1983 and 1939/2009) and three times (1939/1983/2009). Logged sites were those burnt in 1939 and clearcut in 1980–85 or 2009–10, and salvage logged in 2009–10 after a second fire in 2009. In addition, sites that experienced multiple fires and

clearcut logging were those burnt in 1939/1983 and clearcut in 2009–10. All disturbance history categories were replicated 10 times with the exception of forests long-undisturbed (1850: 4 replicates), burnt twice (1939/2009: 11 replicates) and three times (1939/1983/2009: 6 replicates). Natural and human disturbances are typically stand-replacing events in mountain ash ecosystems, making it possible to readily assign any given stand of forest to a specific age cohort. We controlled environmental variables that could influence soil abiotic measures. Sites were characterized by a predominantly southerly aspect, an elevation of ~600–900 m and an annual precipitation class of ‘1,300–1,800 mm’, and were positioned away from drainage lines and ridges, as indicated by topographical wetness indices. Replicate sites representing disturbance history categories were distributed among these environmental conditions without bias. For instance, both long-undisturbed sites and highly-disturbed sites were located in areas of high elevation and precipitation. Furthermore, we recorded the projective foliage cover of vascular plant species in each quadrat on each site using the survey protocol and sample configurations developed by the Australian Department of the Environment, Land, Water and Planning⁵⁶. Projective foliage cover was used as a measure of species abundance and is hereafter referred to as ‘abundance’. We assigned life form categories to each plant species using criteria defined by Bowd et al.³¹, and used the total abundance (sum of the abundance of each plant species in each respective life form category in each site) of each dominant life form—‘Eucalyptus’, ‘Acacia’, ‘Tree’, ‘Shrub’, ‘Ground-fern’ and ‘Tree-fern’—in each of the 81 sites as primary covariates in all generalized linear models to account for their potential effects on soil measures (for example, potential increase in nutrient uptake with increasing abundance/biological fixation of nitrogen by *Acacia* species). ‘Tree ferns’ and ‘ground ferns’ were categorized into separate groups, as tree ferns are structurally a mid-storey tree, differing in size and function from other fern species and mid-storey ‘Trees’⁴⁹. Additionally, we separated ‘Eucalyptus’ and ‘Acacia’ species from other life form groups. This was because *Eucalyptus* trees are the dominant over-storey species within these forests, whereas *Acacia* species dominate the mid-storey and have different ecological roles, such as nitrogen fixation^{31,49}. All other tree species were assigned to the ‘Tree’ life form category. In addition, other environmental factors, such as ‘parent rock’, ‘Australian soil classification (‘dermosol’, ‘sodosol’, ‘tenosol’, collectively known as ‘Dystric nitosols’ according to the world reference base for soil resources 2014⁵⁷)¹³, ‘elevation’ and ‘slope’ (deg) were used as primary factors in our statistical analysis to account for their potential effects on soil composition. Vegetation abundance data were previously reported and discussed in ref. ³¹.

Soil sampling

We sampled all 81 sites during the Australian summer of December 2016–March 2017. Using 1 ha long-term monitoring and newly established plots, we measured quadrats of 25 m × 25 m away from the roadside to account for edge effects⁵⁸. In each site, we collected nine 10 cm × 30 cm soil cores along the perimeter and centre of each plot and stratified and pooled the composite samples by depth (0–10 cm and 20–30 cm)⁵⁹. We took an additional air-tight 50 ml sample of soil for soil moisture determination from each respective depth. Soils were then air-dried and sieved using a 2 mm sieve in preparation for chemistry analysis.

Soil chemistry and composition analysis

We determined the soil particle size distribution of soil samples using the modified pipette method^{27,60}. We treated soils with 10 ml of distilled water, 10 ml of 30% hydrogen peroxide (H₂O₂) and one drop of acetic acid and then heated them to remove organic matter. We added an additional 5 ml of H₂O₂ at 15 min intervals until all organic matter was removed. We then evaporated the soils and treated them with 10 ml of 10% sodium hexametaphosphate (NaHMP) to disperse particles and left them to shake overnight. Using a standardized table of particle sedimentation times, we took 20 ml aliquots of the shaken sample and sieved, evaporated (over-dried at 105 °C) and weighed the remaining sample to determine the sand, silt and clay content⁶⁰. We measured the moisture content of soils gravimetrically and reported this as a percentage of the dry mass. Additional soil chemical tests were conducted by CSBP Laboratories (Perth, Western Australia). Ammonium and nitrate nitrogen contents were determined colorimetrically, following extraction with 2 M potassium chloride (25°C)^{61,62}. Available phosphorus and potassium were measured using the Colwell method^{61,63}. Sulfur levels were determined by the Blair–Lefroy extractable sulfur method⁶⁴. Organic carbon was measured using the Walkley–Black method⁶⁵. The concentrations of soluble salts were estimated by measuring electrical conductivity based on a 1:5 soil/water extract (EC 1:5). pH (CaCl₂) was also measured from the same soil/water extracts, producing two measures of pH, 1:5 soil/water suspension and 1:5 soil/0.01 M CaCl₂^{61,62}. DTPA-extractable trace elements (Cu, Fe, Mn, Zn) were determined by atomic absorption spectroscopy following extraction with DTPA^{61,62}. Boron was measured using inductively couple plasma (ICP) spectroscopy after CaCl₂ extraction^{61,62}. Soil exchangeable cations (Mg, K, Na, Ca) were determined using ICP spectroscopy using a 1:5 soil:water extraction^{61,62}.

Statistical analysis

We ran three sets of generalized linear models. The first determined the influence of the factors ‘disturbance history category’ ($n = 9$), ‘parent-rock’ ($n = 5$), ‘Australian soil classification’ ($n = 3$), slope, elevation and the abundance of dominant plant life forms (‘Acacia’, ‘Eucalyptus’, ‘Groundfern’, ‘Tree-fern’, ‘Shrub’, ‘Tree’), as described by Bowd and colleagues³¹, on all 22 soil measures. The second set of models extrapolated the influence of ‘disturbance history categories’ with respect to the factors (1) clearcutting, (2) salvage logging, (3) number of fires (1, 2, 3) and (4) age (8, 34, 78 years), as well as the environmental variables (5) parent-rock (1, 2, 3, 4, 5) and (6) Australian soil classification (dermosol, sodosol) and the abundance of dominant plant life forms on all 22 soil measures. We analysed a third set of generalized linear models using the same component disturbance history and environmental variables of similarly aged sites last disturbed in 2009 to determine the influence on major soil measures ‘Nitrate’, ‘Available phosphorus’, ‘Available potassium’, ‘Ammonium’, ‘Organic carbon’ and ‘Sulfur’, controlling for successional effects. Appropriate variables were log- or square-root-transformed, and significant outliers were removed to meet assumptions of generalized linear models. Predictions of the value of soil measures with respect to disturbance history categories and the most abundant parent rock (type 3), Australian soil classification (dermosol) and the mean elevation, slope and abundance of dominant life forms for each of the 81 sites were generated using the respective generalized linear models (Fig. 1). The MuMin package and ‘dredge’ function were used to determine which combination of factors best explained any variance in the measure of each soil chemical and compositional variable by ranking Akaike information criterion (AIC) values. The combination of factors that presented the lowest AIC value was used in each generalized linear model. All statistical analyses were conducted using R studio 3.4.3.

Data availability

The data that support the findings of this study are available in the Supplementary Information and from the corresponding author upon request.

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Supplementary Information

1. Results with corresponding tables and figures:

Figs. S1

Tables S1 to S7

We discovered that fire, clearcut logging and salvage logging significantly influenced the composition of soils in the 0-10 cm and 20-30 cm layers of soil. Significant effects were still evident up to at least 8 decades post-fire and 3 decades post-clearcut logging ($p < 0.001$ - $p = 0.05$) (Table S3, S4). For instance, nitrate and available phosphorus were significantly lower across the chronosequence at sites burnt and/or logged and aged 78, 34 and 8 years old, relative to long-undisturbed sites ($p < 0.001$ - $p = 0.05$) (Figure 1, Figure S1, Table S3, S4).

Fire impacts on forest soils

Relative to sites burnt once, forest stands burnt twice in recorded history (since 1850) were characterized by significantly lower levels of ammonium, nitrate, organic carbon, available phosphorus, sulfur, DTPA iron, boron and exchangeable aluminium cations in the 0-10 cm layer of soil ($p < 0.001$ - $p = 0.02$), and ammonium, organic carbon, available phosphorus, exchangeable potassium and aluminum cations, and soil moisture in the lower layer of soil (20-30 cm depth) ($p < 0.001$ - $p = 0.04$) (Figure 2; Table S5, S6). In contrast, soil pH(CaCl₂) and sand content was significantly higher in the 0-10 cm layer of soil, relative to sites burnt once ($p = 0.01$) (Table S5).

In forest stands burnt three times, sulfur, exchangeable aluminium cations and DTPA iron were significantly lower in the top 0-10 cm of soil, relative to sites subject to one fire ($p < 0.001$ - $p = 0.01$) (Figure 2; Table S5). Available potassium, sand content and pH(CaCl₂) were significantly higher in the 0-10 cm of soil ($p < 0.001$ - $p = 0.01$); and exchangeable cations were significantly higher in the 0-10 cm and 20-30 cm layers of soil ($p < 0.001$ - $p = 0.02$) (Figure 2; Table S5, S6).

Logging impacts on forest soils

Clearcut logging resulted in significantly lower levels of ammonium, nitrate, available phosphorus, available potassium, DTPA zinc, DTPA copper, boron, and, exchangeable cations in the 0-10 cm of soil ($p < 0.001$ - $p = 0.04$), and ammonium, organic carbon, available phosphorus, available potassium, exchangeable cations and soil moisture in the lower 20-30 cm layer of soil, relative to unlogged forest ($p < 0.001$ - $p = 0.04$) (Table S5, S6). Clearcut logged

sites had a significantly higher sand content in the 0-10 cm of soil, compared to unlogged sites ($p=0.01$). Salvage logged sites had significantly lower ammonium, DTPA iron, boron and exchangeable cations in the 0-10 cm layer of soil ($p<0.001$ - $p=0.04$), and exchangeable sodium and boron in the 20-30 cm layer of soil, relative to unlogged forest ($p<0.001$) (Figure 2; Table S5, S6).

Lifeform abundance influence on forest soils

We found the abundance of dominant lifeforms significantly influenced key soil measures in the 0-10 cm and 20-30 cm layers of soil in individual component disturbance models ($p<0.05$).

‘Tree’ abundance had a significant negative influence on clay content, boron and soil moisture in the 0-10 cm layer of soil ($p=0.02$ - 0.03); and nitrate, organic carbon, sulfur and soil moisture in the 20-30 cm layer of soil ($p<0.001$ - 0.02). In contrast, ‘tree’ abundance had a significant positive influence on micronutrients and exchangeable cations in the 0-10 cm and 20-30 cm layers of soil ($p<0.001$ - 0.03). ‘Tree-fern’ abundance had a significant positive influence on nitrate, soil conductivity, DTPA iron, DTPA manganese, boron and soil moisture in the 0-10 cm layers of soil ($p=0.001$ - 0.04); and nitrate, clay and sulfur in the 20-30 cm layer of soil ($p<0.001$ - 0.04). The abundance of the ‘Eucalyptus’ lifeform had a significant positive influence on available potassium and exchangeable sodium in the 0-10 cm layer of soil ($p=0.001$ - 0.02); and a significant negative influence on organic carbon in the 20-30 cm layer of soil ($p=0.03$). ‘Ground-fern’ abundance did not significantly influence any soil measures in the 0-10 cm layer of soil, but had a significant positive relationship on available potassium, and exchangeable cations in the 20-30 cm of soil ($p=0.001$ - 0.04). ‘Acacia’ abundance had a significant positive influence on ammonium and exchangeable cations in the 0-10 cm layer of soil ($p=0.01$ - 0.04); and a significant negative influence on available potassium and DTPA Manganese in the 20-30 cm layer of soil ($p<0.001$ - 0.03) (Table S6).

Disturbance impacts on forest soils in similarly aged forests

Our results show strong effects of disturbance history on forests soils across the chronosequence and two soil depths. However, it is unknown whether these effects are due to disturbance itself, or the effects of disturbance on forest stand age and vegetation composition which, in turn, affect soils.

By analyzing a subset of our data with identical stand age (8 years) but with differing prior disturbance histories, we demonstrate that fire and clearcut logging significantly influenced

key soil measures even when controlling for age/successional effects. Sites clearcut in 2009 were characterized by significantly lower concentrations of nitrate, available phosphorus and available potassium in the top 0-10 cm layer of soil ($p<0.001$ - $p=0.03$), and ammonium, organic carbon, available phosphorus and available potassium in the 20-30 cm of soil relative to similarly aged unlogged sites ($p<0.001$ - $p=0.04$). Sites burnt twice (last in 2009) resulted in significantly lower levels of available phosphorus and sulfur in the 0-10 cm of soil ($p=0.02$ - $p=0.03$), and in ammonium, organic carbon and available potassium in the 20-30 cm of soil, relative to similarly aged sites burnt once ($p<0.001$ - $p=0.02$). Sites burnt three times (last in 2009) had significantly lower levels of sulfur in the 0-10 cm of soil ($p<0.01$), and higher levels of available potassium, relative to similarly aged sites burnt once ($p<0.001$)(Figure 3; Table S7).

S1: The disturbance history and number of replicate sites of each of the nine disturbance history categories. F= fire, CC= Clearcut, SL= Salvage logged.

	1850 Fire	1939 Fire	1983 Fire	2009 Fire	1980-85 Clearcut	2009-10 Clearcut	2009-10 Salvage	n=
'1850F'	✓							4
'1939F'		✓						10
'1939/1983F'		✓	✓					10
'1939/2009F'		✓		✓				11
'1939/1983/2009F'		✓	✓	✓				6
'1939F/1980CC'		✓			✓			10
'1939F/2009CC'		✓				✓		10
'1939/2009F/2009SL'		✓		✓			✓	10
'1939/1983F/2009CC'		✓	✓			✓		10

Table S2: Parent rock types and soil types and respective codes used in models.

Parent rock type	Parent rock type code
Extrusive, fluvial: felsic ignimbrites, basalt and andesite lavas, conglomerate, sandstone	1
Extrusive: biotite-hypersthene rhyodacite ignimbrite, recrystallized	2
Intrusive: biotite granodiorite, medium grained subequigranular/generally porphyritic	3
Intrusive: felsic dykes	4
Metamorphic: hornfels	5

Soil type	Soil type code
Dermosol	1
Sodosol	2
Tenosol	3

Fig. S1: Mean abundance of exchangeable cations, micronutrients and particle size across nine different disturbance types, with standard error bars. The y-axis lists disturbance history categories with the year of occurrence of each disturbance event (F= Fire, CC = Clearcut, SL= Salvage logged).

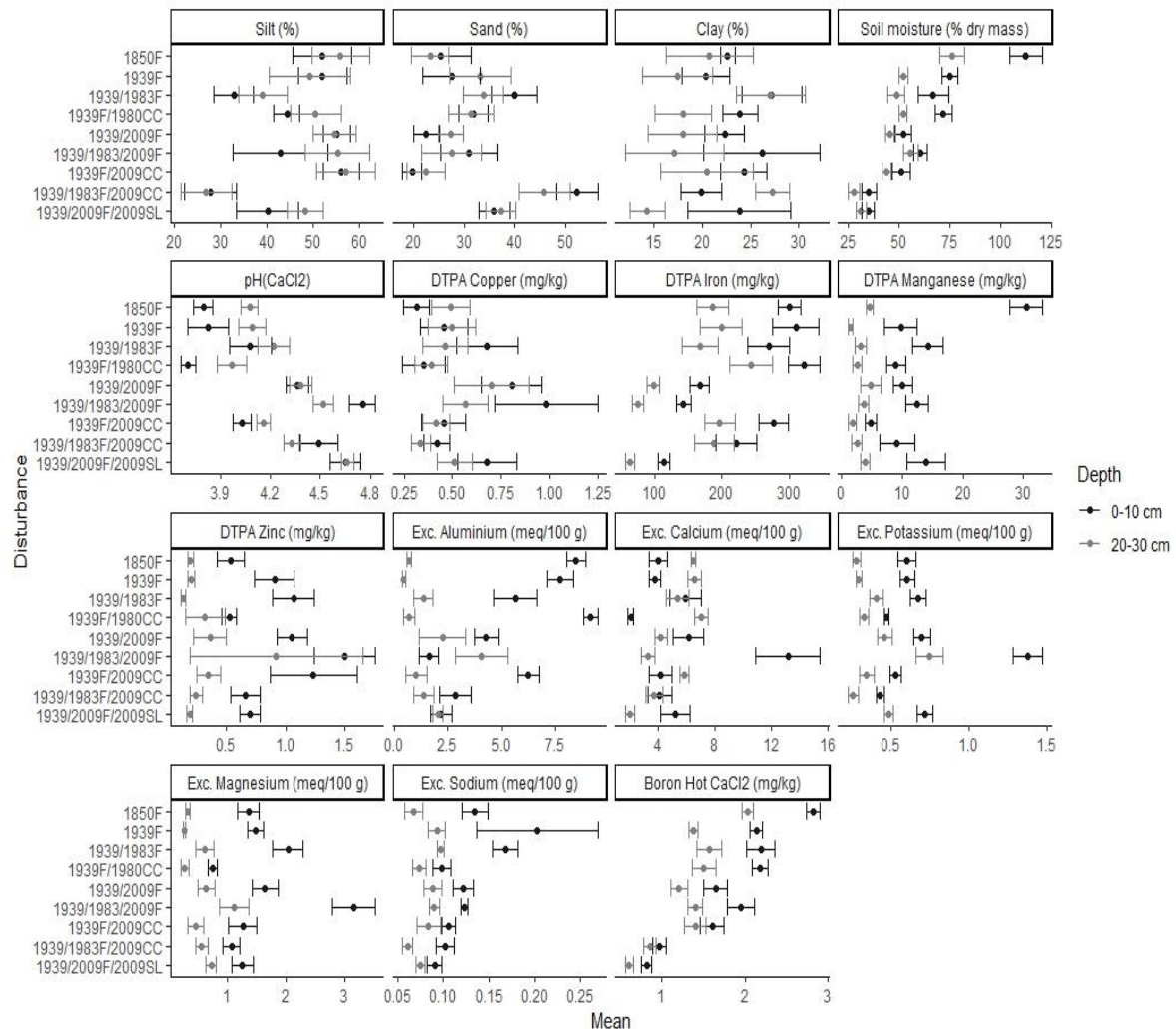


Table S3: Parameter estimates of soil measures with respect to disturbance history category and environmental variables (parent rock type, Australian soil classification, slope, elevation and dominant plant lifeforms) across the 0-10 cm layer of soil depth, generated using generalized linear models. Disturbance history categories are listed by the year of occurrence of each disturbance event (F= Fire, CC = Clearcut, SL= Salvage logged). Red text indicates significant negative influences, and green text indicates significant positive of corresponding factors on each soil variable. E=parameter estimate ($\pm$ standard error).

		(Interc ept)	1939F	1939/1 983F	1939F/1 980CC	1939/2 009F	1939/198 3/2009F	1939F/2 009CC	1939/1983 F/2009CC	1939/2009 F/2009SL
Nitrate (mg/kg) (sqrt)	E = p =	11.33(± 2.72)	8.03(± 1 .72)	8.37(± 1 .80)	5.98(± 1 .69)	7.24(± 1 .60)	7.09(± 1 .67)	9.76(± 1 .79)	12.07(± 1.8 3)	8.78(± 2.21)
Ammonium(mg/kg (log)	E = p =	3.42($\pm$ 0.54)	0.08(± 0 .31)	0.33(± 0 .35)	0.34(± 0 .31)	0.73(± 0 .27)	0.68(± 0 .33)	0.63(± 0 .35)	1.31(± 0.34)	0.73(± 0.27)
Organic Carbon (mg/kg)	E = p =	5.38($\pm$ 0.24)	0.09(± 0 .27)	0.21(± 0 .28)	0.09(± 0 .28)	0.33(± 0 .27)	0.17(± 0 .30)	0.13(± 0 .28)	0.35(± 0.28)	0.74(± 0.28)
Available phosphorus (mg/kg) (log)	E = p =	3.73($\pm$ 0.27)	0.67(± 0 .30)	0.78(± 0 .31)	0.61(± 0 .30)	0.33(± 0 .30)	0.36(± 0 .31)	0.74(± 0 .30)	1.02(± 0.31)	0.80(± 0.38)
Available potassium (mg/kg) (log)	E = p =	5.95($\pm$ 0.28)	0.01(± 0 .17)	0.11(± 0 .17)	0.21(± 0 .17)	0.14(± 0 .16)	0.67(± 0 .19)	0.25(± 0 .18)	0.33(± 0.17)	0.13(± 0.22)
Sulfur (dS/m) (log)	E = p =	2.17($\pm$ 0.37)	0.17(± 0 .24)	0.15(± 0 .24)	0.09(± 0 .23)	0.56(± 0 .23)	0.73(± 0 .26)	0.32(± 0 .25)	0.70(± 0.24)	0.59(± 0.31)
Conductivity (dS/m)(log)	E = p =	1.27($\pm$ 0.56)	0.27(± 0 .29)	0.26(± 0 .31)	0.12(± 0 .28)	0.61(± 0 .26)	0.30(± 0 .30)	0.56(± 0 .29)	0.79(± 0.30)	0.56(± 0.37)
Sand (%)	E = p =	28.03(± 13.05)	4.66(± 7 .46)	3.58(± 7 .90)	3.67(± 7 .33)	4.53(± 6 .68)	0.13(± 7 .25)	8.78(± 7 .45)	8.02(± 7.89)	6.30(± 8.01)
Silt (%)	E = p =	28.62(± 24.09)	9.60(± 1 0.67)	3.52(± 1 1.75)	6.25(± 1 0.45)	4.69(± 9 .53)	3.20(± 11 .36)	10.14($\pm$ 10.97)	2.50(± 11.5 3)	8.36(± 11.1 9)
Clay (%)	E = p =	48.31(± 11.45)	8.79(± 6 .06)	1.84(± 6 .13)	5.49(± 6 .07)	3.73(± 5 .67)	5.64(± 7 .08)	6.54(± 6 .40)	7.09(± 5.91)	4.09(± 5.86)
pH (CaCl ₂)	E = p =	4.58($\pm$ 0.35)	0.12(± 0 .21)	0.17(± 0 .22)	0.21(± 0 .21)	0.35(± 0 .20)	0.79(± 0 .20)	0.10(± 0 .21)	0.46(± 0.22)	0.33(± 0.27)

DTPA Copper (mg/kg) (log)	$E =$ $p =$	2.99(±1.10) 0.01	-1.38(±0.56) 0.02	-0.94(±0.60) 0.12	-1.36(±0.55) 0.02	-0.20(±0.52) 0.70	-0.21(±0.58) 0.71	-1.15(±0.57) 0.05	-1.16(±0.59) 0.05	-1.41(±0.73) 0.06
DTPA Iron (mg/kg)	$E =$ $p =$	70.49(±81.78) 0.39	64.17(±50.07) 0.20	56.94(±52.22) 0.28	62.75(±50.50) 0.22	53.57(±47.26) 0.26	35.05(±54.61) 0.52	53.65(±55.71) 0.34	4.59(±50.68) 0.93	92.16(±64.24) 0.16
DTPA Manganese (mg/kg) (log)	$E =$ $p =$	4.31 (±0.72) 0.00	-1.80 (±0.43) 0.00	-1.58 (±0.45) 0.00	-1.36 (±0.43) 0.00	-1.39 (±0.42) 0.00	-1.40 (±0.48) 0.00	-2.15 (±0.45) 0.00	-1.90 (±0.43) 0.00	-2.29 (±0.56) 0.00
DTPA Zinc (log) (mg/kg)	$E =$ $p =$	1.89(±0.93) 0.05	0.13(±0.43) 0.76	0.21(±0.46) 0.65	0.25(±0.43) 0.57	0.02(±0.40) 0.96	0.29(±0.45) 0.52	0.26(±0.45) 0.56	0.24(±0.45) 0.60	0.20(±0.57) 0.73
Exc. Aluminium (meq./100g)	$E =$ $p =$	2.94(±1.99) 0.15	0.30(±1.14) 0.80	2.42(±1.22) 0.05	1.17(±1.13) 0.30	3.79(±1.02) 0.00	6.63(±1.10) 0.00	2.02(±1.15) 0.08	4.21(±1.23) 0.00	4.99(±1.26) 0.00
Exc. Calcium (meq./100g) (log)	$E =$ $p =$	2.23(±0.70) 0.00	0.25(±0.42) 0.56	0.02(±0.43) 0.96	0.89(±0.43) 0.04	0.09(±0.41) 0.83	0.84(±0.47) 0.08	0.71(±0.48) 0.14	0.62(±0.44) 0.17	0.77(±0.55) 0.17
Exc. Magnesium(meq./100g) (sqrt)	$E =$ $p =$	1.86(±0.31) 0.00	0.09(±0.18) 0.63	0.03(±0.19) 0.86	0.44(±0.19) 0.02	0.05(±0.18) 0.77	0.35(±0.20) 0.09	0.37(±0.21) 0.08	0.40(±0.19) 0.04	0.59(±0.24) 0.02
Exc. Potassium (meq./100g)(log)	$E =$ $p =$	0.11(±0.27) 0.70	0.02(±0.16) 0.92	0.09(±0.17) 0.61	0.22(±0.16) 0.18	0.11(±0.16) 0.50	0.71(±0.18) 0.00	0.23(±0.17) 0.18	0.37(±0.16) 0.03	0.08(±0.22) 0.71
Exc. Sodium (meq./100g)	$E =$ $p =$	0.11(±0.02) 0.00	0.00(±0.02) 0.87	0.02(±0.02) 0.18	0.04(±0.02) 0.03	0.01(±0.02) 0.45	0.00(±0.02) 0.91	0.03(±0.02) 0.11	0.05(±0.02) 0.01	0.06(±0.02) 0.00
Boron (Hot CaCl ₂) (mg/kg)	$E =$ $p =$	3.31(±0.45) 0.00	0.84(±0.24) 0.00	0.79(±0.25) 0.00	0.81(±0.24) 0.00	1.26(±0.23) 0.00	1.07(±0.28) 0.00	1.41(±0.25) 0.00	1.96(±0.24) 0.00	2.13(±0.23) 0.00
Soil Moisture (% dry mass)	$E =$ $p =$	98.18(±17.04) 0.00	18.96(±11.14) 0.09	21.11(±11.74) 0.08	16.56(±10.87) 0.13	39.45(±10.43) 0.00	31.84(±10.90) 0.00	35.53(±11.06) 0.00	42.25(±11.72) 0.00	41.73(±14.26) 0.00

		Pare nt rock 2	Pare nt rock 3	Pare nt rock 4	Pare nt rock 5	Elev ation	Slop e	Sodo sol	Ten osol	Shr ub	Tre e	Tre efer n	Euc aly pts	Aca cia	Gro und fern
Nitrate(mg/kg) (sqrt)	$E =$ $p =$	1.73(±2.27) 0.45	3.88(±2.18) 0.08	0.93(±2.50) 0.71	1.93(±2.17) 0.38			4.70(±1.61) 0.00	1.63(±2.11) 0.44	0.03 (±0.02) 0.05	0.02 (±0.02) 0.21	0.07 (±0.02) 0.01		0.02 (±0.02) 0.18	0.03 (±0.02) 0.13
Ammonium (mg/kg)(log)	$E =$ $p =$		0.08(±0.19) 0.69	0.42(±0.28) 0.14	0.40(±0.18) 0.03	0.00 (±0.00) 0.13					0.01 (±0.00) 0.08	0.01 (±0.00) 0.19	0.01 (±0.00) 0.05	0.01 (±0.00) 0.00	

	$p =$	± 0.5 7)	± 0.5 5)	± 0.6 3)	± 0.5 4)	± 0.5 1)						
	$p =$	0.10	0.02	0.14	0.16	0.01	0.26	0.13	0.25	0.02		
Exc. Aluminium (meq./100g)	$E =$	5.43(± 1.8 0)	4.24(± 1.7 6)	4.25(± 2.0 2)	5.21(± 1.7 6)					0.03 (± 0.01)	0.03 (± 0.01)	0.03 (± 0.02)
	$p =$	0.00	0.02	0.04	0.00					0.04	0.01	0.08
Exc. Calcium (meq./100g) (log)	$E =$					0.00 (± 0.00)	0.94(± 0.43)	0.08(± 0.53)	0.01 (± 0.00)			0.01 (± 0.00)
	$p =$					0.07	0.03	0.88	0.00			0.04
Exc. Magnesium (meq./100g) (sqrt)	$E =$					0.00 (± 0.00)	0.53(± 0.19)	0.02(± 0.23)	0.00 (± 0.00)			0.00 (± 0.00)
	$p =$					0.00	0.01	0.92	0.01			0.18
Exc. Potassium)m eq./100g) (log)	$E =$					0.00 (± 0.00)	0.45(± 0.18)	0.10(± 0.21)	0.00 (± 0.00)			0.00 (± 0.00)
	$p =$					0.05	0.02	0.62	0.10			0.04
Exc. Sodium (meq./100g)	$E =$									0.00 (± 0.00)	0.00 (± 0.00)	0.00 (± 0.00)
	$p =$									0.05	0.00	0.09
Boron (Hot CaCl ₂) (mg/kg)	$E =$					0.00 (± 0.00)					0.00 (± 0.00)	0.00 (± 0.00)
	$p =$					0.29					0.45	0.10
Soil Moisture (% dry mass)	$E =$	- 0.47(± 14.39)	- 17.19 (± 14.03)	- 9.38(± 16.09)	- 9.22(± 14.00)	- 4.80(± 10.26)				26.0 5(± 3.35)	- 0.17 (± 0.09)	0.42 (± 0.15)
	$p =$	0.97	0.23	0.56	0.51	0.64				0.06	0.06	0.01

Table S4: Parameter estimates of soil measures with respect to factors: age, disturbance history category and environmental variables (parent rock type, Australian soil classification, slope, elevation and dominant plant lifeforms) across the 20-30 cm layer of soil, generated using generalized linear models. Disturbance history categories are listed by the year of occurrence of each disturbance event (F= Fire, CC = Clearcut, SL= Salvage logged). Red text indicates significant negative influences, and green text indicates significant positive of corresponding factors on each soil variable. E=parameter estimate ($\pm$ standard error).

		(Intercept)	1939F	1939/1983F	1939F/1980CC	1939/2009F	1939/1983/2009F	1939F/2009CC	1939/2009F/2009SL	1939/1983F/2009CC
Available phosphorus (mg/kg)(log)	E = p =	1.94($\pm$ 0.54) 0.00	- 0.40($\pm$ 0.32) 0.21	- 0.28($\pm$ 0.32) 0.39	- 0.16($\pm$ 0.32) 0.63	- 0.18($\pm$ 0.31) 0.56	- 0.08($\pm$ 0.35) 0.83	- 0.42($\pm$ 0.36) 0.24	- 0.29($\pm$ 0.42) 0.49	- 0.60($\pm$ 0.33) 0.08
Ammonium (mg/kg)(log)	E = p =	2.55($\pm$ 0.30) 0.00	- 0.03($\pm$ 0.16) 0.87	- 0.14($\pm$ 0.17) 0.42	- 0.01($\pm$ 0.16) 0.93	- 0.27($\pm$ 0.15) 0.09	- 0.07($\pm$ 0.19) 0.70	- 0.16($\pm$ 0.17) 0.35	- 0.53($\pm$ 0.16) 0.00	- 0.48($\pm$ 0.16) 0.00
Nitrate(mg/kg)(sqrt)	E = p =	2.82($\pm$ 2.11) 0.19	-3.48($\pm$ 1.05) 0.00	-2.79($\pm$ 1.13) 0.02	-2.16($\pm$ 1.02) 0.04	-2.85($\pm$ 0.95) 0.00	-1.28($\pm$ 1.09) 0.24	-3.69($\pm$ 1.06) 0.00	-3.00($\pm$ 1.37) 0.03	-4.60($\pm$ 1.09) 0.00
Organic carbon (%)	E = p =	4.59($\pm$ 0.83) 0.00	- 0.10($\pm$ 0.50) 0.84	- 0.47($\pm$ 0.51) 0.36	- 0.64($\pm$ 0.50) 0.20	- 0.63($\pm$ 0.49) 0.20	0.05($\pm$ 0.56) 0.93	- 0.05($\pm$ 0.52) 0.93	- 0.49($\pm$ 0.66) 0.46	- 1.52($\pm$ 0.50) 0.00
Available potassium(mg/kg) (log)	E = p =	4.77($\pm$ 0.22) 0.00	0.08($\pm$ 0.22) 0.71	0.32($\pm$ 0.22) 0.15	0.24($\pm$ 0.23) 0.30	0.37($\pm$ 0.22) 0.09	0.82($\pm$ 0.23) 0.00	0.37($\pm$ 0.23) 0.12	0.33($\pm$ 0.28) 0.25	0.13($\pm$ 0.22) 0.58
Sulfur(mg/kg)(log)	E = p =	1.68($\pm$ 0.45) 0.00	0.09($\pm$ 0.22) 0.68	0.08($\pm$ 0.24) 0.73	0.09($\pm$ 0.22) 0.69	0.34($\pm$ 0.20) 0.10	0.49($\pm$ 0.23) 0.04	0.18($\pm$ 0.23) 0.42	0.08($\pm$ 0.29) 0.77	0.11($\pm$ 0.23) 0.64
Conductivity(dS/m)(log)	E = p =	3.64($\pm$ 0.44) 0.00	0.30($\pm$ 0.22) 0.17	0.21($\pm$ 0.23) 0.38	0.09($\pm$ 0.21) 0.67	0.36($\pm$ 0.20) 0.07	0.06($\pm$ 0.23) 0.80	0.30($\pm$ 0.22) 0.18	0.51($\pm$ 0.29) 0.08	0.55($\pm$ 0.23) 0.02
Soil Moisture (%)	E = p =	72.58($\pm$ 9.34) 0.00	- 16.92($\pm$ 5.35) 0.00	- 19.41($\pm$ 29.8) -3.41	- 17.28($\pm$ 5.27) 0.00	- 24.98($\pm$ 4.78) 0.00	- 17.03($\pm$ 5.19) 0.00	- 25.26($\pm$ 5.41) 0.00	- 37.03($\pm$ 5.73) 0.00	- 32.02($\pm$ 6.00) 0.00
Sand (%)	E = p =	9.25($\pm$ 5.56) 0.55	4.03($\pm$ 8.90) 0.65	3.76($\pm$ 9.39) 0.69	1.61($\pm$ 8.69) 0.85	1.51($\pm$ 7.92) 0.85	1.36($\pm$ 8.67) 0.88	3.69($\pm$ 8.93) 0.68	0.04($\pm$ 9.63) 1.00	7.94($\pm$ 9.35) 0.40
Silt (%)	E = p =	104.99($\pm$ 31.95) 0.00	0.27($\pm$ 15.69) 0.99	1.93($\pm$ 16.73) 0.91	0.20($\pm$ 15.67) 0.99	3.95($\pm$ 14.45) 0.79	0.77($\pm$ 16.59) 0.96	4.47($\pm$ 16.26) 0.78	12.79($\pm$ 20.85) 0.54	10.29($\pm$ 16.48) 0.53
Clay (%)	E = p =	21.11($\pm$ 5.78) 0.00	- 6.31($\pm$ 6.44) 0.33	2.61($\pm$ 6.50) 0.69	- 2.05($\pm$ 6.25) 0.74	- 2.42($\pm$ 6.24) 0.70	- 4.66($\pm$ 6.91) 0.50	- 0.51($\pm$ 6.62) 0.94	- 6.07($\pm$ 6.51) 0.35	- 6.06($\pm$ 6.63) 0.36

pH(CaCl ₂)	$E =$ $P =$	4.95(±0.33) < 2e-16	- 0.14(±0.15) 0.36	- 0.07(±0.17) 0.65	- 0.27(±0.15) 0.08	0.09(±0.14) 0.51	0.15(±0.16) 0.33	- 0.10(±0.16) 0.51	0.14(±0.20) 0.49	0.03(±0.16) 0.86
DTPA Copper (mg/kg) (log)	$E =$ $P =$	- 0.98(±0.37) 0.01	- 0.25(±0.40) 0.54	- 0.39(±0.42) 0.35	- 0.38(±0.40) 0.35	0.06(±0.40) 0.88	0.08(±0.44) 0.85	- 0.11(±0.41) 0.79	0.04(±0.41) 0.93	- 0.39(±0.41) 0.34
DTPA Iron (mg/kg)	$E =$ $P =$	- 107.96(±73.89) 0.15	101.28(±45.24) 0.03	112.12(±46.19) 0.02	120.70(±45.38) 0.01	- 9.62(±44.09) 0.83	26.49(±5.27) 0.60	114.44(±47.10) 0.02	27.79(±59.39) 0.64	98.73(±45.28) 0.03
DTPA Manganese(mg/kg) (log)	$E =$ $P =$	1.07(±0.56) 0.06	- 1.32(±0.56) 0.02	- 0.79(±0.57) 0.17	- 0.72(±0.58) 0.22	- 0.67(±0.56) 0.23	- 0.43(±0.59) 0.47	- 0.70(±0.61) 0.26	- 1.20(±0.72) 0.10	- 0.88(±0.60) 0.14
DTPA Zinc (mg/kg) (log)	$E =$ $P =$	- 1.78(±1.00) 0.08	0.32(±0.52) 0.54	0.48(±0.57) 0.40	0.39(±0.51) 0.44	0.16(±0.47) 0.74	0.64(±0.51) 0.21	0.25(±0.53) 0.63	0.69(±0.57) 0.23	0.96(±0.57) 0.09
Exc. Aluminium (meq./100g)	$E =$ $P =$	1.00(±2.37) 0.67	0.70(±1.12) 0.53	- 0.31(±1.21) 0.80	1.26(±1.09) 0.25	- 1.44(±1.02) 0.16	- 1.83(±1.16) 0.12	0.07(±1.14) 0.95	- 1.35(±1.45) 0.36	- 1.98(±1.17) 0.09
Exc. Calcium (meq./100g)(log)	$E =$ $P =$	- 0.44(±0.41) 0.29	- 0.12(±0.45) 0.78	0.71(±0.46) 0.13	- 0.41(±0.44) 0.35	0.82(±0.44) 0.06	1.75(±0.48) 0.00	0.14(±0.46) 0.76	1.05(±0.46) 0.03	0.68(±0.47) 0.15
Exc. Magnesium (meq./100g)(log)	$E =$ $P =$	- 0.94(±0.93) 0.31	0.00(±0.44) 0.99	0.29(±0.48) 0.54	- 0.63(±0.43) 0.15	0.40(±0.40) 0.32	0.89(±0.46) 0.06	0.38(±0.45) 0.40	- 0.33(±0.57) 0.57	0.28(±0.46) 0.55
Exc. Potassium (meq./100g)(log)	$E =$ $P =$	- 1.35(±0.22) 0.00	0.10(±0.22) 0.65	0.32(±0.22) 0.16	0.26(±0.23) 0.26	0.38(±0.22) 0.08	0.89(±0.23) 0.00	0.40(±0.24) 0.10	0.39(±0.29) 0.18	0.03(±0.23) 0.91
Exc. Sodium (meq./100g)(log)	$E =$ $P =$	- 2.54(±0.35) 0.00	0.27(±0.22) 0.22	0.47(±0.23) 0.04	- 0.09(±0.21) 0.66	0.08(±0.20) 0.70	0.29(±0.21) 0.18	0.07(±0.23) 0.78	- 0.18(±0.28) 0.52	- 0.18(±0.23) 0.44
Boron (Hot CaCl ₂)(mg/kg)	$E =$ $P =$	2.08(±0.18) < 2e-16	- 0.69(±0.19) 0.00	- 0.43(±0.19) 0.03	- 0.60(±0.18) 0.00	- 0.71(±0.18) 0.00	- 0.58(±0.20) 0.00	- 0.55(±0.19) 0.01	- 1.42(±0.19) 0.00	- 0.98(±0.19) 0.00

		Sodo sol	Ten sol	Ele vati on	Slo pe	Aca cia	Tre e	Tre e- fern	Euc alyp tus	Gro und- fern	Shr ub	Pare nt rock 2	Pare nt rock 3	Pare nt rock 4	Pare nt rock 5
Available phosphorus (mg/kg) (log)	$E =$ $P =$	- 1.10(±0.33) 0.00	0.54(±0.40) 0.18	0.00(±0.00) 0.01		0.00(±0.00) 0.95	- 0.01(±0.00) 0.01								
Ammonium (mg/kg) (log)	$E =$			0.00(±0.00) - 0.01(±0.00)											

DTPA Manganese(mg/kg) (log)	$E =$ $P =$	1.82(±0.64) 0.01	- 0.77(±0.76) 0.32	0.02 (±0.01) 0.14	- 0.01 (±0.01) 0.04	0.01 (±0.01) 0.04	- 0.01 (±0.01) 0.40	0.02 (±0.01) 0.00							
DTPA Zinc (mg/kg) (log)	$E =$ $P =$			0.02 (±0.02) 0.26		- 0.01 (±0.01) 0.50	- 0.01 (±0.01) 0.01		0.13(±0.87) 0.88	- 0.74(±0.84) 0.38	0.76(±0.96) 0.43	0.25(±0.83) 0.76			
Exc. Aluminium (meq./100g)	$E =$ $P =$	- 3.26(±1.05) 0.00	- 0.07(±1.27) 0.96	0.00 (±0.00) 0.01	- 0.07 (±0.03) 0.01	0.02 (±0.01) 0.13		0.03 (±0.01) 0.00	1.60(±1.45) 0.27	1.72(±1.41) 0.23	0.12(±1.61) 0.94	2.03(±1.39) 0.15			
Exc. Calcium (meq./100g)(log)	$E =$ $P =$					- 0.01 (±0.01) 0.12		0.02 (±0.01) 0.02	- 0.01 (±0.01) 0.02						
Exc. Magnesium (meq./100g)(log)	$E =$ $P =$	1.14(±0.42) 0.01	- 0.41(±0.51) 0.42	0.00 (±0.00) 0.14	0.02 (±0.01) 0.07	- 0.01 (±0.01) 0.03		0.02 (±0.01) 0.00	- 0.01 (±0.00) 0.01	0.62(±0.58) 0.29	0.58(±0.56) 0.31	0.79(±0.63) 0.21	- 0.02(±0.55) 0.97		
Exc. Potassium (meq./100g)(log)	$E =$ $P =$	0.55(±0.25) 0.03	- 0.16(±0.29) 0.59	0.01 (±0.01) 0.07	- 0.01 (±0.00) 0.00		0.00 (±0.00) 0.11	0.00 (±0.00) 0.09							
Exc. Sodium (meq./100g)(log)	$E =$ $P =$	0.08(±0.22) 0.71	- 0.57(±0.27) 0.04			0.00 (±0.00) 0.02	0.00 (±0.00) 0.06	- 0.01 (±0.00) 0.04	0.01 (±0.00) 0.01	0.00 (±0.00) 0.10	- 0.01 (±0.00) 0.01	- 0.04(±0.29) 0.88	- 0.31(±0.28) 0.27	- 0.11(±0.32) 0.72	- 0.22(±0.27) 0.43
Boron (Hot CaCl ₂)(mg/k g)	$E =$ $P =$			- 0.01 (±0.01) 0.09	- 0.01 (±0.00) 0.01	0.01 (±0.00) 0.10		0.00 (±0.00) 0.18							

Table S5: Parameter estimates of soil measures with respect to factors: age, disturbance (fire and clearcut and salvage logging) and environmental variables (parent rock type, Australian soil classification, slope, elevation and dominant plant lifeforms) across the top 0-10 cm layer of soil, generated using generalized linear models. Red text indicates significant negative influences, and green text indicates significant positive of corresponding factors on each soil variable.

		(Intercept)	Clearcut logging	2 Fires	3 Fires	Salvage logging	Age =34 years	Age= 78 years
Ammonium (mg/kg) (sqrt)	$E =$ $P =$	5.84(±1.56) 0.00	-2.28(±0.75) 0.00	- 1.99(±0.82) 0.02	-2.42(±1.21) 0.05	-2.61(±0.78) 0.00	0.95(±0.60) 0.12	0.08(±1.18) 0.95
Nitrate (mg/kg)	$E =$ $P =$	- 8.22(±47.35) 0.86	- 33.91(±16.03) 0.04	- 45.85(±16.54) 0.01	- 23.80(±25.07) 0.35	- 0.62(±25.74) 0.98	21.06(±12.74) 0.10	- 33.52(±23.82) 0.16
Organic carbon (%)	$E =$ $P =$	5.28(±0.12) < 2e-16	-0.05(±0.13) 0.69	- 0.35(±0.13) 0.01	0.15(±0.22) 0.51	-0.31(±0.17) 0.08		
Conductivity (dS/m)	$E =$ $P =$	- 1.68(±0.50) 0.00	-0.15(±0.17) 0.37	- 0.25(±0.17) 0.16	0.09(±0.27) 0.74	0.08(±0.27) 0.78	0.40(±0.14) 0.01	0.12(±0.25) 0.62
Available phosphorus (mg/kg) (log)	$E =$ $P =$	2.69 (±0.40) 0.00	-0.78 (±0.18) 0.00	-0.82 (±0.18) 0.00	-0.39 (±0.29) 0.19	0.05 (±0.33) 0.88	2.69 (±0.40) 0.00	-0.78 (±0.18) 0.00
Silt (%)	$E =$ $P =$	39.34(±18.86) 0.04	-3.76(±4.14) 0.37	- 7.53(±4.30) 0.08	-8.16(±7.58) 0.29	5.79(±5.76) 0.32		
Sand (%)	$E =$ $P =$	5.95 (±13.10) 0.65	14.07 (±5.28) 0.01	15.99 (±5.73) 0.01	21.79 (±8.36) 0.01	0.07 (±5.38) 0.99	3.44 (±4.17) 0.41	17.41 (±7.99) 0.03
Available potassium(mg/kg)(log)	$E =$ $P =$	6.14(±0.18) < 2e-16	-0.36(±0.06) 0.00	0.04(±0.06) 0.48	0.58(±0.11) 0.00	-0.28(±0.16) 0.08		
Clay (%)	$E =$ $P =$	43.74(±8.00) 0.00	-0.77(±2.59) 0.77	2.90(±2.78) 0.30	0.67(±4.72) 0.89	-0.43(±3.68) 0.91		
Sulfur(mg/kg)(log)	$E =$ $P =$	1.99(±0.28) 0.00	-0.12(±0.12) 0.33	- 0.32(±0.12) 0.01	-0.52(±0.20) 0.01	-0.04(±0.23) 0.85	0.45(±0.09) 0.00	0.45(±0.18) 0.02
pH (CaCl ₂)	$E =$ $P =$	4.90(±0.41) < 2e-16	0.06(±0.13) 0.64	0.38(±0.14) 0.01	0.73(±0.20) 0.00	-0.10(±0.21) 0.63	- 0.28(±0.10) 0.01	- 0.14(±0.19) 0.48
DTPA Copper (mg/kg)(log)	$E =$ $P =$	2.51(±0.99) 0.01	-0.75(±0.33) 0.03	- 0.07(±0.35) 0.84	0.08(±0.52) 0.88	-0.98(±0.53) 0.07	- 0.43(±0.26) 0.10	- 1.08(±0.49) 0.03
DTPA Iron(mg/kg)	$E =$	77.97 (±91.88)	-9.08 (±21.07)	-79.92 (±21.43)	-127.16 (±33.37)	-170.88 (±30.45)		

	$P =$	0.40	0.67	0.00	0.00	0.00		
DTPA Manganese(mg/kg) (sqrt)	$E =$ $P =$	3.29 (±0.79) 0.00	0.11 (±0.29) 0.70	0.11 (±0.25) 0.67	0.36 (±0.42) 0.39	-0.85 (±0.65) 0.20	3.29 (±0.79) 0.00	0.11 (±0.29) 0.70
DTPA Zinc (mg/kg) (log)	$E =$ $P =$	2.05(±0.65) 0.00	-0.42(±0.16) 0.01	0.17(±0.15) 0.26	0.36(±0.25) 0.17	0.02(±0.20) 0.90		
Exc. Aluminium(meq./100)	$E =$ $P =$	0.99(±2.21) 0.65	0.11(±0.91) 0.90	- 3.07(±0.94) 0.00	-5.18(±1.40) 0.00	1.68(±1.46) 0.25	2.58(±0.72) 0.00	1.54(±1.35) 0.26
Exc. Calcium(meq./100) (log)	$E =$ $P =$	2.08(±0.45) 0.00	-0.63(±0.16) 0.00	0.24(±0.15) 0.12	1.05(±0.26) 0.00	-0.81(±0.39) 0.04		
Exc. Potassium(meq./100)(log)	$E =$ $P =$	0.04 (±0.18) 0.84	-0.36 (±0.06) 0.00	-0.02 (±0.06) 0.73	0.60 (±0.10) 0.00	-0.17 (±0.16) 0.29		
Exc. Sodium(meq./100)	$E =$ $P =$	0.12(±0.01) < 2e-16	-0.04(±0.01) 0.00	0.00(±0.01) 0.94	0.00(±0.02) 0.80	-0.07(±0.01) 0.00		
Exc. Magnesium (meq./100)(log)	$E =$ $P =$	0.63 (±0.16) 0.00	-0.30 (±0.06) 0.00	0.03 (±0.05) 0.52	0.24 (±0.09) 0.01	-0.48 (±0.14) 0.00	0.63 (±0.16) 0.00	-0.30 (±0.06) 0.00
Soil moisture (% dry mass)	$E =$ $P =$	78.72(±19.38) 0.00	-2.65(±6.60) 0.69	5.96(±7.01) 0.40	0.93(±10.30) 0.93	-5.49(±6.77) 0.42	18.23(±5.25) 0.00	14.29(±9.81) 0.15
Boron (Hot CaCl ₂)(mg/kg)	$E =$ $P =$	2.28(±0.19) < 2e-16	-0.59(±0.15) 0.00	0.61(±0.15) 0.00	-0.36(±0.24) 0.14	-0.84(±0.15) 0.00	0.40(±0.12) 0.00	0.29(±0.23) 0.21

		Parent rock 2	Parent rock 3	Parent rock 4	Parent rock 5	Elevation	Slope	Sodosol	Eucalyptus	Ground-fern	Acacia	Shrub	Tree	Tree-fern
Ammonium (sqrt)(mg/kg)	$E =$ $P =$		0.63(±0.62) 0.31	1.29(±0.99) 0.2	0.94(±0.60) 0.12	0.003 (±0.00) 0.07			0.02(±0.01) 0.13		0.02(±0.01) 0.03			
Nitrate (mg/kg)	$E =$ $P =$	34.41(±33.85) 0.31	56.26(±33.30) 0.10	7.02(±37.63) 0.85	26.18(±33.27) 0.43	0.06(±0.04) 0.09		49.81(±25.53) 0.06				0.29(±0.23) 0.21		0.75(±0.35) 0.04
Organic carbon (%)	$E =$ $P =$													
Conductivity (dS/m)	$E =$ $P =$	- 0.97(±0.36) 0.01	- 0.95(±0.36) 0.01	- 1.04(±0.40) 0.01	- 0.95(±0.35) 0.01	0.00(±0.00) 0.05		0.47(±0.27) 0.09		0.01(±0.00) 0.14				0.01(±0.00) 0.03
Available phosphorus (log)(mg/kg)	$E =$ $P =$					0.00 (±0.00) 0.13	0.02 (±0.02) 0.15	2.75 (±0.69) 0.00			-0.01 (±0.01) 0.09		0.01 (±0.01) 0.03	0.03 (±0.01) 0.00

Silt (%)	$E =$ $P =$	4.04(± 15.49)	- 14.48(± 15.27)	3.79(± 17.17)	9.80(± 15.19)	0.02(± 0.02)		
Sand (%)	$E =$ $P =$	-3.88 (± 11.41)	13.55 (± 11.16)	3.47 (± 12.65)	-4.19 (± 11.18)			0.13 (± 0.07)
Available potassium(log)	$E =$ $P =$					0.00(± 0.00)	0.54(± 0.18)	0.00(± 0.00)
Clay (%)	$E =$ $P =$					0.01	0.00	0.02
	$E =$ $P =$					- 0.03(± 0.01)		- 0.17(± 0.07)
Sulfur (log)(mg/kg)	$E =$ $P =$					0.00(± 0.00)	- 0.58(± 0.24)	0.00(± 0.00)
pH (CaCl ₂)	$E =$ $P =$	- 0.70(± 0.28)	- 0.66(± 0.28)	- 0.57(± 0.32)	- 0.72(± 0.28)	0.00(± 0.00)	0.01(± 0.01)	0.51(± 0.20)
DTPA Copper (log)(mg/kg)	$E =$ $P =$	- 2.06(± 0.71)	- 1.56(± 0.69)	- 1.06(± 0.79)	- 1.57(± 0.69)	0.00(± 0.00)	1.00(± 0.53)	
DTPA Iron(mg/kg)	$E =$ $P =$	94.94 (± 70.24)	161.15 (± 69.13)	80.26 (± 77.70)	112.27 (± 67.83)	0.19 (± 0.07)	-3.34 (± 1.32)	-0.81 (± 0.47)
DTPA Manganese(sqrt) (mg/kg)	$E =$ $P =$					0.00(± 0.00)	0.61(± 0.18)	0.01(± 0.00)
DTPA Zinc (log)(mg/kg)	$E =$ $P =$	- 0.93(± 0.52)	- 1.26(± 0.51)	- 0.92(± 0.58)	- 0.80(± 0.51)	0.00(± 0.00)		0.01(± 0.00)
Exc. Aluminium(meq./100)	$E =$ $P =$	5.70(± 1.92)	3.92(± 1.89)	4.42(± 2.13)	4.81(± 1.88)	- 1.87(± 1.38)		0.04(± 0.01)
Exc. Calcium(log)(meq./100)	$E =$ $P =$					0.00(± 0.00)	0.95(± 0.43)	0.01(± 0.00)
Exc. Potassium(log)(meq./100)	$E =$ $P =$					0.00 (± 0.00)	0.49 (± 0.18)	0.00 (± 0.00)
Exc. Sodium(meq./100)	$E =$ $P =$							0.00(± 0.00)

Exc. Magnesium(log) (meq./100)	$E =$					0.00 (±0.0 0)	0.46 (±0.15)			0.00 (±0.0 0)	0.00 (±0.0 0)	
	$p =$					0.00	0.00			0.05	0.01	
Boron (Hot CaCl ₂)(mg/kg)	$E =$									- 0.01(±0.00)	0.01(±0.00)	
	$p =$									0.03	0.01	
Soil moisture (% dry mass)	$E =$	- 0.52(± 13.91)	- 17.43(± 13.66)	- 6.79(± 15.54)	- 10.08(± 13.65)	- 0.02(±0.02)					- 0.21(±0.09)	0.42(±0.14)
	$p =$	0.97	0.21	0.66	0.46	0.23					0.03	0.00

Table S6: Parameter estimates of soil measures with respect to factors: age, disturbance (fire and clearcut and salvage logging) and environmental variables (parent rock type, Australian soil classification, slope, elevation and dominant plant lifeforms) across the 20-30 cm layer of soil, generated using generalized linear models. Red text indicates significant negative influences, and green text indicates significant positive of corresponding factors on each soil variable.

		(Intercept)	2 Fires	3 Fires	Clearcut logging	Salvage logging	Age =34 years	Age= 78 years
Nitrate (mg/kg)	$E =$ $p =$	-13.01 ($\pm$ 18.28) 0.48	-7.26 ($\pm$ 6.51) 0.27	9.72 ($\pm$ 9.56) 0.31	-9.16 ($\pm$ 6.12) 0.14	-0.89 ($\pm$ 9.91) 0.93	8.49 ($\pm$ 4.87) 0.09	-12.69 ($\pm$ 9.09) 0.17
Organic carbon (%)	$E =$ $p =$	5.71($\pm$ 0.17) < 2e-16	$\bar{0.55(\pm 0.16)}$ 0.00	0.24($\pm$ 0.27) 0.37	$\bar{-0.55(\pm 0.15)}$ 0.00	0.21($\pm$ 0.40) 0.60		
Conductivity(dS)(log)	$E =$ $p =$	-3.24 ($\pm$ 0.25) < 2e-16	-0.19 ($\pm$ 0.12) 0.11	0.27 ($\pm$ 0.17) 0.13	-0.10 ($\pm$ 0.11) 0.35	-0.06 ($\pm$ 0.20) 0.75	0.22 ($\pm$ 0.09) 0.02	-0.14 ($\pm$ 0.17) 0.40
Available phosphorus(mg/kg)(sqrt)	$E =$ $p =$	1.85($\pm$ 0.54) 0.00	$\bar{0.57(\pm 0.23)}$ 0.02	0.08($\pm$ 0.37) 0.83	$\bar{-0.62(\pm 0.22)}$ 0.01	0.31($\pm$ 0.41) 0.46	0.32($\pm$ 0.17) 0.07	0.54($\pm$ 0.34) 0.11
Silt(%)	$E =$ $p =$	88.02($\pm$ 18.07) 0.00	$\bar{5.76(\pm 5.62)}$ 0.31	2.73($\pm$ 9.32) 0.77	-4.81($\pm$ 5.32) 0.37	6.83($\pm$ 13.62) 0.62		
Sand(%)	$E =$ $p =$	10.38($\pm$ 13.03) 0.43	1.32($\pm$ 4.06) 0.75	3.53($\pm$ 6.72) 0.60	3.30($\pm$ 3.84) 0.39	14.91($\pm$ 9.82) 0.13		
Clay(%)	$E =$ $p =$	18.86($\pm$ 4.18) 0.00	$\bar{7.99(\pm 3.11)}$ 0.01	2.01($\pm$ 5.18) 0.70	4.48($\pm$ 3.26) 0.17	4.80($\pm$ 7.88) 0.54		
Available potassium(mg/kg) (log)	$E =$ $p =$	5.37($\pm$ 0.17) < 2e-16	$\bar{0.21(\pm 0.13)}$ 0.11	0.22($\pm$ 0.19) 0.27	$\bar{-0.26(\pm 0.12)}$ 0.04	0.06($\pm$ 0.22) 0.78	0.09($\pm$ 0.10) 0.33	$\bar{0.52(\pm 0.19)}$ 0.01
Ammonium(mg/kg)(sqrt)	$E =$ $p =$	3.45 ($\pm$ 0.64) 0.00	$\bar{-0.71 (\pm 0.28)}$ 0.01	-0.34 ($\pm$ 0.43) 0.43	$\bar{-1.03 (\pm 0.27)}$ 0.00	-0.37 ($\pm$ 0.49) 0.45	0.78 ($\pm$ 0.21) 0.00	-0.22 ($\pm$ 0.39) 0.57
Sulfur(mg/kg)(log)	$E =$ $p =$	1.22($\pm$ 0.39) 0.00	0.08($\pm$ 0.14) 0.58	0.03($\pm$ 0.21) 0.90	0.24($\pm$ 0.13) 0.07	0.32($\pm$ 0.21) 0.14	0.32($\pm$ 0.11) 0.01	0.33($\pm$ 0.19) 0.10
pH(CaCl ₂)	$E =$ $p =$	4.92 ($\pm$ 0.29) < 2e-16	0.10 ($\pm$ 0.10) 0.30	0.19 ($\pm$ 0.14) 0.19	-0.07 ($\pm$ 0.09) 0.45	0.10 ($\pm$ 0.15) 0.49	$\bar{-0.15 (\pm 0.07)}$ 0.04	-0.10 ($\pm$ 0.13) 0.44
DTPA Copper (mg/kg)(log)	$E =$ $p =$	$\bar{1.14(\pm 0.25)}$ 0.00	$\bar{0.03(\pm 0.20)}$ 0.88	0.25($\pm$ 0.33) 0.46	-0.12($\pm$ 0.19) 0.54	0.23($\pm$ 0.30) 0.44		
DTPA Iron (mg/kg)	$E =$	$\bar{134.03(\pm 94.03)}$	$\bar{18.39(\pm 31.88)}$	$\bar{13.45(\pm 46.93)}$	47.84($\pm$ 29.1.)	$\bar{24.60(\pm 47.44)}$	42.08($\pm$ 23.1.)	57.49($\pm$ 44.0.)

	$P =$	0.16	0.57	0.78	0.11	0.61	0.07	0.20
DTPA Manganese (mg/kg)(log)	$E =$ $P =$	0.50(±0.44)	0.25(±0.33))	0.00(±0.49))	-0.09(±0.32)	0.40(±0.55)	0.23(±0.26))	0.98(±0.49)) 0.05
DTPA Zinc(mg/kg)(log)	$E =$ $P =$	-1.52(±0.85)	0.27(±0.25))	0.55(±0.39))	0.32(±0.26)	0.23(±0.38)		
Exc. Aluminium (meq./100g)	$E =$ $P =$	1.82 (± 2.08)	-1.84 (± 0.72)	-2.39 (± 1.03)	-0.47 (± 0.65)	-0.21 (± 1.08)	1.09 (± 0.53)	0.15 (± 0.97)
Exc. Calcium (meq./100g)	$E =$ $P =$	-0.50(±0.25)	0.84(±0.21))	1.82(±0.36))	-0.09(±0.22)	0.26(±0.31)		
Exc. Potassium (meq./100g)	$E =$ $P =$	0.51(±0.07)	0.11(±0.05))	0.20(±0.08))	-0.18(±0.05)	0.00(±0.09)	0.04(±0.04))	0.24(±0.07)) 0.00
Exc. Sodium (log) (meq./100g)	$E =$ $P =$	-2.00(±0.22)	0.05(±0.08))	0.06(±0.14))	-0.42(±0.09)	0.45(±0.13)		
Exc Magnesium(log) (meq./100g)	$E =$ $P =$	-0.39(±0.55)	0.47(±0.24))	0.87(±0.37))	-0.15(±0.23)	0.69(±0.43)	0.29(±0.19))	0.29(±0.35)) 0.42
Soil Moisture (%)	$E =$ $P =$	58.66(±8.92)	12.40(±3.95))	3.19(±5.68))	11.16(±3.68))	0.25(±6.03)	6.20(±2.92))	5.03(±5.47)) 0.36
Boron (Hot CaCl ₂)(mg/kg)	$E =$ $P =$	0.75(±0.13)	0.34(±0.10))	0.28(±0.16))	-0.36(±0.10)	0.57(±0.18)	0.10(±0.08))	0.36(±0.15)) 0.02

		Elevatio n	Slope	Sodosol	Parent rock 2	Parent rock 3	Parent rock 4	Parent rock 5	Tree	Tree- fern	Acacia	Shrub	Eucalyptus	Ground- fern
Nitrate (mg/kg)	$E =$ $P =$	0.04 (± 0.01)		-26.78 (± 9.75)	17.57 (± 12.90)	18.19 (± 12.67)	-2.28 (± 14.42)	14.15 (± 12.66)	-0.20 (± 0.09)	0.40 (± 0.13)				
Organic carbon (%)	$E =$ $P =$			-0.76(± 0.45)					0.01(±0.0)				0.01(±0.01)	
Conductivity(dS)(log)	$E =$ $P =$	0.00 (±0.00)		-0.73 (±0.22)					0.00 (±0.00)	0.01 (±0.00)			0.00 (±0.00)	
Available phosphorus(mg/kg)(sqrt)	$E =$	0.00(±0.00)	-0.02(±0.01)	-1.91(± 0.44)									0.06	

	$p =$							± 0.01	± 0.01	
								0.03	0.02	0.02
Exc. Potassium (meq./100g)	$E =$	0.09(± 0.09)						0.00(± 0.00)		0.00(± 0.00)
	$p =$	0.32						0.03		0.06
Exc. Sodium (log) (meq./100g)	$E =$	0.00(± 0.00)						-0.01(± 0.00)	0.01(± 0.00)	-0.01(± 0.00)
	$p =$	0.10						0.07	0.01	0.00
Exc Magnesium(log) (meq./100g)	$E =$	0.00(± 0.00)	0.01(± 0.01)	1.06(± 0.46)				-0.01(± 0.01)	-0.01(± 0.00)	0.01(± 0.01)
	$p =$	0.18	0.30	0.02				0.22	0.03	0.04
Soil Moisture (%)	$E =$	-10.71(± 5.58)	4.69(± 7.77)	6.04(± 7.65)	3.04(± 8.62)	4.64(± 7.64)		-0.14(± 0.05)	0.12(± 0.08)	0.09(± 0.06)
	$p =$	0.06	0.55	0.43	0.73	0.55		0.01	0.14	0.12
Boron (Hot CaCl_2)(mg/kg)	$E =$	-0.01(± 0.00)	-0.36(± 0.19)					0.00(± 0.00)	0.00(± 0.00)	
	$p =$	0.02	0.06					0.01	0.06	

Table S7: Parameter estimates of soil chemical and measures with respect to factors: disturbance (fire and clearcut and salvage logging) and environmental variables (parent rock type, Australian soil classification, slope, elevation and dominant plant lifeforms) across the 0-10 cm and 20-30 cm layers of soil and sites last disturbed in 2009, generated using generalized linear models. Red text indicates significant negative influences, and green text indicates significant positive of corresponding factors on each soil variable.

Soil measure	Depth		(Intercept)	2 Fires	3 Fires	Clearcut logging	Salvage logging
Nitrate (sqrt)(mg/kg)	0-10 cm	$E =$	5.86(± 1.04)	-	-	-	-
		$p =$	0.00	0.65(± 0.74)	0.32(± 1.16)	-1.85(± 0.80)	1.57(± 1.27)
Nitrate (mg/kg)	20-30 cm	$E =$	5.09(± 9.66)	0.39	0.78	0.03	0.23
		$p =$	0.60	8.76(± 4.50)	2.16(± 6.76)	-2.58(± 5.68)	12.22(± 7.30)
Ammonium(mg/kg)(sqrt)	0-10 cm	$E =$	6.56(± 0.84)	-	-	-	-
		$p =$	0.00	0.66(± 0.71)	0.89(± 1.02)	-0.93(± 0.79)	-1.03(± 0.82)
Ammonium(mg/kg)(sqrt)	20-30 cm	$E =$	4.31(± 0.61)	0.36	0.39	0.24	0.22
		$p =$	0.00	0.94(± 0.34)	0.61(± 0.46)	-0.76(± 0.36)	-0.51(± 0.35)
Organic carbon (%)	0-10 cm	$E =$	5.24(± 0.26)	-	-	-	-
		$p =$	<2e-16	0.42(± 0.23)	0.14(± 0.33)	-0.06(± 0.21)	-0.45(± 0.23)
Organic carbon (%)	20-30 cm	$E =$	5.01(± 0.87)	0.07	0.66	0.78	0.06
		$p =$	0.00	1.53(± 0.35)	0.73(± 0.50)	-0.86(± 0.32)	0.25(± 0.59)
Available phosphorus (mg/kg)(log)	0-10 cm	$E =$	3.48(± 0.29)	-	-	-	-
		$p =$	0.00	0.55(± 0.22)	0.60(± 0.35)	-0.99(± 0.24)	-0.12(± 0.38)
Available phosphorus (mg/kg)(log)	20-30 cm	$E =$	2.38	0.02	0.10	0.00	0.75
		$p =$	0.00	-0.11	-0.13	-0.45 (± 0.18)	-0.21 (± 0.33)
Available potassium (mg/kg)(log)	0-10 cm	$E =$	5.83(± 0.12)	-	-	-	-
		$p =$	< 2e-16	0.18(± 0.10)	0.48(± 0.15)	-0.46(± 0.10)	-0.16(± 0.17)
Available potassium (mg/kg)(log)	20-30 cm	$E =$	5.87(± 0.25)	0.09	0.00	0.00	0.34
		$p =$	< 2e-16	0.55(± 0.19)	0.03(± 0.27)	-0.65(± 0.23)	-0.41(± 0.29)
Sulfur (mg/kg)(sqrt)	0-10 cm	$E =$	3.48(± 0.24)	-	-	-	-
		$p =$	< 2e-16	0.43(± 0.19)	0.90(± 0.29)	-0.23(± 0.19)	-0.23(± 0.34)
Sulfur (mg/kg)(sqrt)	20-30 cm	$E =$	1.63(± 0.47)	0.03	0.00	0.23	0.49
		$p =$	0.00	0.43(± 0.23)	0.18(± 0.33)	0.76(± 0.31)	0.93(± 0.36)

Soil measure	Depth		Sodo sol	Slope	Elevation	Parent rock 3	Parent rock 4	Parent rock 5	Shrub	Acacia	Tree-fern	Eucalyptus	Tree	Ground-fern
Nitrate (sqrt)(mg/kg)	0-10 cm	$E =$	5.08(± 1.26)	0.08(± 0.04)					0.03 (± 0.01)	0.03 (± 0.01)	0.26 (± 0.09)			
		$p =$	0.00	0.05					0.02	0.03	0.00			

Nitrate (mg/kg)	20-30 cm	$E =$	- 24.70 (±5.83)	0.03(±0.01)	- 6.55(±4.45)	- 14.74 (±6.10)	- 11.67 (±3.40)	0.12 (±0.06)	1.90(±0.41)
		$p =$	0.00	0.01	0.15	0.02	0.00	0.06	0.00
Ammonium(mg/kg)(sqrt)	0-10 cm	$E =$			0.66(±0.68)	1.03(±0.84)	0.64(±0.51)	0.03(±0.01)	0.02(±0.01)
		$p =$			0.33	0.23	0.21	0.00	0.06
Ammonium(mg/kg)(sqrt)	20-30 cm	$E =$		0.00(±0.00)	0.03(±0.30)	0.80(±0.39)	0.36(±0.24)	0.01(±0.00)	0.01(±0.00)
		$p =$		0.03	0.92	0.05	0.13	0.06	0.21
Organic carbon (%)	0-10 cm	$E =$						0.01(±0.01)	
		$p =$						0.12	
Organic carbon (%)	20-30 cm	$E =$	- 1.48(±0.61)	0.00(±0.00)					- 0.01(±0.01)
		$p =$	0.02	0.11					0.13
Available phosphorus (mg/kg)(log)	0-10 cm	$E =$	0.52(±0.38)					0.01 (±0.00)	0.01(±0.00)
		$p =$	0.18					0.07	0.11
Available phosphorus (±mg/kg)(±log)	20-30 cm	$E =$	-0.97 (±0.34)	0.00 (±0.00)					-0.01 (±0.00)
		$p =$	0.01	0.23					0.01
Available potassium (mg/kg)(log)	0-10 cm	$E =$	0.27(±0.17)						0.00(±0.00)
		$p =$	0.12						0.07
Available potassium (mg/kg)(log)	20-30 cm	$E =$	0.60(±0.25)	0.01(±0.01)	0.27(±0.18)	0.35(±0.24)	0.15(±0.14)	0.01(±0.00)	0.03(±0.02)
		$p =$	0.02	0.18	0.15	0.15	0.31	0.00	0.05
Sulfur (mg/kg)(sqrt)	0-10 cm	$E =$	0.53(±0.34)					0.01 (±0.00)	
		$p =$	0.13					0.10	
Sulfur (mg/kg)(sqrt)	20-30 cm	$E =$	1.54(±0.30)	0.00(±0.00)	0.42(±0.22)	0.57(±0.31)	0.38(±0.19)	0.05(±0.02)	- 0.01(±0.00)
		$p =$	0.00	0.04	0.07	0.08	0.05	0.03	0.00

Chapter 3

Fire and logging regimes alter functional communities of fungi

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Abstract

Fungi perform critical functions in forest ecosystems. They stabilize soils, provide important food resources for animals, form symbiotic mycorrhizal relationships with ~80% of terrestrial plant species, and facilitate decomposition, biogeochemical cycling and the transfer of resources between plants. Global increases in the frequency of ecological disturbances are driving major changes to the structure and function of forests. However, the impacts of disturbance on below-ground fungal communities are largely unknown. Here for the first time, we used DNA and RNA metabarcoding across two soil depths to explore how these often-cryptic communities are influenced by disturbances in some of the world's tallest and most carbon-dense forests, the Mountain Ash forests of southeastern Australia. We provide evidence that the number of fires, clearcut logging and salvage logging can alter the composition of fungal communities, and the relative abundance and richness of functional groups, controlling for spatial variation, time since disturbance and other environmental variables. The responses of fungal communities differed between logged forest and forest burned by wildfire alone. For instance, clearcut logging resulted in a lower richness of total symbiotrophic fungi and arbuscular mycorrhizal (AM) fungi across both soil depths. Similarly, two and three wildfires resulted in a lower richness of AM fungi, but were associated with increases in the richness of ectomycorrhizal (EcM) fungi in the 0-10 cm depth of soil. In contrast, post-fire salvage logged forests had a higher richness of pathotrophic and saprotrophic fungi, relative to unlogged forests. Disturbance impacts were evident across both RNA and DNA-derived datasets, reinforcing our findings that both active (RNA and DNA) and potentially inactive (DNA) fungal communities are significantly altered by disturbance. Our study shows that disturbance-driven changes to fungal communities may have implications for the diversity and expected function of forest ecosystems.

Keywords: *disturbance regimes, wildfire, fungi, clearcut logging, Eucalyptus regnans, community ecology*

Manuscript highlights

- We describe the fungal biome of an iconic Australian forest using metabarcoding.
- Natural and human disturbances in this ecosystem altered fungal communities.
- Disturbance impacts on fungi may have functional implications in forests.

INTRODUCTION

Wildfire is a major driver of the structure and function of forests worldwide, and influences both above and below-ground ecological patterns, processes and biological communities (Ashton 1981; Bond and others 2005; Bowman and others 2009; Seidl and others 2014a; Fraver and others 2017). In recent decades, widespread climatic changes and increases in anthropogenic disturbance have increased the frequency and intensity of wildfires across many terrestrial ecosystems (Bond and others 2005; Bowman and others 2009; Seidl and others 2014b). Novel intensities and frequencies of wildfires now characterize disturbance patterns in conifer forests of the Pacific north-west of the USA (Odion and others 2004; Thompson and others 2007), Brazilian Amazonian rainforests (Cochrane and Laurance 2008), European forests (Seidl and others 2014b), and the wet sclerophyll forests of southeastern Australia (Lindenmayer, Hobbs, Likens, Krebs, & Banks, 2011; Taylor, McCarthy, & Lindenmayer, 2014; Zylstra, 2018). The impact of disturbances on above-ground communities in these ecosystems are well characterised (Barlow and others 2016; Blair and others 2016; Welch and others 2016; Thom and others 2017). However, how disturbances affect functionally critical, below-ground soil communities, like fungi are comparatively poorly understood (Hartmann and others 2012; Kurth and others 2013; Egidi and others 2016; Bahram and others 2018).

Advances in DNA sequencing technology have paved the way for the exploration of cryptic soil microbial communities, including fungi, enabling a detailed understanding of the ecological functions of biodiversity components in forest ecosystems (Bálint and others 2016). Fungi are the most diverse and abundant eukaryotic microbial community in soils, and have key functions in ecosystems (Bahram and others 2018). These include: **(a)** stabilizing soils and preventing nutrient leaching (Claridge and others 2009; Martínez-García and others 2017), **(b)** facilitating decomposition, biogeochemical cycling (Lundell and others 2014), and the transfer of resources between plants (including carbon and nitrogen), which increases plant seedling survival (Teste and others 2009; Klein and others 2016; Martin and others 2016), **(c)** acting as an important animal food source (Trappe and others 2005; Nuske and others 2019), and **(d)** forming symbiotic mycorrhizal relationships with ~90% of terrestrial plant families (Selosse and others 2006; Martin and others 2016; Bahram and others 2018).

Globally, forest ecosystems are colonized by, and depend on, mycorrhizal fungi that form complex underground networks, commonly described as the “wood-wide web” (Martin and

others 2016). Mycorrhizal fungi play an integral role in the global carbon cycle, where the majority either form a mantle around (ecto-mycorrhizal) or penetrate (arbuscular mycorrhizal) plant root tips, assisting in the acquisition of nitrogen and phosphorus in exchange for carbon, receiving up to 20-40% of plant photosynthates (Selosse and others 2006; Averill and others 2014; Martin and others 2016). Millions of hectares of mycorrhizal-dependent forests are subjected to intensive clearcut and salvage logging annually (Cochrane & Laurance, 2008; Correia, Raulier, Bouchard, & Filotas, 2018; Leverkus, Lindenmayer, Thorn, & Gustafsson, 2018; Lindenmayer and others, 2011; Seidl and others, 2014). The cumulative effect of these disturbances, coupled with climatic changes, and subsequent increases in the intensity and frequency of wildfires can alter the structure and function of fungal communities (Cairney and Bastias 2007; Hartmann and others 2012; Egidio and others 2016; Reazin and others 2016; Dove and Hart 2017; Day and others 2019). This can have cascading effects on plant communities (Scott and others 2013; van der Putten and others 2013), decomposition rates and carbon cycling (Averill and others 2014; Philpott and others 2018) through biological interactions and feedbacks (Wardle and others 2004; van der Putten and others 2013; Averill and others 2014; Teste and others 2017; Philpott and others 2018).

Previous studies in boreal and temperate forests across the globe have found short-term to mid-term changes in fungal communities following single disturbance events (Byrd, Parker, Vogler, & Cullings, 2000; Chen & Cairney, 2002; Day and others, 2019; Hartmann and others, 2012; Jones and others, 2003; Mah, Tackaberry, Egger, & Massicotte, 2001; McMullan-Fisher, May, & Keane, 2002; Reazin and others, 2016; Whitman and others, 2019; Wilhelm and others, 2017). However, comparatively few studies have observed longer-term effects (Visser 1995; Varenium and others 2016; Mushinski and others 2018) or cumulative effects of altered disturbance regimes on fungal communities. Further, a majority of these studies have focused solely on mycorrhizal fungi, with little consideration of total fungal communities and their respective functional traits (Cairney & Bastias, 2007; Taylor and others, 2010). Here, we address these knowledge gaps by simultaneously quantifying the responses of total fungal communities and their respective functional traits to both wildfire and clearcut and salvage logging across a multi-decadal chronosequence in Mountain Ash (*Eucalyptus regnans*) forests in southeastern Australia. Specifically, to do this, we used metabarcoding to identify fungi from DNA and RNA, across two depths of forest soils to address two important questions: 1. What is the effect of the number of fires on fungal community composition and functional groups of fungi? 2. What is the effect of clearcut

logging and post-fire salvage logging on fungal community composition and functional groups of fungi?

While some fungal species possess heat-resistant mycelia and spore banks that allow them to withstand the impacts of wildfire and post-logging slash-burning, others can perish under extreme soil temperatures generated by wildfires (Jones and others 2003; Carlsson and others 2012; Kurth and others 2013; Glassman and others 2016; Day and others 2019). Wildfire also can alter the composition and function of fungal communities by modifying host-plant communities (Goldmann et al. 2015; Tedersoo and others, 2008) and abiotic soil environments (Bowd, Banks, Strong, & Lindenmayer, 2019; Reazin and others, 2016) through the volatilization of soil nutrients and organic matter (Goldmann and others 2015; Pellegrini and others 2018) and post-fire erosion and nutrient leaching (Rab 2004; Hartmann and others 2012, 2014; Lacroix and others 2016). These impacts are more pronounced with increasing fire frequency, which can alter fungal community composition by reducing fungal biomass, diversity, the occurrence of sensitive species, and increasing early successional species that are tolerant of fire (Buscardo and others, 2015; Cairney & Bastias, 2007; Day and others, 2019; Dove & Hart, 2017; Glassman and others, 2016; Goldmann and others, 2015; Holden & Treseder, 2013; McMullan-Fisher and others, 2011). The recovery of fungal communities post-fire can take over a decade in some ecosystems, which may influence their respective functional roles (Visser 1995; Cairney and Bastias 2007; Dooley and Treseder 2012; Holden and Treseder 2013).

In clearcut and post-fire salvage logging operations, all vegetation within an area of forest is cleared and the remaining 'slash' and debris is then usually burnt and reseeded with the dominant tree species, producing a new homogenous cohort of forest (Ashton, 1976; Flint, Fagg, 2007; Florence, 1996). Due to the intensity and compounding nature of these human disturbances, the respective impacts on biological communities and soil environments can be more extensive than the impacts of natural wildfire alone (Blair and others, 2016; Bowd, Lindenmayer, Banks, & Blair, 2018; Byrd and others, 2000; Hartmann and others, 2012, 2014; Hume, Han, Chen, Taylor, & Han, 2018; Varenium and others, 2016). Clearcut logging can destroy fungal habitats including above and below-ground biological legacies such as large dead trees/ wood and plant root systems (Blair and others, 2016; Goldmann and others, 2015; Josefsson, Olsson, & Östlund, 2010; Lindenmayer & McCarthy, 2002; Seidl, Rammer, and others, 2014), and alter soil nutrients and compact soils, reducing water infiltration, hydraulic conductivity and increasing erosion and nutrient leaching (Bowd and others, 2019;

Hartmann and others, 2012, 2014; Kishchuk and others, 2015; Lacroix and others, 2016; Rab, 2004). These impacts can alter fungal community composition and mycorrhizal associations for multiple decades (Holden and Treseder 2013; Buscardo and others 2015; Goldmann and others 2015; Varenium and others 2016; Pressler and others 2019).

METHODS

Site description

We carried out this study in the ectomycorrhizal tall and carbon-dense Mountain Ash forests of the Victorian Central Highlands in southeastern Australia (Ashton 1976a) (Figure 1, S1). These temperate, high-rainfall ‘wet sclerophyll’ forests are characterized by a tall canopy dominated by the world’s tallest flowering plant, *Eucalyptus regnans* (Mountain Ash), with a midstorey dominated by *Acacia* species, an understorey consisting of broad-leaved shrubs, tree-ferns and a dense ground layer rich in fern and mesophytic herb species (Ashton, 2000; Blair and others, 2016; Bowd and others, 2018). These forests typically experience cool and humid climatic conditions in the winter and summer months and receive an annual precipitation of between 1300-1500 mm (Ashton and Attiwill 1994). However, periodic hot, dry summers and wildfires also occur, and have increased in frequency in recent decades (Bowman, Murphy, Neyland, Williamson, & Prior, 2014; Taylor, McCarthy, & Lindenmayer, 2014). The abiotic soil environments of these forests consist primarily of well-drained, acidic, deep, Dermosols derived from granitic rock (Ashton & Attiwill, 1994; Bowd and others, 2019; Burns and others, 2015). pH ranges from 3.4-5.2, nitrate and phosphorus content averages approximately 23 mg/kg and 50 mg/kg respectively, and organic carbon content typically exceeds 5 % in dominant stands last burnt in 1939 (Bowd and others, 2019).



Figure 1. Example stands of Mountain Ash forests that have experienced different disturbance regimes. The top image is forest burnt in 1939 and then regenerated following fire (taken in 2017), and the bottom image is forest that experienced wildfire followed by post-fire salvage logging in 2009 (taken in approx. 2014).

The Victorian Central Highlands support ~157,000 ha of Mountain Ash forests, 80% of which are broadly designated for timber harvesting and pulp production, with the remaining 20% located in closed water catchments and national parks (Langford 1976; Burns and others 2015). Historically, these forests experience infrequent, high-intensity wildfires every 75-150 years, which typically result in a new homogenous regrowth cohort of the dominant obligate seeder, *E. regnans* (Ashton, 1976; McCarthy, Gill, & Lindenmayer, 1999). The frequency of these fires appears to have increased and some areas have experienced multiple high-severity fires over the past decadal including those in 1926, 1932, 1939, 1983 and most recently in 2009 (Ashton, 1981; Lindenmayer and others, 2011). In 1939, >70% of these forests were burnt and many were subsequently salvage logged, the regrowth of which is the primary resource of wood for the timber industry (Florence, 1996; Lindenmayer & Ough, 2006; Lindenmayer & Franklin, 1997). More recently, the 2009 fires burnt 53 400 ha of Mountain Ash forest, the majority of which was regrowth from earlier fires in 1939 (Burns and others 2015). This has resulted in a large cohort of young, dense and fire-prone regrowth with limited structural diversity (Lindenmayer and others, 2012; Taylor, McCarthy and Lindenmayer, 2014).

In addition to fire, Mountain Ash forests have experienced ongoing clearcut logging since the 1970s (Flint & Fagg, 2007; Florence, 1996). Clearcut logging involves the clearing of all understory vegetation and the removal of the target tree species (*E. regnans*) within a 15-40 ha area (Flint & Fagg, 2007; Florence, 1996; Lindenmayer and others, 2011). Remaining debris or 'slash' is then burnt and aerially seeded with the dominant tree species (Chambers & Attiwill, 1994; Flint & Fagg, 2007; Lindenmayer and others, 2011). Salvage (post-fire) logging can be described as clearcut logging that occurs after a high-intensity fire, with the exception that there is no post-clearcut slash burn if post-fire regeneration is adequate (Blair and others, 2016; Lindenmayer & Ough, 2006).

Study design

We selected nine disturbance histories for our study: five experienced fire-only and the remaining four were clearcut or salvage logged. Fire-only sites were forests long-undisturbed (unburnt since 1850s), burnt once (1939 fire), twice (1939/1983 and 1939/2009) and three times (1939/1983/2009). Logged sites which regenerated after fire in 1939 were then clearcut between 1980-1985 or between 2008-2010. In addition, we included sites which experienced multiple fires and clearcut logging, including those burnt in 1939 and 1983 and clearcut in

2008-10, and those burnt in 1939 and 2009 and salvage logged in 2009-10. All disturbance histories were replicated at least 10 times, with the exception of forests long-undisturbed (1850s, n=4) and three times (1939/1983/2009, n=6) (Table 1).

Table 1. Disturbance histories and number of replicate sites of each of the nine disturbance histories. F= fire, CC= Clearcut logged, SL= Salvage logged. DNA and RNA samples were collected at all sites, however some RNA samples were discarded as a result of DNA contamination and low read numbers. Therefore, for RNA samples, ‘Number of sites’ reflects those used in analyses after rarefaction.

Disturbance history	1850 Fire	1939 Fire	1983 Fire	2009 Fire	1980-85 Clearcut	2008-10 Clearcut	2009-10 Salvage	Number of sites DNA	Number of sites RNA
‘1850F’	✓							4	4
‘1939F’		✓						10	9
‘1939/1983F’		✓	✓					10	8
‘1939/2009F’		✓		✓				11	10
‘1939/1983/2009F’		✓	✓	✓				6	6
‘1939F/1980CC’		✓			✓			10	9
‘1939F/2009CC’		✓				✓		10	7
‘1939F/2009F/2009SL’		✓		✓			✓	10	8
‘1939/1983F/2009CC’		✓	✓			✓		10	10

We measured quadrats of 25 m x 25 m during a consistent seasonal period in the austral summer between December 2016 - early March 2017 (mean precipitation: December 2016: 62.2 mm; January 2017: 66.8 mm; February 2017: 64.0; March 2017: 68.0 mm (Bureau of Meteorology 2019)). Our 81 field sites were characterized by a predominantly southerly aspect, were located at an elevation of ~600-900 meters, experienced an annual precipitation of between 1300-1800 mm, and were positioned away from drainage lines and ridges. For consistency, we followed the microbiological sampling protocol described by the Australasian BASE (Biomes of Australian Soil Environments) project (Bissett and others 2016). Specifically, at each site, we collected nine, 10 cm x 30 cm soil cores along the perimeter and in the centre of each quadrat and stratified, pooled and mixed each soil sample by depth (0-10 cm and 20-30 cm). From the 0-10 cm and 20-30 cm composite soil samples for each site, we collected subsamples of soil (approximately 100 grams per sample) and stored them at -20°C for later DNA analysis. Further, from the 0-10 cm soil depth sample, we

took an additional 2 x 2 grams of soil for RNA extraction. We placed these samples in 15 mL falcon tubes containing 5 ml of MO BIO's LifeGuard™ Soil Preservation Solution, USA and stored them at -20°C for two months, and at -80°C thereafter. DNA from 0-10 cm and 20-30 cm depths of soil and RNA from 0-10 cm depth of soil, are hereafter referred to as sample types.

Metabarcoding analysis

DNA extraction and sequencing was undertaken by the BASE project, according to the methods described by Bissett et al. (2016). Briefly, DNA was extracted in triplicate (3 x 0.25g) using MO BIO power soil kits and extractions combined. The fungal ITS1 region, utilising primers ITS1F (Gardes and Bruns 1993) and ITS4 (White and others 1990), was amplified and the fragment bidirectionally sequenced (paired end 300 bp) using the Illumina MiSeq platform. Primers were utilised on the Illumina platform using Golay barcodes (Caporaso and others 2012). While this method has a high coverage of fungal diversity and is appropriate for the context of this study, like all amplicon-based methods, it has some limitations, including its inability to capture taxa with longer ITS1 regions (Taylor and others 2016).

We extracted RNA using MO BIO RNA Powersoil® Total RNA Isolation Kit in accordance with the manufacturer's instructions. We treated extracted RNA with DNase using Qiagen DNA Max Kit in accordance with manufacturer's instructions to remove DNA contamination. We reverse-transcribed RNA to synthesise cDNA using the Superscript IV cDNA synthesis kit, 9 ul of RNA, and the reverse ITS4 primer in accordance with manufacturer's instructions, along-side positive and negative controls described by Anderson *and others*, 2007 to control for potential DNA contamination (Anderson and Parkin 2007). We performed PCRs using DreamTaq PCR kit and the ITS1F and ITS4 primers and used gel electrophoresis (1.5% agarose) on PCR products to detect potential contaminants in positive and negative controls. We discarded contaminated samples.

Consistent with the extracted DNA, RNA amplicons were generated from cDNA and the fungal ITS region was amplified and sequenced as above. Metabarcoding analysis for both the cDNA (RNA) and DNA samples were conducted as per Bissett and others, (2016). In summary, the ITS1 gene region was extracted from R1 reads using ITSx v1.0.11 (Bengtsson-Palme and others 2013), OTUs were clustered at 97% sequence similarity and chimeras removed using usearch (v9.0.2132, 64-bit) (-cluster_otus -minsize 4) (using uchime

algorithm) and sequences mapped back to OTUs generate abundances (-usearch_global –strand plus –id 0.97 -maxaccepts 56 -top_hit_only -maxrejects 256). Primers were removed during the ITSx process. Further, the UPARSE algorithm was used (implemented in usearch via the cluster_otus command) to reduce the potential of oversplitting of low quality sequences. Rare OTUs and singletons with <4 reads total across sample datasets (RNA 0-10 cm, DNA 0-10 cm and DNA 20-30 cm) were removed.

We assigned taxonomy to each OTU using the Wang method (Wang and others 2007) as employed by MOTHUR (v1.39.1) (Schloss and others 2009) and the UNITE v6 species hypothesis database (Abarenkov and others 2010) using a probability cutoff of 60% (Cutler and others, 2017; Hartmann and others, 2012; Wang and others, 2007). Where possible, we reclassified fungal OTUs formally described as belonging to the Zygomycota phylum to updated phyla groups identified in Terdersoo et al., (2018). We removed OTUs unclassified at the phylum level by the Bayesian classifier.

Using FUNGuild v1.0 flat database, we assigned functional groups to 34%, 32% and 37% of rarefied fungal OTUs in the 0-10 cm (DNA, RNA) and the 20-30 cm (DNA) depths of soil respectively based on trophic strategies: ‘symbiotroph’, ‘pathotroph’ and ‘saprotroph’ using ‘highly probable/probable matches’(Nguyen and others 2016). 1) Symbiotrophic fungi exchange resources with hosts; 2) saprotrophic fungi receive nutrients by breaking down dead hosts; and 3) pathotrophic fungi receive nutrients by harming hosts (Nguyen and others 2016). Fungal OTUs assigned to multiple functional groups: ‘Pathotroph’, ‘Pathotroph-Saprotroph’, ‘Pathotroph-Saprotroph-Symbiotroph’ were included in all respective functional groups for downstream analysis (Phillips and others 2019). Further, we separated symbiotrophic fungi into two dominant guilds for downstream analysis: arbuscular mycorrhizal fungi (AM) and ectomycorrhizal fungi (EcM). While FUNGuild is widely used in fungal community research, it is important to note that given our sampling was of bulk soil, we cannot be certain that fungal OTUs assigned to functional groups were fulfilling their respective functional roles at the time of sampling. Therefore, ‘highly probable’ and ‘probable’ fungal OTUs assigned to functional groups should be regarded as potentially/likely fulfilling respective functional roles.

Statistical analyses

We generated a total of 9,964,060 ITS1 fungal sequence reads from DNA samples across 81 sampling sites and 6,315,586 ITS1 fungal sequence reads from RNA samples across 71 sampling sites. We rarefied the abundance of each OTU to the lowest number of reads for each sample type (0-10 cm DNA sample = 19,943 ; 20-30 cm DNA sample = 24,382; 0-10 cm RNA sample = 8356) using the *rarefy_even_depth* function in the *phyloseq* (McMurdie and Holmes 2013) package in R to account for the uneven library sizes between samples (after removing unclassified OTUs) (Weiss and others, 2015). We discarded 10 samples in the RNA sample type that had less than 5,000 raw sequence reads (Table 1). We assessed sampling efficacy at the 97% OTU level using the *rarecurve* function in *vegan* (Oksanen and others 2013)(Figure S2).

To assess the influence of spatial structure on the composition of fungal communities, we used dbMEM analysis (distance-based Moran's eigenvector maps)(originally, PCNM analysis) on the residuals of detrended, hellinger transformed abundance data for each sample using the *adespatial* package in R (Dray and others 2017; Borcard and others 2018). To select the most influential dbMEMs eigenvectors, we applied a forward selection process on those with positive spatial correlation using a double stopping criteria (Blanchet and others 2008). Thereafter, we used these selected dbMEMs as a proxy for spatial explanatory variables in our multivariate analyses (Borcard and others 2018).

Using the *adonis* function in the *vegan* package we used a permutational-based multivariate ANOVA (PERMANOVA) to quantify the influence of disturbance (No. fires, clearcut logging, salvage logging), time since disturbance and spatial variation (dbMEMs)) on the composition of fungal communities based on euclidian dissimilarity index of hellinger transformed abundance data for each sample. Thereafter, we used the *pairwise.adonis* package to make post-hoc pairwise comparisons between the influence of the number of fires and time since disturbance on the composition of fungal communities based on the same dissimilarity index (Martinez Arbizu 2020). We carried out variance partitioning using the *varpart* function in the R package *vegan* to evaluate the contribution of disturbance, time since disturbance and spatial variation (significant dMEMs) on fungal community composition across each sample types using adjusted R^2 values.

We used generalized linear regression models (GLM) to determine the influence of component individual disturbances of the nine disturbance histories ('0 fires (since 1850s)', '1

fire', '2 fires', '3 fires', 'clearcut logging', 'salvage logging') on the richness and relative abundance of fungal functional groups: symbiotrophs (total symbiotrophs (arbuscular mycorrhizal (AM) and ectomycorrhizal (EcM)), and AM and EcM fungi indepedantly), saprotrophs, pathotrophs, controlling for time since disturbance and environmental variables (Australian soil classification (Dermosol, Sodosol, Tenosol, parent-rock type (Table S1), elevation, slope, and historical silviculture events and thinning (30-40 years prior to clearcut and salvage logging events in 1980-1985 or 2008-2010 (8 sites). We employed the *dredge* function from the *MuMin* package in R (Bartoń 2013) (parameters: disturbance variables = fixed factors; rank= AICc) to select the combination of factors with the lowest AICc for each respective model. We detected no significant multi-collinearity between variables used in each model (variance inflation factors, VIF <10)(*car* package in R (Fox and Weisberg 2019). We used negative binomial generalised linear models with full model dispersion parameters to account for overdispersion using the *MASS* package in R (Venables and Ripley 2002).

We used the statistical package *Indicspecies* (Cáceres and Legendre 2009) in R to identify fungal OTUs that were significantly ($p < 0.001$) associated with, or 'indicative' of, the nine disturbance histories across the three sample types using the function *multipatt* with 999 permutations. To account for potential type 1 errors, we only reported indicator species that were highly significant indicators ($p < 0.001$) of specific disturbance histories.

We generated variograms using model residuals (bins= min. and max. distance between sites) for each response variable to test for spatial auto-correlation using the *geoR* (Ribeiro Jr. and Diggle 2001) package in R. We found no evidence of spatial auto-correlation in any of our response variables (Figure S3).

We generated figures using the *ggplot2* (Wickham 2016) statistical package in R. All analyses were conducted using R 3.6.3.

RESULTS

Summary

From rarefied samples, we found a total of 8967 OTUs across all disturbance history and sample types. Of these OTUs, 3269 were found in DNA samples from both soil depths, and 1629 were found in both DNA and RNA samples.

Specifically, from rarefied DNA samples, we found 6588 fungal OTUs from 1,554,127 ITS1 sequences in the 0-10 cm depth of soil, and 4683 fungal OTUs from 1,927,185 ITS1 sequences in the 20- 30 cm depth of soil. These OTUs were represented by eight phyla: Ascomycota, Basidiomycota, Chytridiomycota, Glomeromycota, Kickxellomycota, Mortierellomycota, Mucoromycota and Basidiobolomycota. We also identified a small number of OTUs assigned only to the phyla Zygomycota at the highest resolution. OTUs belonging to the Basidiomycota and Ascomycota were dominant in the 0-10 cm and 20-30 cm depths of soil, accounting for >90% of classified OTUs and total sequences.

In 0-10 cm RNA samples, we identified 3304 OTUs from 577,705 ITS1 sequences. Of these, OTUs belonging to the Ascomycota and Basidiomycota were dominant (>80% of total sequences; and >90% of classified OTUs).

Fungal OTU richness varied across disturbance histories and was highest in DNA samples from the 0-10 cm of soil and lowest in RNA samples from the 0-10 cm depth of soil. Typically, the richness of fungal OTUs increased with the number of fires across all sample types, however, varied in logged sites of the same age (Figure 2).

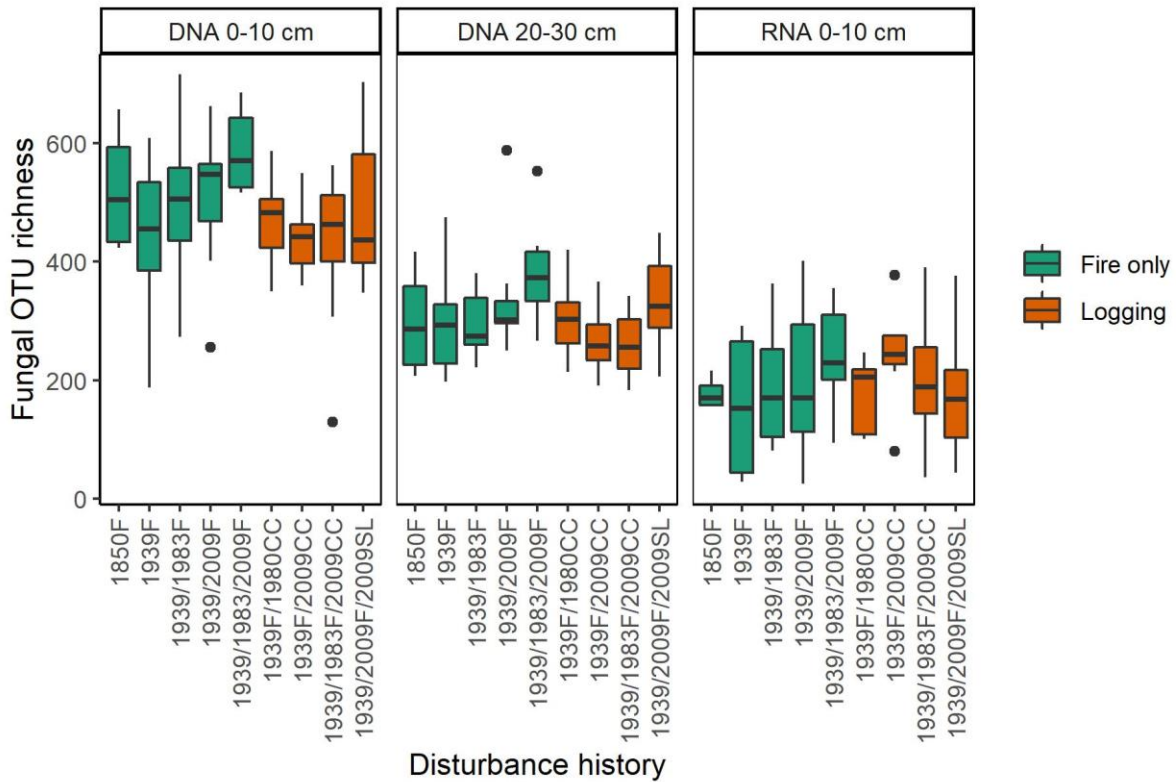


Figure 2. Box plot of the richness of total fungi across nine disturbance histories, with respect to the sample type (DNA 0-10 cm, DNA 20-30 cm, RNA 0-10 cm). Boxes represent the interquartile range (IQR) between the first and third quartiles (25th and 75th percentiles, respectively), and the horizontal line inside the box defines the median. Whiskers represent the lowest and highest values within 1.5 times the IQR from the first and third quartiles, respectively.

We identified 31 dominant fungal OTUs (top 20 most abundant from each sample type) from our dataset, across all disturbance histories. Of these, 32 % were Basidiomycetes, 39% were Ascomycetes, 26% belonged to the Mortierellomycota phyla and one saprotroph belonged to the Mucoromycota phyla. *Cryptococcus* had the highest mean relative abundance across all sample types. *Sebacina* sp had a higher mean relative abundance in older forests that were unlogged, and *Sordariales* sp and *Umbelopsis* sp had a higher mean relative abundance in logged sites (Figure 3).

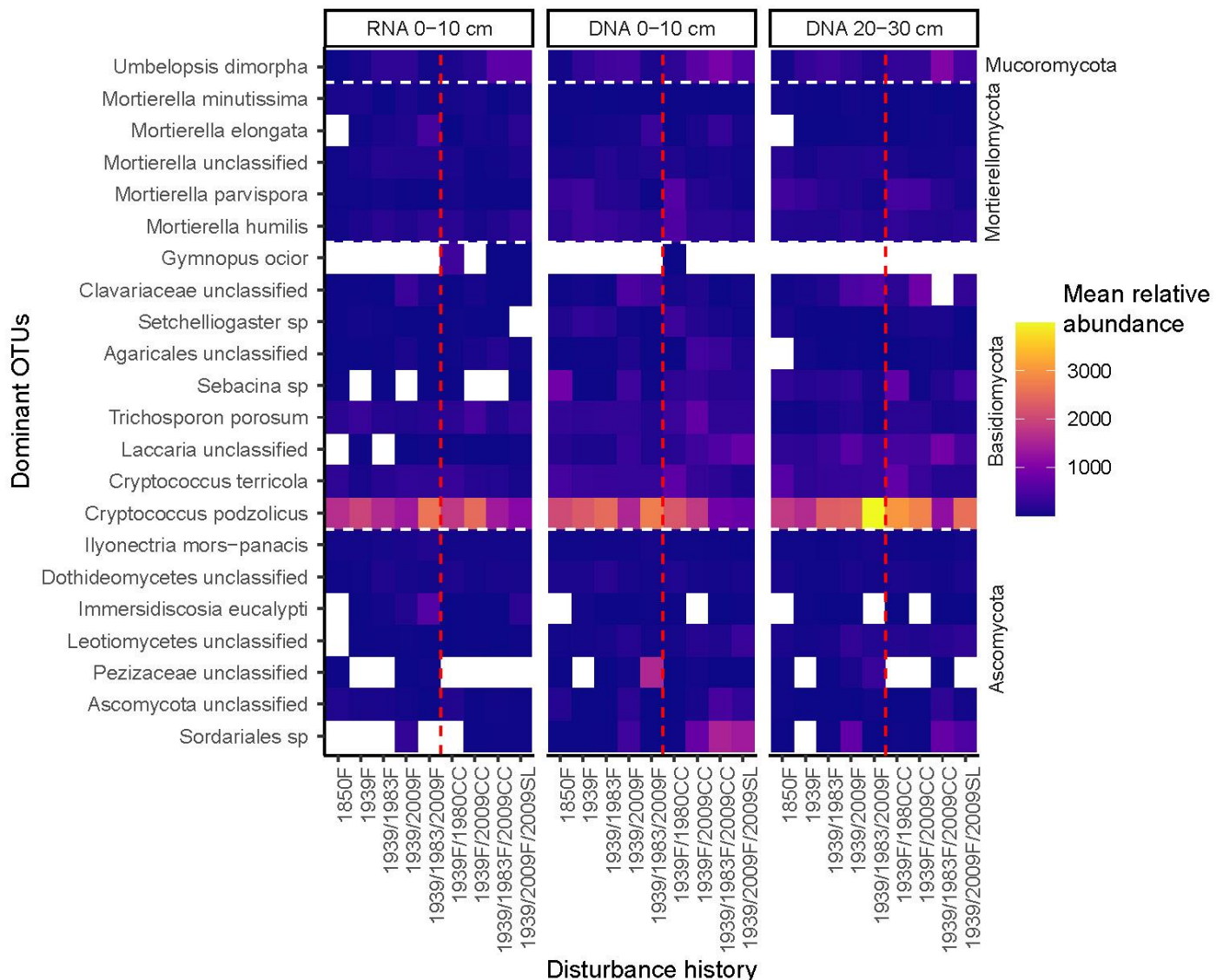


Figure 3. Mean relative abundance of dominant fungal genera (top 20 most abundant read count (after rarefaction) in each sample type) with respect to disturbance histories. Red line = indicates logged sites, white line = delineates fungal phyla.

Fungal community composition

Fungal community composition was significantly influenced by the number of fires, clearcut logging, post-fire salvage logging, time since disturbance (log) and spatial dbMEMs across all DNA samples from both soil depths (Table 2). The number of fires and clearcut logging also significantly influenced the fungal community composition in RNA samples from the 0-10 cm soil depth. Variance partitioning using adjusted R^2 values indicated that disturbances (clearcut logging + salvage logging + no. wildfires) explained the highest proportion of variance across all sample types, relative to time since disturbance (log) and spatial variation (significant dbMEMs). However, most of the variance in these communities was largely unexplained (Figure S4).

Table 2. Influence of disturbance and spatial variables (dbMEM (MEM) eigenvectors) on the fungal community composition as indicated using permutational multivariate analysis of variance (PERMANOVA). Respective pairwise comparisons are located in Table S2.

		Df	SumsOfSqs	MeanSqs	F	R2	p=	
DNA 0-10 cm	<i>No. fires</i>	3	4.71	1.57	2.51	0.08	0.00	***
	<i>Clearcut logging</i>	1	1.58	1.58	2.53	0.03	0.00	***
	<i>Salvage logging</i>	1	1.67	1.67	2.67	0.03	0.00	***
	<i>TSD (log)</i>	1	1.07	1.07	1.70	0.02	0.00	**
	<i>Spatial MEM2</i>	1	0.63	0.63	1.00	0.01	0.41	
	<i>Spatial MEM3</i>	1	0.96	0.96	1.54	0.02	0.01	**
	<i>Residuals</i>	72	45.01	0.63		0.81		
	<i>Total</i>	80	55.62			1.00		
DNA 20-30 cm	<i>No. fires</i>	3	4.16	1.39	2.23	0.08	0.00	***
	<i>Clearcut logging</i>	1	1.40	1.40	2.25	0.03	0.00	***
	<i>Salvage logging</i>	1	1.11	1.11	1.78	0.02	0.00	**
	<i>TSD (log)</i>	1	1.20	1.20	1.93	0.02	0.00	***
	<i>Spatial MEM 2</i>	1	0.57	0.57	0.92	0.01	0.68	
	<i>Spatial MEM 3</i>	1	0.98	0.98	1.58	0.02	0.00	**
	<i>Spatial MEM 5</i>	1	1.08	1.08	1.73	0.02	0.00	**
	<i>Residuals</i>	71	44.12	0.62		0.81		
RNA 0-10 cm	<i>No. fires</i>	3	2.74	0.91	1.60	0.07	0.00	***
	<i>Clearcut logging</i>	1	1.13	1.13	1.97	0.03	0.00	**
	<i>Salvage logging</i>	1	0.52	0.52	0.90	0.01	0.72	
	<i>TSD (log)</i>	1	0.43	0.43	0.75	0.01	0.98	
	<i>Spatial MEM 2</i>	1	0.66	0.66	1.16	0.02	0.23	
	<i>Residuals</i>	63	36.00	0.57		0.87		
	<i>Total</i>	70	41.47			1.00		

Post-hoc pairwise tests indicated significant differences between the composition of fungal communities in forests unburnt (since 1850), burnt once, twice and three times across all sample types ($p < 0.05$), except for pairwise tests between forests unburnt and burnt once in DNA and RNA samples from the 0-10 cm soil depth; and between forests burnt once and twice, and once and three times in RNA samples. Moreover, pairwise tests between the composition of fungal communities across different times since disturbance (167, 34, 8 years) indicated significant differences between forests last disturbed 8 years prior and all other times since disturbance across DNA samples. In contrast, pairwise tests between forests last disturbed 167, 34 and 8 years ago across all sample types were not significant, with the exception of pairwise tests between forests last disturbed 167 and 34 years ago in DNA samples from the 20-30 cm depth of soil (Table S2).

Functional groups of fungi

Saprotrophic fungi were the most species rich in all samples types and were most abundant across DNA and RNA samples from the 0-10 cm depth of soil. In contrast, symbiotrophic ectomycorrhizal fungi were the most abundant in DNA samples from the 20-30 cm depth of soil. The number of fires, clearcut logging and salvage logging significantly influenced the relative abundance and richness of fungal functional groups, controlling for environmental variables and time since disturbance (log). Disturbance impacts were most extensive on symbiotrophic fungi, but the nature of impacts (positive or negative) differed between disturbances. For instance, the richness of total symbiotrophic fungi (EcM and AM) significantly declined with clearcut logging across both soil depths (DNA samples), and their respective relative abundance increased in forests burnt once in the 0-10 cm depth of soil (DNA samples). Further analysis of symbiotrophic fungal responses to disturbance revealed differences between EcM and AM fungi. Specifically, sites burnt twice ($p = 0.01$) and three times ($p = 0.05$) supported a significantly higher richness of EcM fungi, and sites burnt once ($p = 0.04$) supported a significantly higher relative abundance of EcM fungi in the 0-10 cm soil depth (DNA samples) ($p = 0.03$), relative to long-unburnt sites.

In contrast, the richness of AM fungi significantly declined in forests burnt once, twice and three times in DNA and RNA samples from the 0-10 cm depth of soil ($p = 0.00$). Further, clearcut logging was associated with declines in AM richness across both depths of soil ($p = 0.00-0.03$) (DNA samples). Salvage logging was also associated with declines in AM richness in the 0-10 cm depth of soil ($p = 0.02$) (DNA samples), and the relative abundance of AM fungi was significantly lower in forests burnt once, twice and clearcut forests in the 0-10

cm depth of soil (DNA)($p=0.00-0.01$); in forests burnt once, twice and three times in RNA samples ($p=0.00-0.01$), and in forests burnt once in DNA samples from the 20-30 cm depth of soil ($p=0.02$).

Salvage logging was associated with increases in the richness of saprotrophic fungi in the 20-30 cm depth of soil ($p=0.03$) and pathotrophic fungi ($p=0.00$) in the 0-10 cm depth of soil (DNA samples). In contrast, clearcut logging was associated with a significantly lower richness of pathotrophic fungi in the 20-30 cm depth of soil ($p=0.04$). Moreover, forests burnt once and twice were associated with a significantly lower relative abundance of pathotrophic fungi ($p=0.01-0.02$) (Figure 4; Table S3).

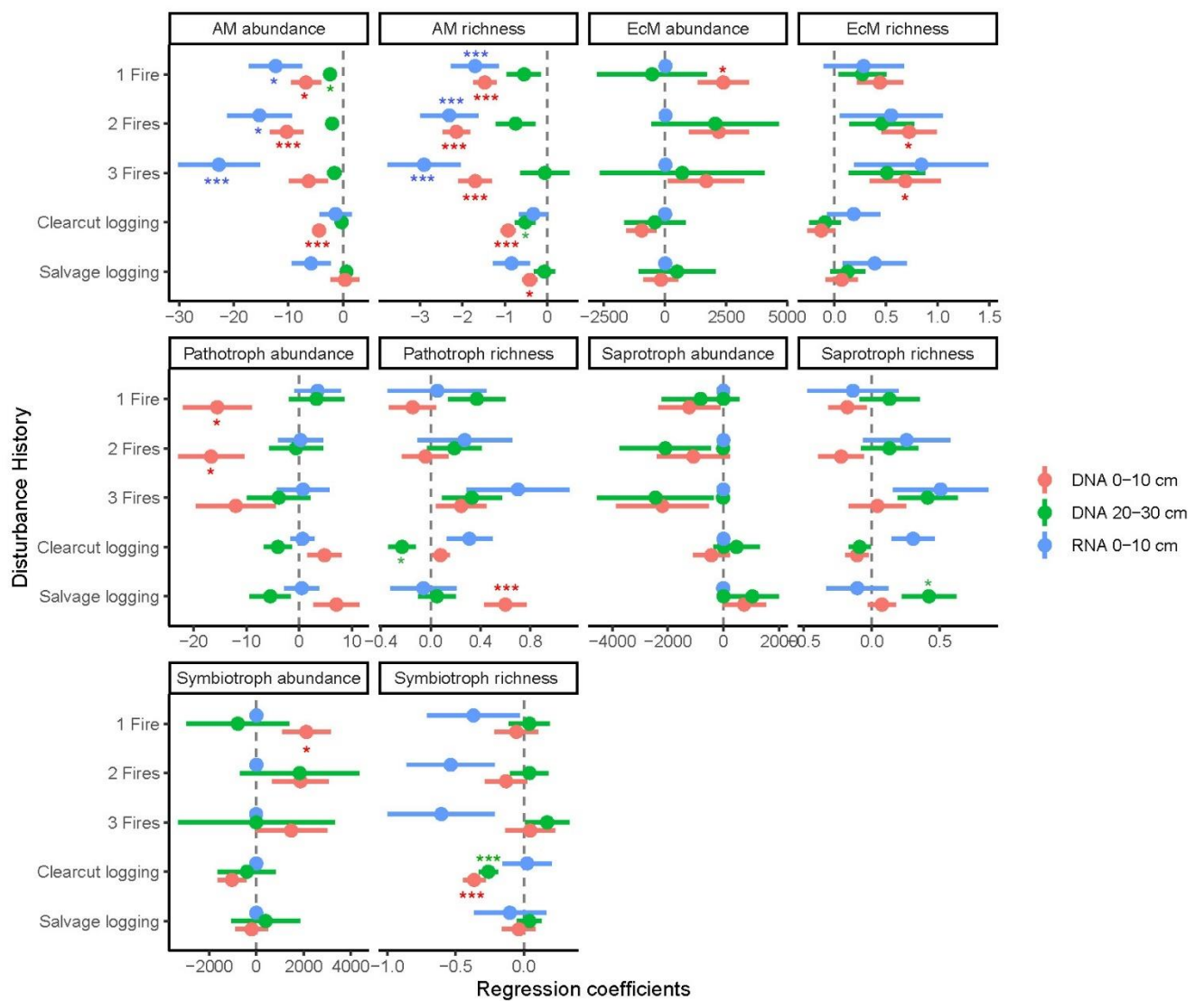


Figure 4. Coefficients from generalized linear models of the richness and abundance fungal functional group, and total fungal richness with respect to disturbance history sample type (DNA 0-10 cm, DNA 20-30 cm and RNA 0-10 cm). A complete list of the influence of the factors and covariates generated using these models is shown Table S3. *p<0.05, **p<0.01, ***p<0.001. See Table S3 for further detail.

Indicator analysis

Multipatt indicator species analysis identified several OTUs that were significant ($p < 0.001$), strong indicators of the nine different disturbance histories across all sample types ($\text{IndVal} > 0.75$) (Figure 5, Table S4).

In forests unburnt since 1850, indicator species were primarily basidiomycetes and ascomycetes, pooled across all sample types. These comprised several OTUs that were only indicative of this site type including: ectomycorrhizal *Cortinarius* sp. (2 OTUs), *Laccaria* sp. (1 OTU), *Lactarius* sp. (1 OTU), *Russula* sp. (2 OTUs), and saprotrophic *Agaricus* sp (1 OTU) and *Mortiella* sp. (5 OTUs). Forests burnt three times, last in 2009, also were uniquely indicated by several species, pooled across all sample types. These included a large number of AM fungal OTUs (7 OTUs) belonging to the Glomeromycota phyla, such as *Diversispora* sp., and saprotrophic fungal OTUs (25 OTUs): *Hypoxyton*, *Leohumicola*, *Leucoagaricus*, *Hemimycena*, *Physisporinus* and *Ramicandelaber* sp. The large number of indicators associated with sites unburnt since 1850 and those burnt three times, demonstrates their respective distinct fungal community compositions that differed from one another and other disturbance histories (Figure 5, Table S4). Other disturbance histories were characterized by lower numbers of unique indicator OTUs across the soil depths, many of which were not specific to individual disturbance histories (Figure 5, Table S4).

Pooled across all sample types, forests unburnt since 1939, 1983 and last logged in 1980s were indicated by ectomycorrhizal *Lactarius* and *Setchelliogaster* sp., and saprophytic *Umbelopsis* and *Leohumicola* sp. Further, AM Archaeosporaceae sp. and *Entoloma* sp. were indicative of sites logged in 2009 only, and saprotrophic, *Cladophialophora* sp. were indicative of sites burnt in 1983 and logged in 2009 only, pooled across all sample types. All forests logged in 2009 were also indicated by AM Glomeromycetes, plant pathogen: *Perisporiopsis*, and saprotrophic: *Leohumicola* and *Geminibasidium* sp., pooled across all sample types. Similarly salvage logged forests were also indicated by plant pathogen: *Perisporiopsis*, and saprotrophic *Leohumicola*, *Tetracladium*, *Trechispora*, *Umbelopsis* species. However, plant pathogen *Truncatella* sp, ectomycorrhizal *Inocybe* sp. and saprotrophic *Trechispora* sp. were indicative of salvage logged sites only (pooled across all sample types).

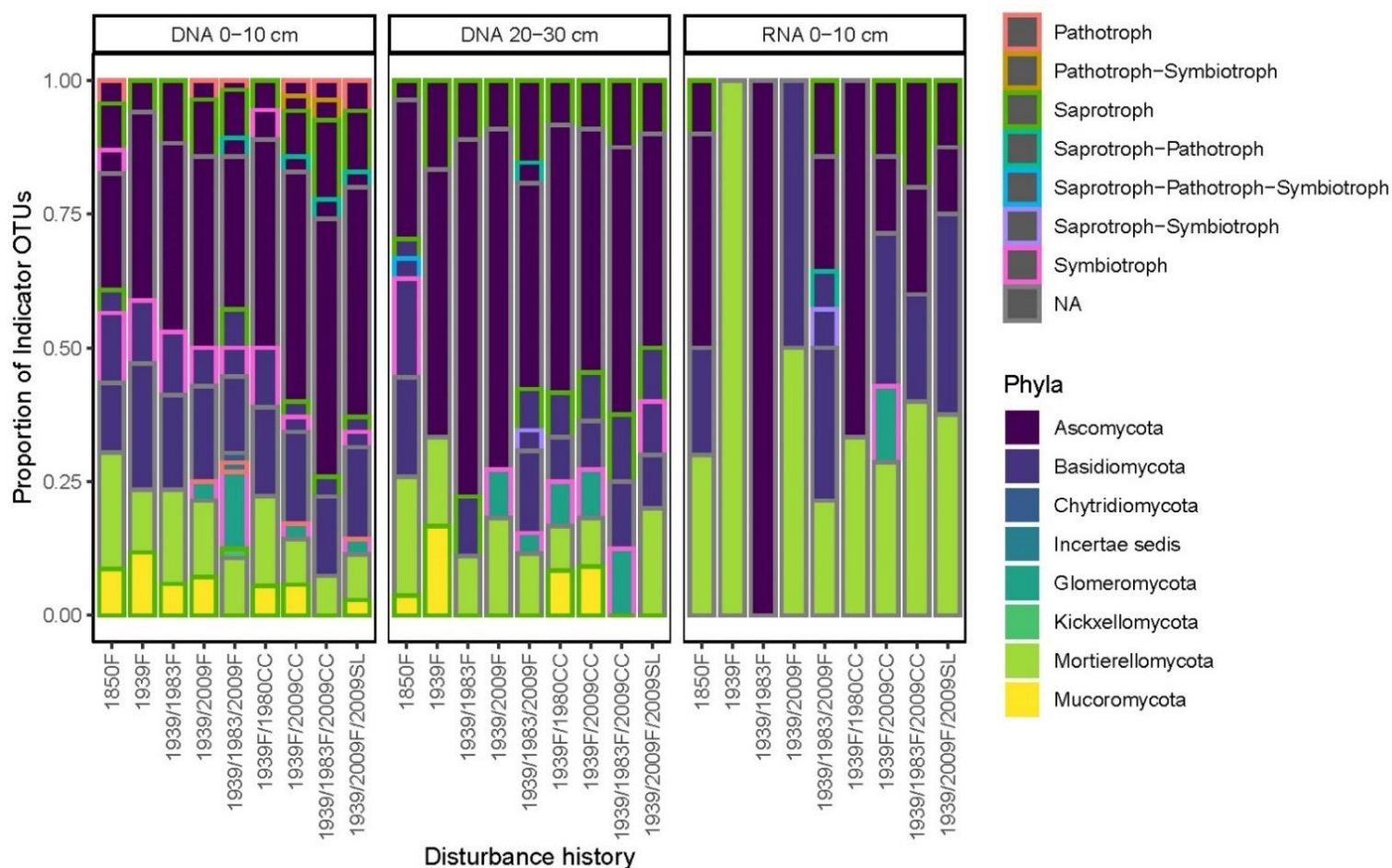


Figure 5. Proportion of indicator fungal OTUs by phyla (and functional groups within phyla) for each of the nine disturbance histories, across the two sample depths. Indicator OTUs are those that were strong, highly significant ($\text{IndVal} > 0.75$; $p < 0.001$) indicators for disturbance history.

DISCUSSION

Using a detailed sampling approach, we provide compelling empirical evidence that the composition of fungal communities and the relative abundance and richness of fungal functional groups are significantly altered by fire and clearcut and post-fire salvage logging events in the Mountain Ash forests of southeastern Australia. Symbiotrophic fungi were disproportionally impacted by disturbances relative to other functional groups of fungi. For instance, clearcut logging was associated with a lower richness of total symbiotrophic fungi and AM fungi across both soil depths. Similarly, two and three wildfires were associated with a lower richness of AM fungi, but a higher richness of EcM fungi in the 0-10 cm depth of soil. In contrast, post-fire salvage logged forests had a higher richness of pathotrophic and saprotrophic fungi, relative to unlogged forests. Changes in the relative abundance and richness of functional groups of fungi can have functional implications in forest ecosystems, and impact plant growth and seedling survival (Scott and others 2013; van der Putten and others 2013), and decomposition rates and carbon cycling (Averill and others 2014; Maron and others 2018; Philpott and others 2018). Our study may be one of the first reports of disturbance effects on fungal communities using DNA and RNA metabarcoding. Our results provide an important and timely insight into the disturbance responses of fungal communities (Treseder and Mack 2004; Cairney and Bastias 2007; Buscardo and others 2015).

In forest ecosystems across the globe, the impacts of fire on fungal communities can last up to 15 years in boreal forests (Dooley and Treseder 2012), 32 years in Ponderosa pine forests (Kurth and others 2013), 41 years in Jack pine forests (Visser 1995), and presumably longer in temperate forests that experience frequent high-severity fire (Dooley and Treseder 2012). In southeastern Australian Mountain Ash forests, for the first time, we found that disturbances produced unique fungal community compositions for at least 8 years in the 0-10 cm (from RNA and DNA samples), and for up to at least 34 years in the 20-30 cm soil depths post-disturbance.

Long-undisturbed forests produced some of the most diverse and species rich fungal community compositions across the nine disturbance histories and were strongly indicated by a large number of unique ectomycorrhizal species. This may be partially explained by age-related canopy closure and a subsequent increase in carbon allocation to root symbionts, as described in boreal forests (Visser 1995; Twieg and others 2007). A number of fungal OTUs

that were indicators of, or dominant in, these long-undisturbed sites were absent from all other disturbance histories. This suggests that some of these taxa may be sensitive to fire, and therefore may be restricted to long-undisturbed forests. Typically, these forests have a greater complexity of available habitats than disturbed forests, and can support diverse and sensitive species (Tedersoo and others 2008; Lindenmayer and Laurance 2017; Watson and others 2018). This may explain the high richness and number of unique indicator OTUs found in these sites. For instance, long-undisturbed forests have deep, organic soil horizons rich in key nutrients (Bowd and others, 2019), diverse microclimates (Ough and Murphy 2004), living and dead biological legacies (Lindenmayer & Laurance, 2017; Seidl and others 2014), and a rich biodiversity, including plants that can support fungal species (Tedersoo and others 2008), and mycophagous animals that can distribute their propagules (Claridge and Lindenmayer 1998; Trappe and others 2005). However, RNA rarefactions curves indicated these forests had the lowest gamma diversity, which may indicate a low turnover of active fungal species in the absence of recent perturbations.

In some post-fire forest ecosystems, an increased availability of new niches, microclimates and resilient fungal communities, including early successional and cosmopolitan taxa, can increase richness and diversity in the short-term (Sun and others, 2015). We found evidence of this in sites burnt three times which supported the most species rich and diverse fungal community composition across sample types, relative to other disturbance histories (Figure 2). These novel fungal community compositions also supported a significantly higher richness of ectomycorrhizal fungi, and a significantly lower abundance of arbuscular mycorrhizal fungi, relative to long-unburnt sites. Despite this, sites burnt three times were strongly indicated by a large number of arbuscular mycorrhizal fungi and saprotrophic fungi. This contrasts from the large number of indicator ectomycorrhizal fungal OTUs that characterized the DNA samples gathered from older, less-disturbed sites. The dominance of ectomycorrhizal fungi as indicator species in older, less-disturbed sites suggests that organic soil horizons are well-developed (Bowd and others 2019). In contrast, the prevalence of arbuscular mycorrhizal fungi as indicator taxa in highly disturbed sites suggests a low accumulation of surface litter and likely reflects a change in host plant species relative abundance (Treseder and Mack 2004; Selosse and others 2006).

The recolonization of fungal species after fire is dependent on the suitability of environmental conditions (Dang and others 2017), survival of nearby plant hosts, fungal dispersal success from nearby populations (Glassman and others 2016), and inoculum sources

such as subterranean deposits of hyphae or the fungal spore bank (Glassman and others, 2016; McMullan-Fisher and others, 2011). Therefore, the fire-induced shifts in fungal community composition observed in this study could be explained by these unmeasured factors, and by the combination of extreme soil temperatures that can be reached during a fire ($>500^{\circ}\text{C}$) and the associated death of some species (Jones and others 2003; Carlsson and others 2012; Kurth and others 2013; Glassman and others 2016), changes in the populations of spore-spreading mycophagous mammals (Nuske and others 2019), or shifts in soil nutrient pools (Bowd and others, 2019; Hume and others, 2018) and vegetation communities (Blair and others, 2016; Bowd and others, 2018; Ough, 2001). Communities that occupy different soil depths can respond differently to disturbances, with those in the topsoil typically more vulnerable to direct disturbance impacts (Liu and others 2015). This likely explains the pronounced disturbance impacts we observed in the topsoil. Further, disturbances may shift the composition of fungal communities that maintain functional roles due to high rates of functional redundancy and complementarity (Jones and others 2010; Maron and others 2018). However, our study provides evidence that disturbances, especially logging, may result in a unique fungal community composition that may alter respective functional roles (increase in pathogens, decrease in symbionts).

Altered fungal community composition can subsequently influence the respective functional roles that fungi have in ecosystems including plant growth and seedling survival (Scott and others 2013; van der Putten and others 2013), and decomposition rates and carbon cycling (Averill and others 2014; Maron and others 2018; Philpott and others 2018) through biological interactions and feedbacks (Wardle and others 2004; van der Putten and others 2013; Averill and others 2014; Teste and others 2017; Philpott and others 2018). However, the interactions between fungal and plant communities, and soil environments in disturbed forests requires further research attention to quantify direct functional implications.

Clearcut and post-fire salvage logging impacts on fungi

We found fungal community composition differed between sites that were logged and unlogged, and those that were burnt by different numbers of wildfires. This indicates that disturbance frequency and origin (natural or anthropogenic) are major drivers of the composition of fungal communities across all sample types and soil depths. While previous studies have found short-term compositional changes in symbiotic fungal communities post-clearcut logging (Byrd and others 2000; Mah and others 2001; Hartmann and others 2012), comparatively few investigations have quantified longer-term effects (Varenium and others

2016; Mushinski and others 2018). We found that clearcut logging resulted in compositional changes and significant reductions in the relative abundance and richness of functional groups of fungi controlling for time since disturbance, other disturbances and spatial autocorrelation. Specifically, clearcut logging had the largest adverse impact on symbiotrophic fungi, relative to the impacts of wildfire alone. For instance, clearcut logging was associated with a lower richness of total symbiotrophic fungal OTUs and a lower richness and abundance of AM fungal OTUs. This may be explained by the combination of the physical disturbances associated with logging, that may severely damage root systems and remove organic matter (Mushinski and others 2018) and the post-logging high-intensity ‘slash-burn’ of remaining vegetation and debris. These disturbances can directly destroy fungal biomass and inoculum sources (Dooley and Treseder 2012), alter the availability of saprotrophic fungal habitat (Josefsson and others 2010), and/or significantly alter soil environmental conditions that can impact the composition of fungal communities (Bowd and others, 2019; Dooley & Treseder, 2012; Hume and others, 2018; Goldmann and others, 2015). Further, fungal species that demonstrate strong host preference (of plant species that may be absent) i.e., some symbiotrophs, or sensitive species also may be vulnerable to disturbance-induced changes in plant communities (Tedersoo and others 2008; Hartmann and others 2014; Goldmann and others 2015; de Groot and others 2016; Merges and others 2018).

Long-term changes in fungal community composition and declines in the richness of symbiotrophic fungi in clearcut sites could impact the functional integrity of forest ecosystems and their resilience in the event of future perturbations (Dooley and Treseder 2012; Hartmann and others 2012, 2014). For instance, previous research has demonstrated that clearcut logging can alter plant community composition, and result in lower concentrations of key soil nutrients, relative to unlogged forest (Blair and others, 2016; Bowd and others, 2019; Hume and others, 2018; Prest, Kellman, & Lavigne, 2014).

While symbiotrophic fungi can be severely impacted by clearcut logging, saprotrophic and pathotrophic fungal species can be more resistant to the impacts of disturbance and subsequently can become more diverse in some ecosystems (Hartmann and others 2014; Varenium and others 2016; Mushinski and others 2018). This is because some of these fungi likely benefit from changes to the physical environment associated with logging such as exposed organic matter, vegetation dieback and physical breakdown of soil aggregates (Hartmann and others 2014). This could explain the significant increase in pathotrophic and saprotrophic fungal richness with post-fire salvage logging that we observed in our study.

However, our findings also may reflect functional complementarity that exists among fungi in some environments, where more resilient species occupy post-disturbance environments and fulfil functional requirements (Jones and others 2010).

RNA and DNA based fungal analysis

We utilized metabarcoding technology from both DNA and RNA extracted from the 0-10 cm soil depth to identify fungal communities. While using fungal community assessments based on DNA is useful in the identification of soil fungi, DNA samples may be from organisms that are dead, metabolically inactive or ‘relic extracellular DNA’ and consequently may be functionally less important when considering the impact of disturbance on community composition (Anderson and Parkin 2007; Carini and others 2017). Using both DNA and RNA based community assessments may allow for identification of metabolically-active species (Anderson and Parkin 2007; Bastias and others 2007; Baldrian and others 2012; van der Linde and others 2012). However, the detectability of ‘active’ species using RNA can be highly variable, which may limit its application (Blazewicz and others 2013). Nevertheless, we found a number of dominant OTUs from DNA samples that were not found in some RNA samples (Figure 3). This suggests that some of these OTUs may have been metabolically inactive. We also identified a number of dominant RNA OTUs that were not found in DNA samples. This suggests that our DNA samples did not capture the full diversity of fungal soil communities or may reflect their heterogeneity within each sample type, including rare species. Future research is required to quantify the differences between RNA and DNA derived communities at greater taxonomic resolution.

Across all sample types and disturbance histories, many fungal OTUs were unable to be identified beyond the phylum level, including those that were highly abundant and strong indicators of disturbance histories (Figure 3,5). This is a major limitation in molecular studies and highlights a fundamental need for future research to identify these species and their respective functional roles. Under-sampling diversity is common in soil microbial ecology studies, due to the large heterogeneity in soil environments and lack of replication (Lemos, Fulthorpe, Triplett, & Roesch, 2011; O’Brien and others, 2016; Taylor and others, 2010). However, other studies have indicated that over 10,000 DNA sequences per sample should be sufficient to detect major trends in microbial communities in similar environments (Lemos and others 2011). Therefore, it is likely we have covered a large proportion of fungal diversity, especially in the 0-10 cm DNA samples (19,943 sequences per sample) and in the 20-30 cm DNA samples (24,382 sequences per sample). However, as indicated by rarefaction

curves, an increase in the number of sequences derived from each sample in each sample type would increase the number of fungal OTUs found (Figure S2). The consistent significant impacts of disturbance on fungal communities that we quantified across all sample depths (accounting for potential niche separation) and sample types (RNA and DNA) strengthens the confidence of our findings that “active” fungal communities are significantly altered by disturbance.

By describing fungal communities derived from both DNA and RNA, our study contributes a comprehensive and large dataset characterizing Australian fungal taxa, which have been grossly under sampled, relative to those in North America and Europe. Further, the indicator species we identified in this study provide a pool of candidates for autecological studies. However, because many of these fungal OTUs are yet to be formally described beyond the phyla level, this will require intensive collection of sporophores.

Management implications

Climatic changes and anthropogenic disturbance are increasing the frequency of large stand-replacing fires globally (Bowman and others 2009, 2011; Van Der Werf and others 2017). Collectively, these disturbances are driving major changes in the structure and function of forests. However, little is known about the long-term impacts of disturbance on vital soil microbial communities (Hartmann and others 2012; Kurth and others 2013; Egidi and others 2016; Bahram and others 2018). Here, we have demonstrated that disturbances can alter the composition of fungal communities for up to at least 8 years in the topsoil and 34 years in the subsoil, and significantly influence the richness and relative abundance of functional groups of fungi.

Fire and anthropogenic disturbances are predicted to increase in severity and frequency in the coming decades (Bowman and others 2009, 2011). Therefore, it is likely that the composition of fungal communities and the richness and relative abundance of fungal functional groups will continue to be altered by compounding disturbances. These changes could locally displace species more characteristic of long-undisturbed forests and impair the key ecological functions that fungi provide. For instance, because mycorrhizal fungi mobilize nutrients including N and P that are otherwise unavailable to plants, declines in the richness and abundance of symbiotrophic fungi may have adverse impacts on plant growth and seedling survival (Finlay 2008). To best preserve the vital functions fungal communities, have in both

above and below ground ecosystems, it is important to manage forests to maintain the full suite of fungal diversity. Therefore, where possible, older less-disturbed forests should be conserved, and anthropogenic perturbations such as clearcut logging should be limited.

ACKNOWLEDGEMENTS

We thank the Mycological Society of America, The Paddy Pallin Foundation, The Ecological Society of Australia's: Holsworth Wildlife Fund, the Centre of Biodiversity Analysis, and volunteers who assisted in data collection for their support, and contributions to this study.

We acknowledge the contribution of the BASE project partners (DOI: 10.4227/71/561c9bc670099), an initiative supported by Bioplatforms Australia with funds provided by the Australian Commonwealth Government through the National Collaborative Research Infrastructure Strategy.

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Data availability

rDNA and rRNA sequence reads have been submitted to the NCBI SRA under bioproject PRJNA317932 and biosample accessions SAMN11293827- SAMN11294174.

SUPPLEMENTARY TEXT

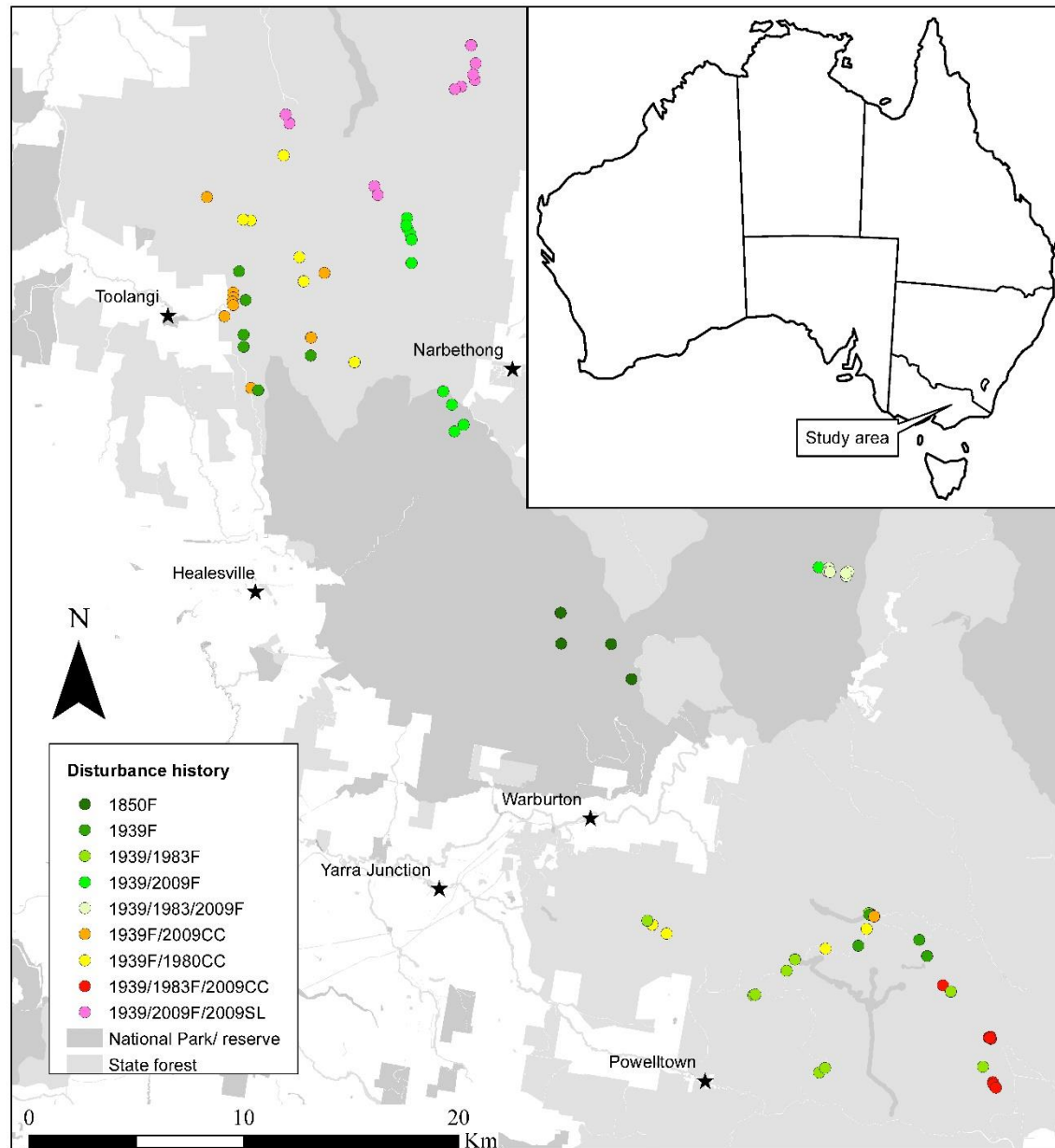


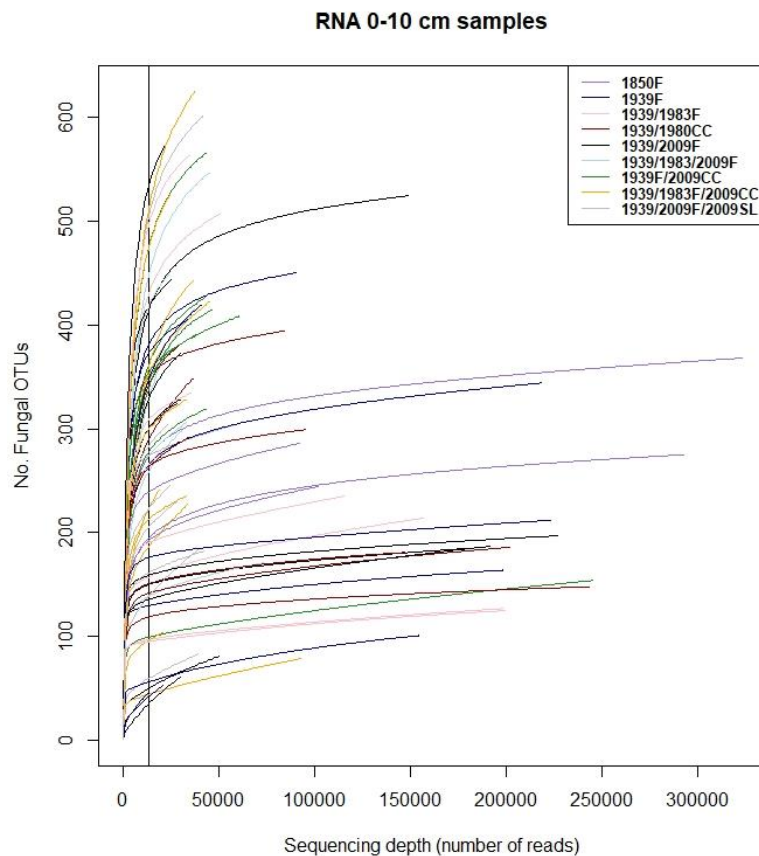
Figure S1. Location of study sites within the southeastern, Victorian Central Highlands in Australia, with respect to National Parks and reserves and State forest.

Table S1. Parent rock types and soil types and respective codes used in models.

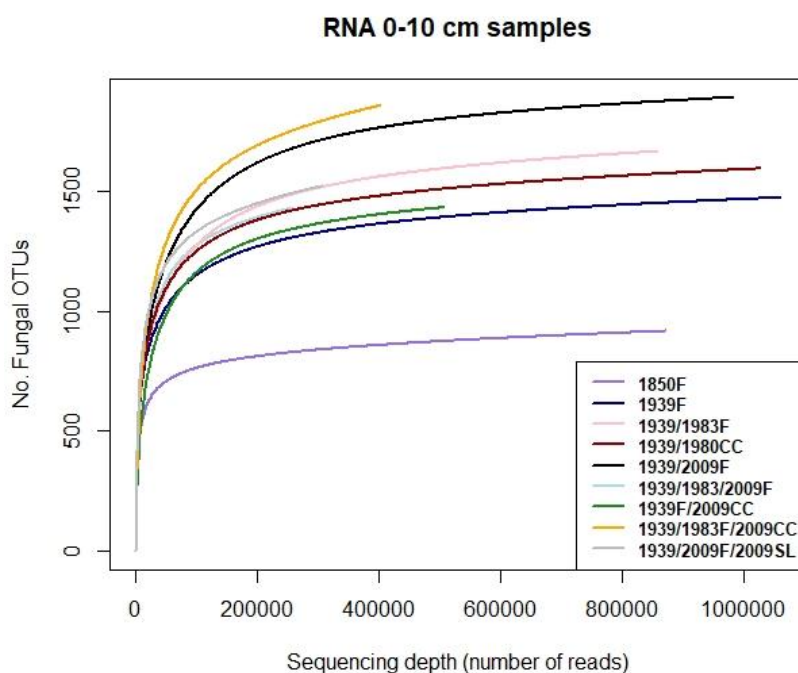
Parent rock type	Parent rock type code
Extrusive, fluvial: felsic ignimbrites, basalt and andesite lavas, conglomerate, sandstone	1
Extrusive: biotite-hypersthene rhyodacite ignimbrite, recrystallized	2
Intrusive: biotite granodiorite, medium grained subequigranular/generally porphyritic	3
Intrusive: felsic dykes	4
Metamorphic: hornfels	5

Soil type	Soil type code
Dermosol	1
Sodosol	2
Tenosol	3

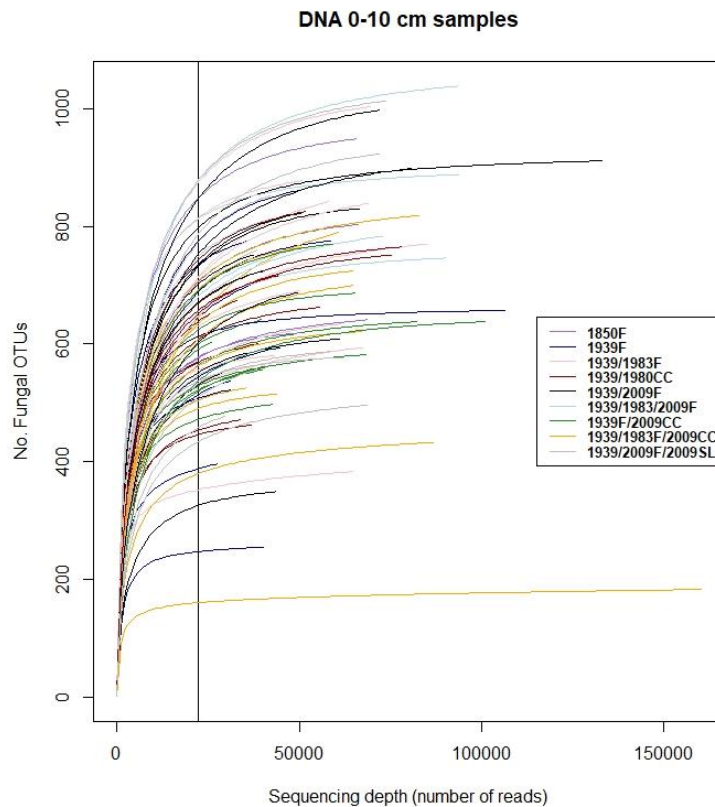
Figure S2. Rarefaction curves for all samples within each sample type (DNA 0-10 cm, DNA 20-30 cm and RNA 0-10 cm) with respect to disturbance histories; and all samples pooled across respective disturbance histories for each sample type.



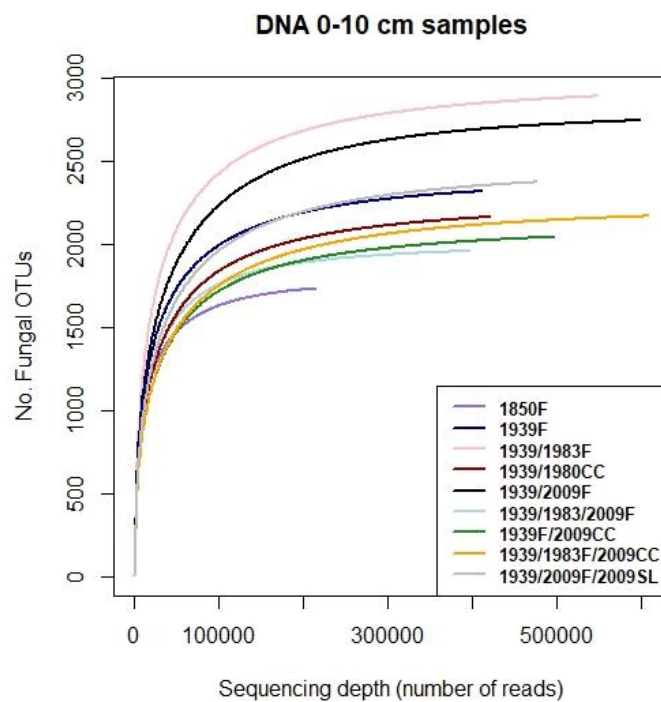
a) Rarefaction curves for each sample within the RNA 0-10 cm sample type, and with respect to disturbance histories. The vertical line is indicative of the sequencing depth that was used in the rarefaction.



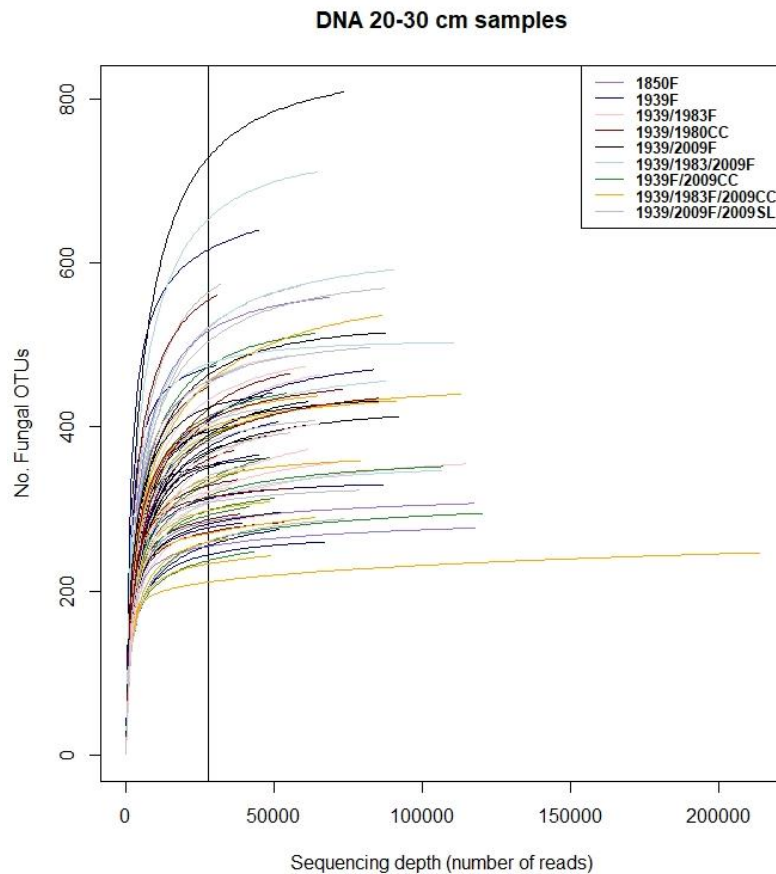
b) Rarefaction curves of all samples pooled across respective disturbance histories within the RNA 0-10 cm sample type.



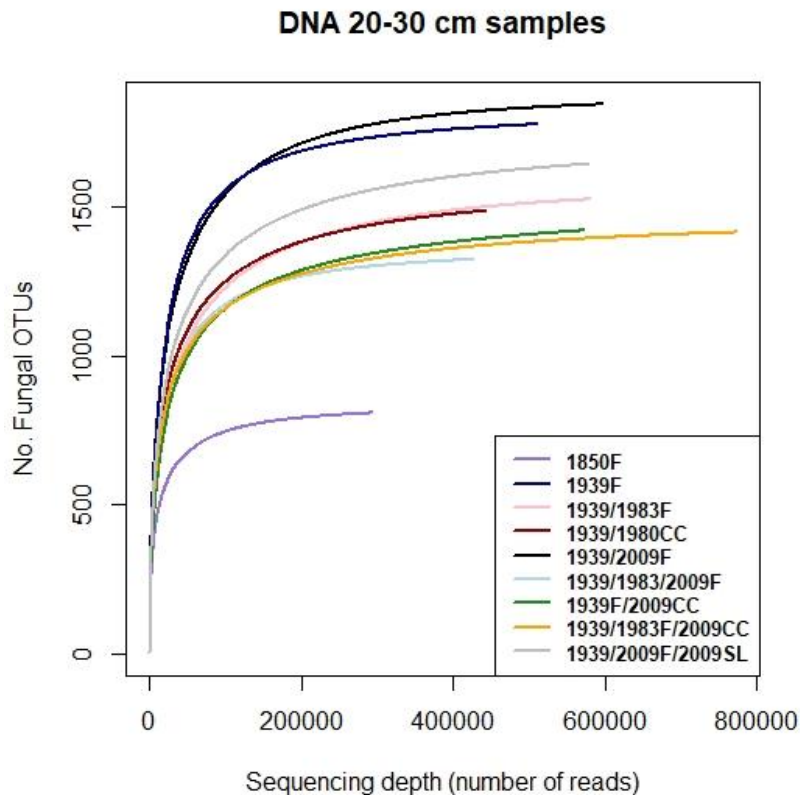
c) Rarefaction curves for each sample within the DNA 0-10 cm sample type, and with respect to disturbance histories. The vertical line is indicative of the sequencing depth that was used in the rarefaction.



d) Rarefaction curves of all samples pooled across respective disturbance histories within the DNA 0-10 cm sample type.



e) Rarefaction curves for each sample within the DNA 20-30 cm sample type, and with respect to disturbance histories. The vertical line is indicative of the sequencing depth that was used in the rarefaction.



f) Rarefaction curves of all samples pooled across respective disturbance histories within the DNA 20-30 cm sample type.

Table S2. Post-hoc pairwise comparisons between the number of **a)** fires, **b)** time since disturbance on fungal community composition across sample types.

a)	Pairwise comparison	Df	SumsOfSqs	F	R2	p=	p (Holm)
DNA 0-10 cm	1 fire vs 2 fires	1	1.82	2.73	0.04	0.00	0.01
	1 fire vs 0 fires	1	0.90	1.43	0.04	0.02	0.13
	1 fire vs 3 fires	1	1.98	3.23	0.09	0.00	0.01
	2 fires vs 0 fires	1	1.19	1.70	0.04	0.00	0.02
	2 fires vs 3 fires	1	1.79	2.63	0.06	0.00	0.01
	0 fires vs 3 fires	1	1.24	2.06	0.20	0.00	0.02
DNA 20-30 cm	1 fire vs 3 fires	1	1.53	2.43	0.07	0.00	0.01
	1 fire vs 2 fires	1	1.47	2.20	0.03	0.00	0.01
	1 fire vs 0 fires	1	1.18	1.83	0.05	0.01	0.04
	2 fires vs 3 fires	1	1.44	2.18	0.05	0.00	0.01
	0 fires vs 3 fires	1	1.21	2.18	0.21	0.00	0.02
	2 fires vs 0 fires	1	1.29	1.91	0.04	0.00	0.01
RNA 0-10 cm	1 fire vs 2 fires	1	0.65	1.11	0.02	0.21	1.00
	1 fire vs 3 fires	1	0.74	1.37	0.05	0.04	0.23
	1 fire vs 0 fires	1	0.93	1.64	0.06	0.01	0.06
	2 fires vs 3 fires	1	1.22	2.09	0.05	0.00	0.01
	2 fires vs 0 fires	1	1.10	1.81	0.05	0.00	0.02
	0 fires vs 3 fires	1	0.89	1.80	0.18	0.00	0.02

b)

	Pairwise comparison	Df	SumsOfSqs	F	R2	p=	p (Holm)
DNA 0-10 cm	TSD = 8 vs TSD = 167	1	1.13	1.66	0.03	0.01	0.04
	TSD = 8 vs TSD = 34	1	1.26	1.86	0.03	0.00	0.01
	TSD = 8 vs TSD = 78	1	1.49	2.19	0.03	0.00	0.01
	TSD = 167 vs TSD = 34	1	0.84	1.26	0.10	0.09	0.56
	TSD = 167 vs TSD = 78	1	0.80	1.20	0.09	0.11	0.63
	TSD = 34 vs TSD = 78	1	0.59	0.89	0.05	0.78	1.00
DNA 20-30 cm	TSD = 8 vs TSD = 78	1	1.19	1.76	0.03	0.00	0.01
	TSD = 8 vs TSD = 34	1	1.05	1.60	0.02	0.00	0.01
	TSD = 8 vs TSD = 167	1	1.24	1.85	0.03	0.00	0.01
	TSD = 34 vs TSD = 78	1	0.75	1.14	0.06	0.23	1.00
	TSD = 167 vs TSD = 78	1	1.08	1.53	0.11	0.04	0.25
	TSD = 167 vs TSD = 34	1	1.20	2.00	0.14	0.00	0.01
RNA 0-10 cm	TSD = 8 vs TSD = 78	1	0.85	1.46	0.03	0.03	0.18
	TSD = 8 vs TSD = 34	1	0.53	0.92	0.02	0.58	1.00
	TSD = 8 vs TSD = 167	1	1.06	1.86	0.03	0.00	0.02
	TSD = 34 vs TSD = 78	1	0.56	0.88	0.06	0.79	1.00
	TSD = 167 vs TSD = 78	1	0.87	1.36	0.11	0.02	0.14
	TSD = 167 vs TSD = 34	1	0.84	1.38	0.12	0.03	0.20

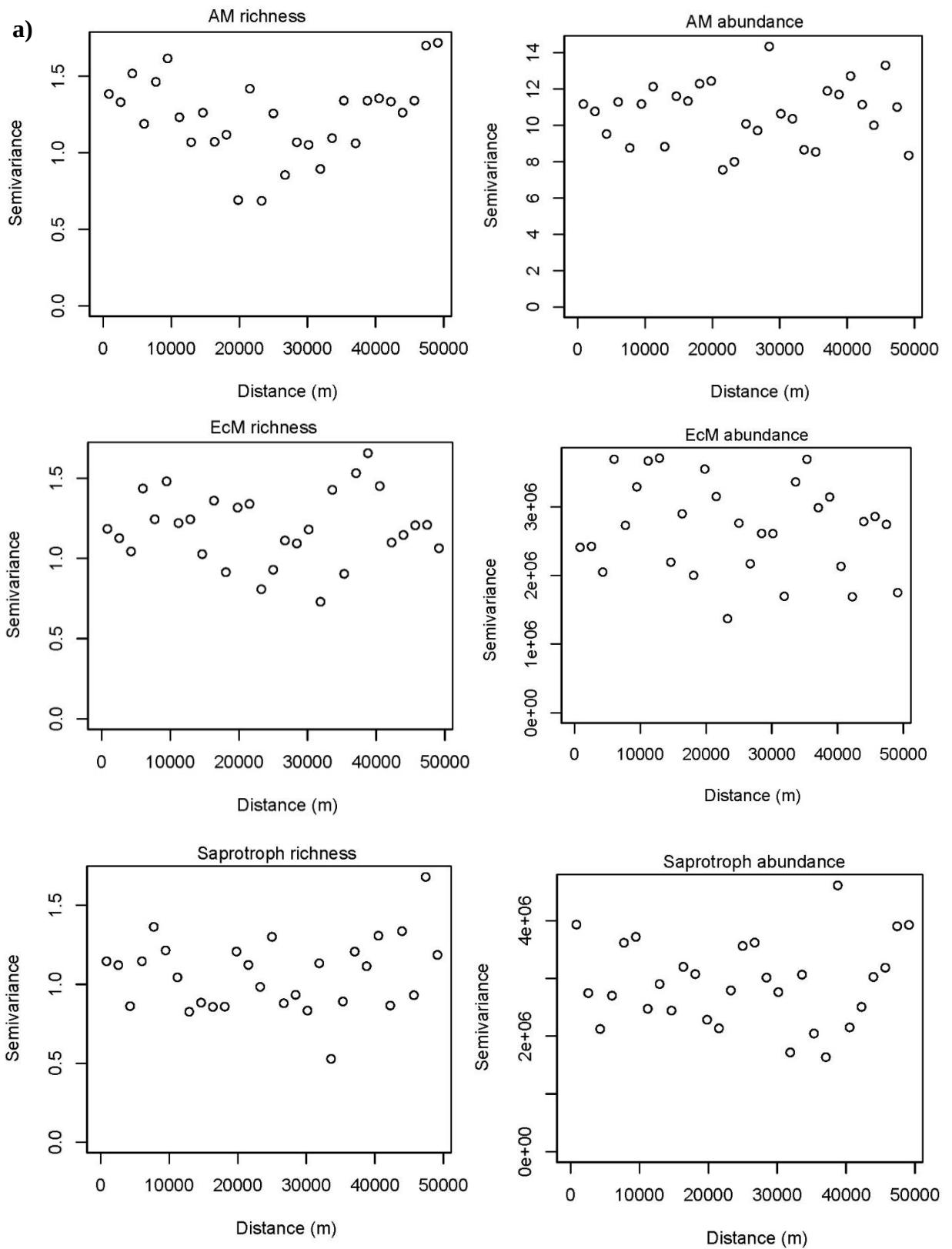
Table S3. Parameter estimates and standard errors from linear regression models of the richness and abundance of each fungal functional group with respect to sample type (DNA 0-10 cm, DNA 20-30 cm and RNA 0-10 cm), disturbance type, time since last disturbance (TSD(log)), and other environmental and site variables. Bold text indicates a significant association ($p < 0.05$) between the corresponding variables.

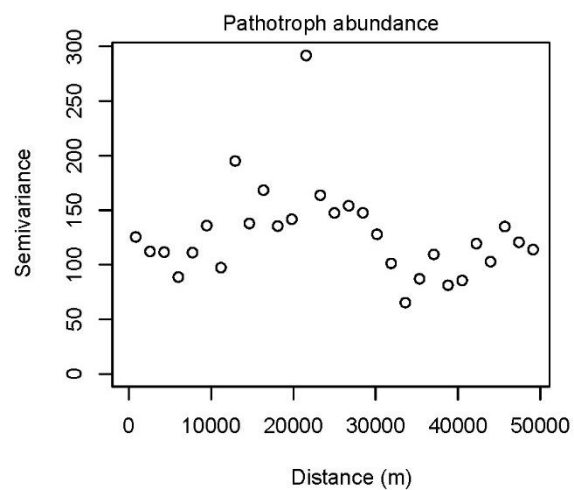
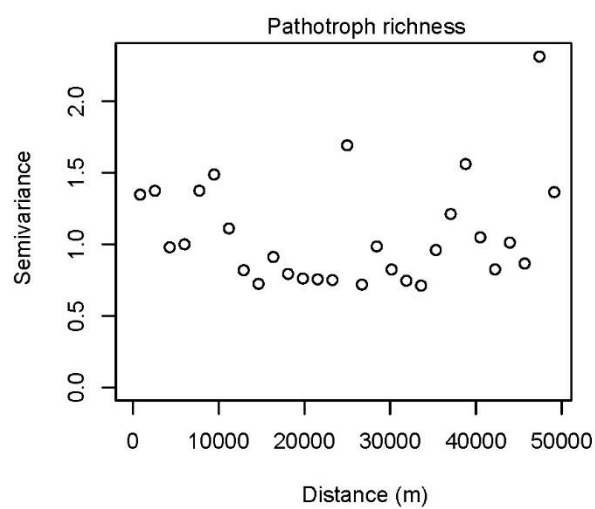
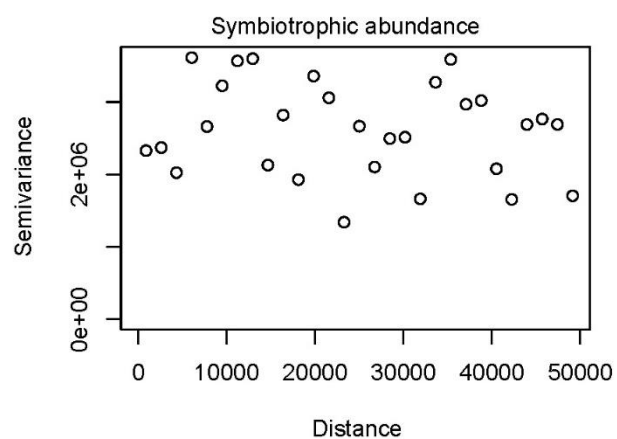
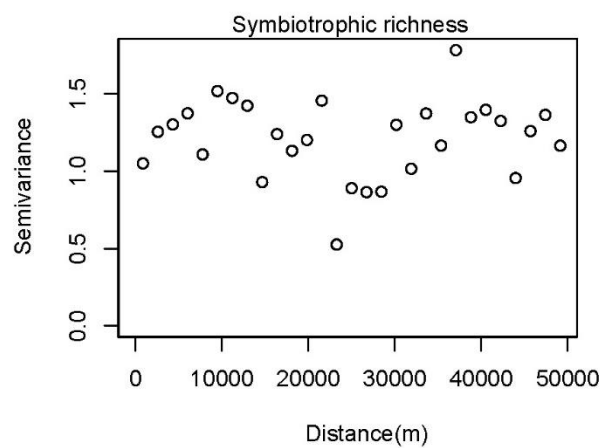
Response	Sample		(Intercept)	1 Fire	2 Fires	3 Fires	Clearcut logging	Salvage logging	TSD (log)	R2
EcM richness	DNA 0-10 cm	Estimate	2.05	0.44	0.72	0.69	-0.13	0.07	0.32	0.31
		SE	0.47	0.22	0.27	0.34	0.14	0.16	0.08	
		p=	0.00	0.05	0.01	0.05	0.36	0.64	0.00	
	DNA 20-30 cm	Estimate	2.54	0.27	0.46	0.51	-0.09	0.13	0.16	0.32
		SE	0.66	0.23	0.31	0.37	0.15	0.17	0.10	
		p=	0.00	0.24	0.14	0.17	0.56	0.45	0.09	
	RNA 0-10 cm	Estimate	-0.15	0.28	0.55	0.84	0.19	0.39	0.47	0.14
		SE	0.92	0.39	0.50	0.65	0.26	0.31	0.17	
		p=	0.87	0.47	0.27	0.20	0.47	0.21	0.01	
EcM abundance	DNA 0-10 cm	Estimate	-566.30	2374.90	2189.20	1678.00	-960.90	-174.10	772.10	0.22
		SE	2091.80	1040.70	1221.90	1554.40	614.10	705.60	372.30	
		p=	0.79	0.03	0.08	0.28	0.12	0.81	0.04	
	DNA 20-30 cm	Estimate	1408.67	-531.51	2047.12	696.97	-421.03	489.71	2557.94	0.33
		SE	5483.91	2233.24	2594.05	3364.92	1255.78	1558.89	758.38	
		p=	0.80	0.81	0.43	0.84	0.74	0.75	0.00	
	RNA 0-10 cm (sqrt)	Estimate	-12.96	11.12	13.83	10.06	-1.79	-0.78	4.46	0.12
		SE	14.25	6.66	8.12	10.25	3.99	4.84	2.58	
		p=	0.37	0.10	0.09	0.33	0.66	0.87	0.09	
Symbiotrophic richness (all)	DNA 0-10 cm	Estimate	4.00	-0.06	-0.13	0.05	-0.36	-0.04		0.31
		SE	0.15	0.16	0.15	0.18	0.08	0.12		
		p=	< 2e-16	0.73	0.40	0.80	0.00	0.76		
	DNA 20-30 cm	Estimate	3.88	0.04	0.04	0.17	-0.26	0.04		0.51
		SE	0.37	0.15	0.14	0.16	0.07	0.09		
		p=	0.00	0.79	0.79	0.30	0.00	0.67		
	RNA 0-10 cm	Estimate	2.89	-0.37	-0.54	-0.60	0.02	-0.10		0.08
		SE	0.29	0.34	0.32	0.39	0.18	0.26		
		p=	0.00	0.28	0.10	0.13	0.90	0.70		
Symbiotrophic abundance (all)	DNA 0-10 cm	Estimate	13.46	2116.47	1867.43	1475.49	-1035.50	-203.64	715.47	0.22
		SE	2062.26	1025.99	1204.58	1532.46	605.43	695.59	366.99	
		p=	0.99	0.04	0.13	0.34	0.09	0.77	0.06	
	DNA 20-30 cm	Estimate	5028.55	-791.71	1834.40	-5.18	-405.95	390.56	2520.28	0.35
		SE	5409.36	2181.44	2532.24	3319.16	1223.93	1459.25	738.53	
		p=	0.36	0.72	0.47	1.00	0.74	0.79	0.00	
	RNA 0-10 cm (sqrt)	Estimate	20.20	0.64	-0.96	-11.01	-3.89	-5.48		0.08
		SE	5.56	6.33	6.05	7.18	3.19	4.60		
		p=	0.00	0.92	0.87	0.13	0.23	0.24		

Response	Sample		(Intercept)	1 Fire	2 Fires	3 Fires	Clearcut logging	Salvage logging	TSD (log)	R2
AM richness	DNA 0-10 cm	Estimate	6.85	-1.48	-2.14	-1.70	-0.93	-0.42	-0.76	0.58
		SE	0.55	0.27	0.32	0.39	0.17	0.18	0.10	
		p=	< 2e-16	0.00	0.00	0.00	0.00	0.02	0.00	
	DNA 20-30 cm	Estimate	4.09	-0.55	-0.75	-0.06	-0.52	-0.07	-0.40	0.49
		SE	0.79	0.40	0.47	0.57	0.24	0.25	0.14	
		p=	0.00	0.18	0.11	0.91	0.03	0.78	0.01	
	RNA 0-10 cm	Estimate	6.00	-1.70	-2.31	-2.91	-0.33	-0.84	-0.76	0.18
		SE	1.19	0.56	0.68	0.85	0.34	0.43	0.22	
		p=	0.00	0.00	0.00	0.00	0.33	0.05	0.00	
AM abundance	DNA 0-10 cm (sqrt)	Estimate	28.69	-6.79	-10.31	-6.30	-4.39	0.36	-3.21	0.48
		SE	4.56	2.72	3.01	3.58	1.24	2.61	0.75	
		p=	0.00	0.01	0.00	0.08	0.00	0.89	0.00	
	DNA 20-30 cm (log)	Estimate	8.81	-2.38	-2.01	-1.58	-0.26	0.63	-0.70	0.32
		SE	1.63	0.97	1.08	1.28	0.44	0.94	0.27	
		p=	0.00	0.02	0.07	0.22	0.55	0.51	0.01	
	RNA 0-10 cm (sqrt)	Estimate	36.52	-12.34	-15.29	-22.72	-1.38	-5.86	-3.82	0.16
		SE	10.38	4.85	5.92	7.47	2.91	3.53	1.88	
		p=	0.00	0.01	0.01	0.00	0.64	0.10	0.05	
Saprotroph abundance	DNA 0-10 cm	Estimate	8005.80	-1234.90	-1086.40	-2200.10	-435.00	738.80	-945.00	0.21
		SE	2249.80	1113.80	1311.50	1668.30	657.30	782.40	400.80	
		p=	0.00	0.27	0.41	0.19	0.51	0.35	0.02	
	DNA 20-30 cm	Estimate	9312.60	-824.40	-2094.00	-2445.20	469.60	1039.60	-1289.40	0.22
		SE	2808.90	1397.40	1640.70	2087.30	824.60	947.40	499.90	
		p=	0.00	0.56	0.21	0.25	0.57	0.28	0.01	
	RNA 0-10 cm (sqrt)	Estimate	60.08	-4.33	1.25	-5.83	1.14	-11.58		0.19
		SE	14.41	8.81	8.50	9.97	3.19	8.34		
		p=	0.00	0.62	0.88	0.56	0.72	0.17		
Saprotroph richness	DNA 0-10 cm	Estimate	5.05	-0.18	-0.23	0.04	-0.11	0.07	-0.09	0.32
		SE	0.28	0.14	0.17	0.21	0.08	0.10	0.05	
		p=	<2e-16	0.20	0.18	0.84	0.20	0.47	0.09	
	DNA 20-30 cm	Estimate	3.51	0.13	0.13	0.41	-0.09	0.42	0.75	0.40
		SE	0.37	0.22	0.21	0.22	0.08	0.20	0.31	
		p=	0.00	0.57	0.53	0.07	0.24	0.03	0.02	
	RNA 0-10 cm	Estimate	3.18	-0.14	0.26	0.51	0.30	-0.11		0.24
		SE	0.64	0.34	0.32	0.35	0.16	0.23		
		p=	0.00	0.68	0.43	0.15	0.06	0.64		
Pathotroph abundance	DNA 0-10 cm (sqrt)	Estimate	47.22	-15.51	-16.66	-11.99	4.77	7.02		0.11
		SE	5.79	6.51	6.23	7.47	3.16	4.33		
		p=	0.00	0.02	0.01	0.11	0.13	0.11		
	DNA 20-30 cm (sqrt)	Estimate	30.69	3.27	-0.60	-3.88	-4.04	-5.47		0.12
		SE	5.01	5.21	5.07	5.98	2.58	3.88		
		p=	0.00	0.53	0.91	0.52	0.12	0.16		
	RNA 0-10 cm (sqrt)	Estimate	18.14	3.47	0.24	0.70	0.63	0.48		0.05
		SE	3.85	4.38	4.22	4.96	2.23	3.23		
		p=	0.00	0.43	0.96	0.89	0.78	0.88		
Pathotroph richness	DNA 0-10 cm	Estimate	3.66	-0.15	-0.04	0.24	0.08	0.60		0.40
		SE	0.19	0.19	0.18	0.20	0.07	0.17		
		p=	< 2e-16	0.44	0.82	0.23	0.27	0.00		
	DNA 20-30 cm	Estimate	1.94	0.37	0.19	0.33	-0.23	0.05	1.24	0.16
		SE	0.53	0.23	0.22	0.24	0.11	0.15	0.49	
		p=	0.00	0.12	0.40	0.18	0.04	0.73	0.01	
	RNA 0-10 cm	Estimate	1.74	0.05	0.27	0.70	0.31	-0.06		0.19
		SE	0.79	0.40	0.38	0.41	0.18	0.26		
		p=	0.03	0.90	0.47	0.09	0.09	0.82		

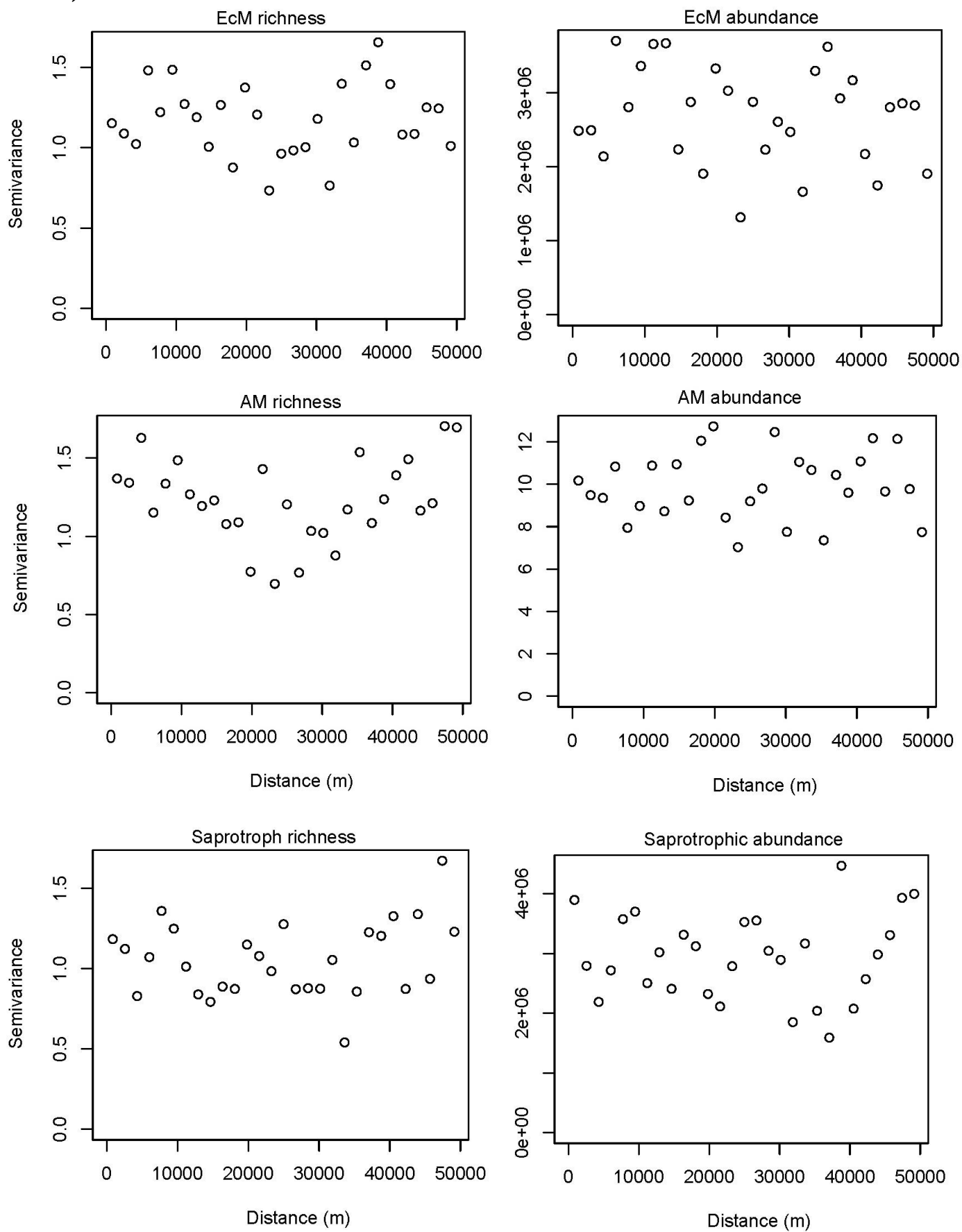
Response	Sample	Parent rock 2	Parent rock 3	Parent rock 4	Parent rock 5	Soil type 2	Soil type 3	Thinning	Historical silviculture	Slope	Elevation
EcM richness	DNA 0-10 cm	Estimate									
		SE									
		p=									
	DNA 20-30 cm	Estimate	0.46	0.18	-0.01	0.04					
		SE	0.36	0.35	0.40	0.35					
		p=	0.20	0.60	0.98	0.91					
	RNA 0-10 cm	Estimate									
		SE									
		p=									
EcM abundance	DNA 0-10 cm	Estimate									
		SE									
		p=									
	DNA 20-30 cm	Estimate								82.79	-4.34
		SE								66.68	3.74
		p=								0.22	0.25
	RNA 0-10 cm (sqrt)	Estimate									
		SE									
		p=									
Symbiotrophic richness (all)	DNA 0-10 cm	Estimate								0.01	
		SE								0.01	
		p=								0.13	
	DNA 20-30 cm	Estimate	0.48	0.28	0.17	0.02					0.00
		SE	0.26	0.25	0.29	0.25					0.00
		p=	0.06	0.28	0.56	0.95					0.11
	RNA 0-10 cm	Estimate									
		SE									
		p=									
Symbiotrophic abundance (all)	DNA 0-10 cm	Estimate									
		SE									
		p=									
	DNA 20-30 cm	Estimate						-2379.00			-7.02
		SE						1440.52			3.75
		p=						0.10			0.07
	RNA 0-10 cm (sqrt)	Estimate									
		SE									
		p=									

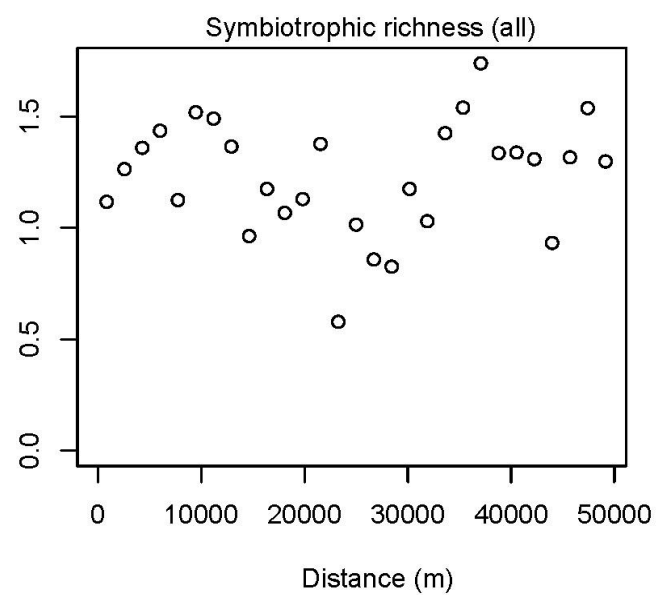
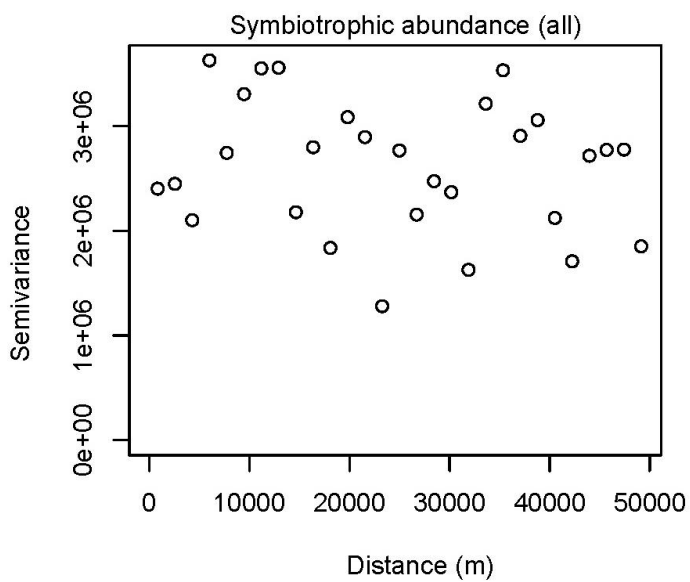
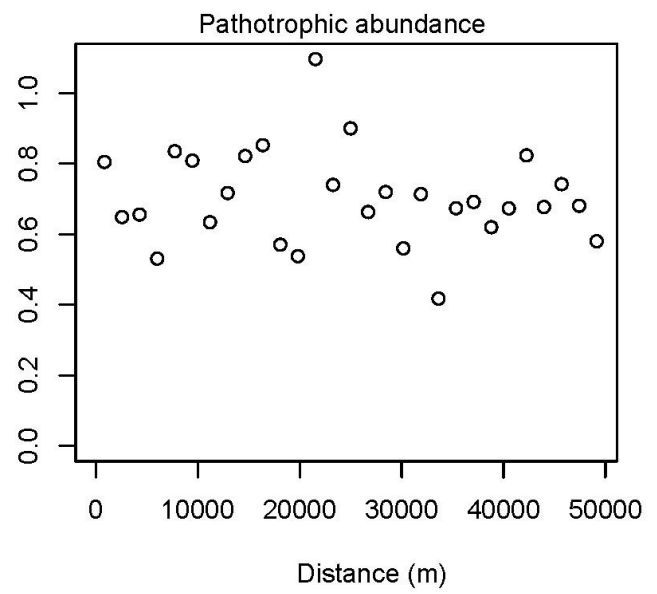
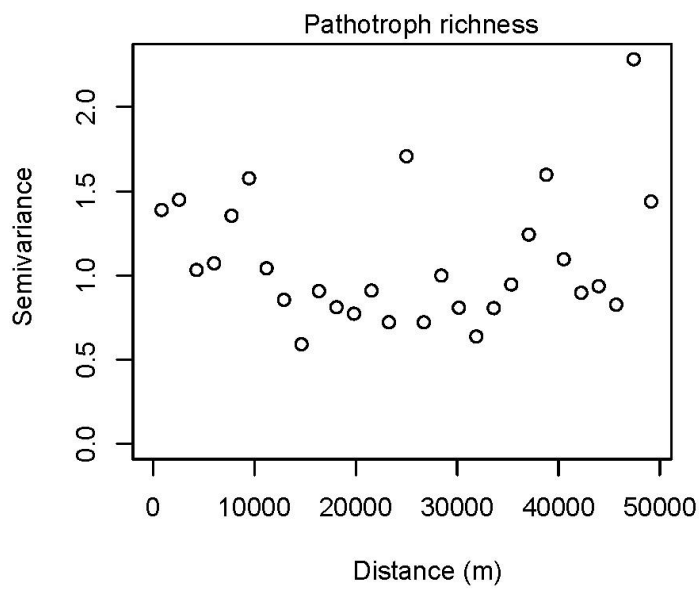
Response	Sample		Parent rock 2	Parent rock 3	Parent rock 4	Parent rock 5	Soil type 2	Soil type 3	Thinning	Historical silviculture	Slope	Elevation
AM abundance	DNA 0-10 cm (sqrt)	<i>Estimate</i>					-2.98	8.33				
		<i>SE</i>					2.74	3.46				
		<i>p=</i>					0.28	0.02				
	DNA 20-30 cm (log)	<i>Estimate</i>					-1.27	-2.57			-0.04	
		<i>SE</i>					0.98	1.24			0.02	
		<i>p=</i>					0.20	0.04			0.08	
	RNA 0-10 cm (sqrt)	<i>Estimate</i>										
		<i>SE</i>										
		<i>p=</i>										
Saprotroph abundance	DNA 0-10 cm	<i>Estimate</i>								-1847.50		
		<i>SE</i>								1156.20		
		<i>p=</i>								0.11		
	DNA 20-30 cm	<i>Estimate</i>										
		<i>SE</i>										
		<i>p=</i>										
	RNA 0-10 cm (sqrt)	<i>Estimate</i>					21.84	12.36				-0.04
		<i>SE</i>					9.53	11.09				0.01
		<i>p=</i>					0.03	0.27				0.01
Saprotroph richness	DNA 0-10 cm	<i>Estimate</i>									0.01	
		<i>SE</i>									0.00	
		<i>p=</i>									0.03	
	DNA 20-30 cm	<i>Estimate</i>	0.52	0.54	0.53		-0.24	-0.69				
		<i>SE</i>	0.31	0.34	0.31		0.21	0.29				
		<i>p=</i>	0.10	0.12	0.09		0.25	0.02				
	RNA 0-10 cm	<i>Estimate</i>	0.19	0.29	-1.41	0.71						
		<i>SE</i>	0.58	0.58	0.66	0.57						
		<i>p=</i>	0.74	0.61	0.04	0.22						
Pathotroph abundance	DNA 0-10 cm (sqrt)	<i>Estimate</i>										
		<i>SE</i>										
		<i>p=</i>										
	DNA 20-30 cm (sqrt)	<i>Estimate</i>									-0.31	
		<i>SE</i>									0.17	
		<i>p=</i>									0.08	
	RNA 0-10 cm (sqrt)	<i>Estimate</i>										
		<i>SE</i>										
		<i>p=</i>										
Pathotroph richness	DNA 0-10 cm	<i>Estimate</i>					-0.60	0.15			0.01	
		<i>SE</i>					0.19	0.25			0.00	
		<i>p=</i>					0.00	0.54			0.04	
	DNA 20-30 cm	<i>Estimate</i>	1.09	0.95	1.03				-0.29			
		<i>SE</i>	0.49	0.54	0.49				0.16			
		<i>p=</i>	0.03	0.08	0.04				0.08			
	RNA 0-10 cm	<i>Estimate</i>	0.46	0.60	-1.36	1.02						
		<i>SE</i>	0.72	0.72	0.88	0.71						
		<i>p=</i>	0.53	0.41	0.13	0.16						



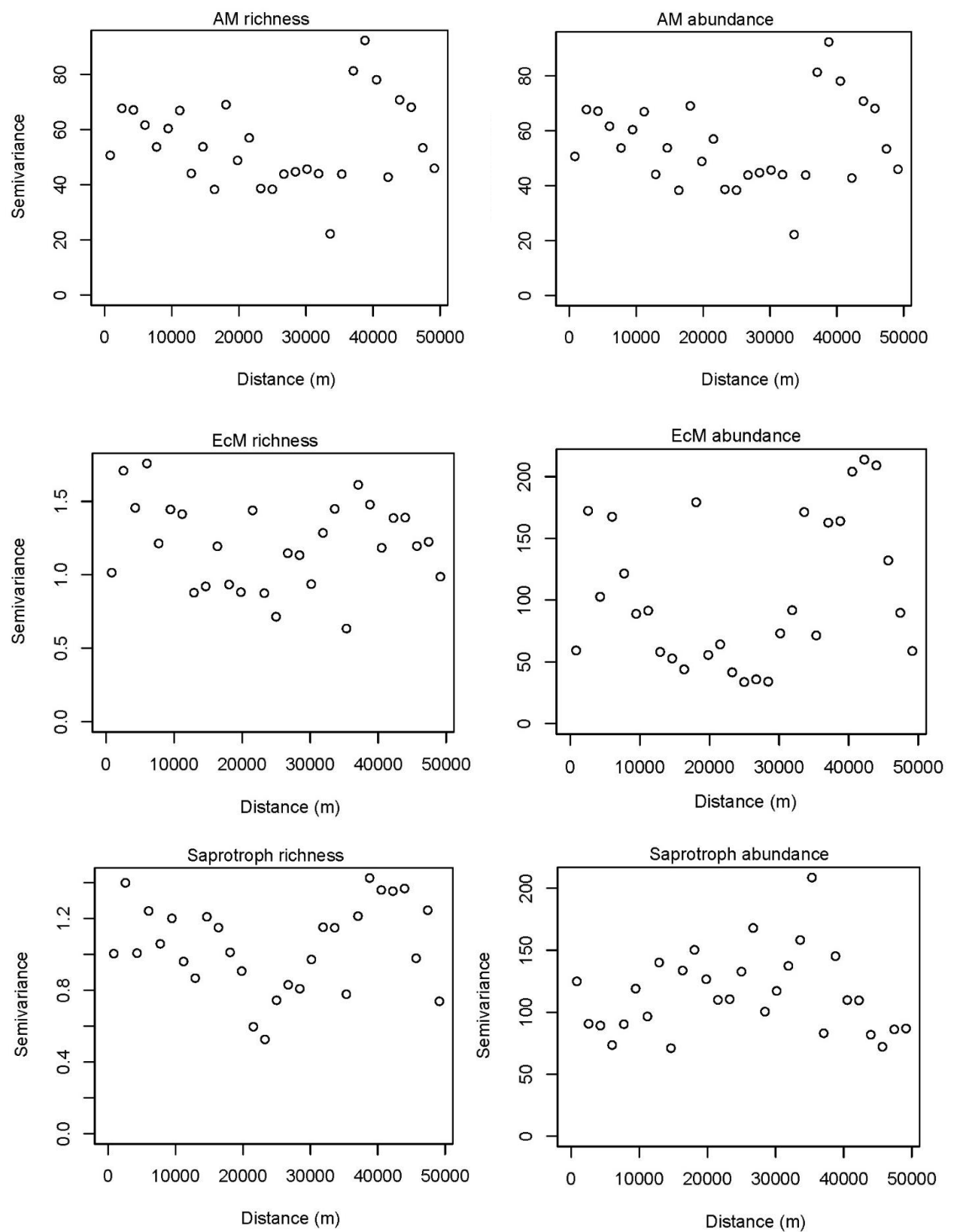


b)





c)



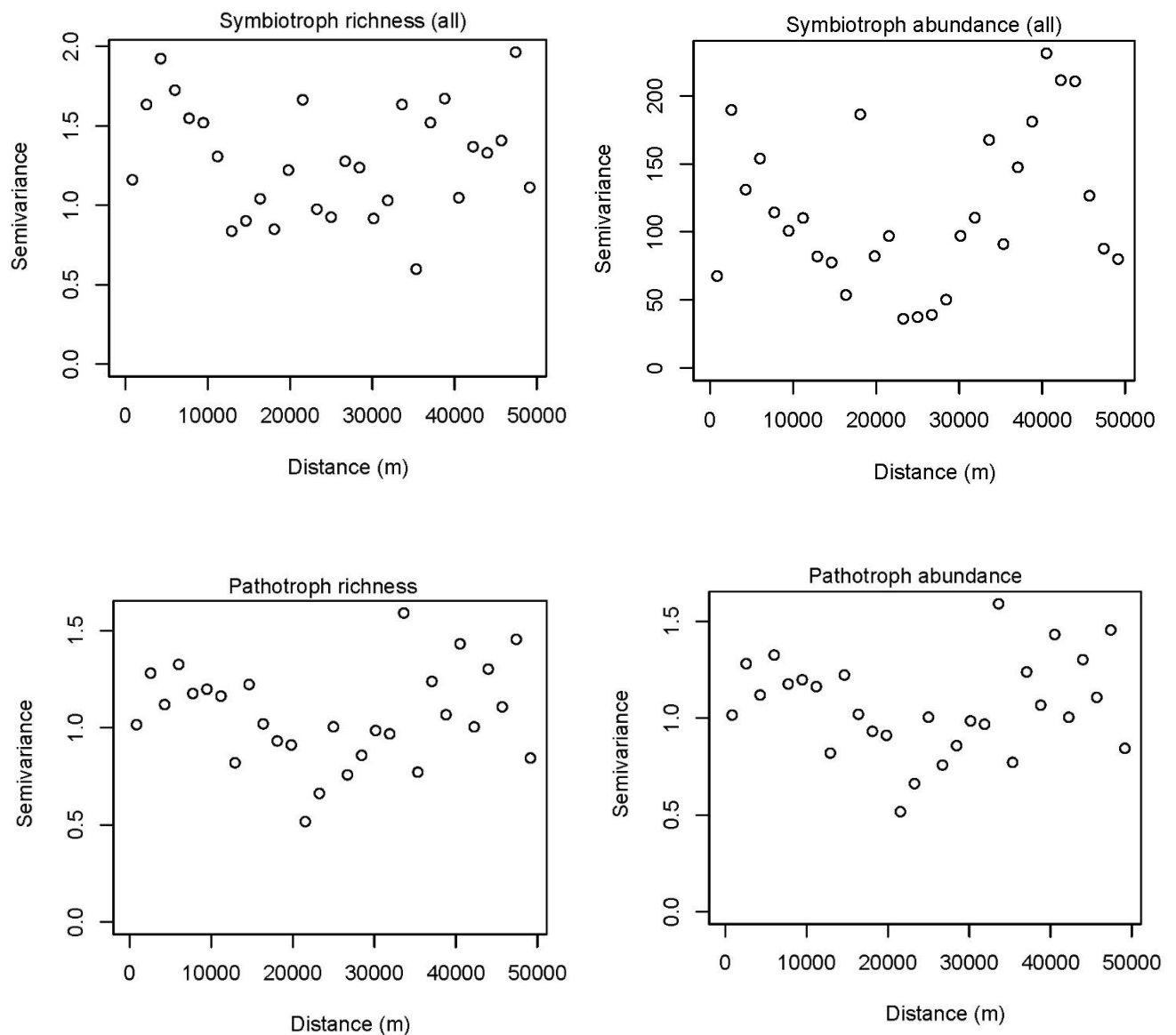
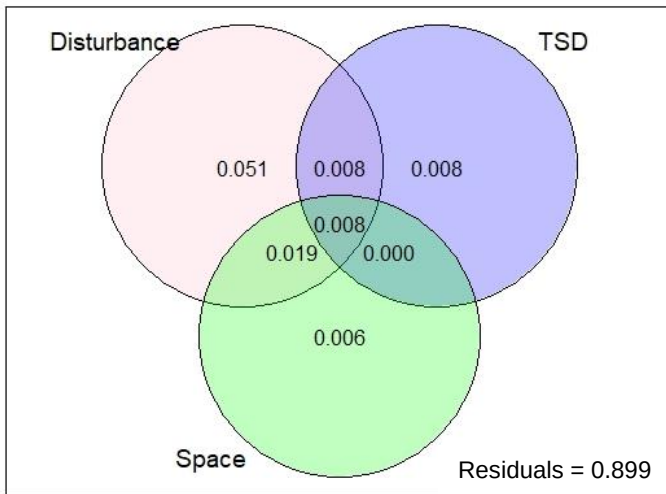
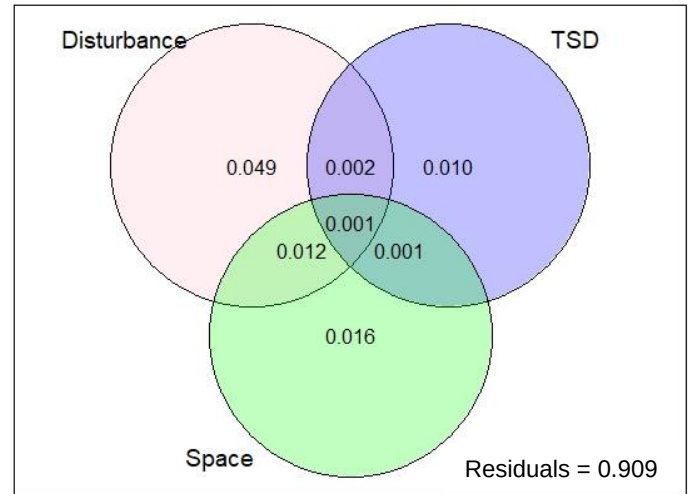


Figure S3. Variograms generated using residual values from each linear regression model for all response variables (richness of fungal OTUs (total, saprotrophic, symbiotrophic and pathotrophic), and relative abundance of fungal OTUs (saprotrophic, symbiotrophic and pathotrophic) across sample types (DNA 0-10 cm (a), DNA 20-30 cm (b) and RNA 0-10 cm (c).

DNA 0-10 cm



DNA 20-30 cm



RNA 0-10 cm

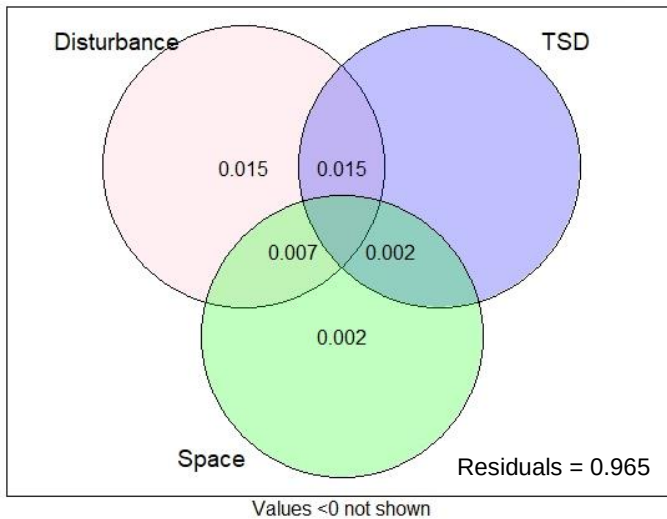


Figure S4. Variance in the community composition of fungal communities explained by disturbance variables (No. Fires, clearcut logging and salvage logging), time since disturbance (log transformed) (TSD), and positive spatial eigenvectors (dbMEMs).

Table S4. Count of indicator OTUs ($p < 0.001$; $\text{IndVal} > 0.75$) by phylum (and functional group within phyla) across each sample, with respect to different disturbance histories.

Sample	Phylum	Functional group	Guild	1850F	1939F	1939/19	1939/1939F	1939F/2	1939/1983	1939/2009
DNA 0-10 cm	Ascomycota	Pathotroph	Plant Pathogen	1	0	0	1	1	0	1
		Pathotroph-Symbiotroph	Ericoid Mycorrhizal	0	0	0	0	0	1	1
		Saprotroph	Plant Saprotroph-Wood Saprotroph	0	0	0	2	0	0	0
		Saprotroph	Soil Saprotroph	1	0	0	0	0	1	0
		Saprotroph	Undefined Saprotroph	1	1	2	3	1	2	4
	Basidiomycota	Saprotroph-Pathotroph	Animal Pathogen-Undefined Saprotroph	0	0	0	2	0	1	1
		Symbiotroph	Ectomycorrhizal	1	0	0	0	1	0	0
		Undefined	Undefined	5	6	6	16	10	7	15
		Saprotroph	Undefined Saprotroph	1	0	0	3	0	1	1
		Saprotroph	Wood Saprotroph	0	0	0	1	0	0	0
	Chytridiomycota	Symbiotroph	Ectomycorrhizal	3	2	2	3	2	1	0
		Undefined	Undefined	3	4	3	8	5	3	6
		Undefined	Undefined	0	0	0	1	0	0	0
		Symbiotroph	Arbuscular Mycorrhizal	0	0	0	8	1	0	1
		Pathotroph	Animal Pathogen	0	0	0	1	0	0	0
DNA 20-30 cm	Ascomycota	Saprotroph	Undefined Saprotroph	0	0	0	1	0	0	0
		Saprotroph	Undefined Saprotroph	0	1	1	3	1	1	1
		Saprotroph-Pathotroph	Animal Pathogen-Undefined Saprotroph	0	0	0	1	0	0	0
		Undefined	Undefined	7	3	6	10	7	6	5
		Saprotroph	Undefined Saprotroph	1	0	1	2	0	1	1
	Basidiomycota	Saprotroph	Plant Saprotroph-Wood Saprotroph	1	0	0	1	0	0	0
		Saprotroph	Undefined Saprotroph	0	1	1	3	1	1	1
		Saprotroph-Pathotroph	Animal Pathogen-Undefined Saprotroph	0	0	0	1	0	0	0
		Undefined	Undefined	7	3	6	10	7	6	5
		Saprotroph	Undefined Saprotroph	1	0	1	2	0	1	1
	Glomeromycota	Saprotroph	Wood Saprotroph	0	0	0	0	0	0	0
		Saprotroph-Pathotroph-Symbiotroph	Endophyte-Plant Pathogen-Undefined Saprotroph	1	0	0	0	0	0	0
		Saprotroph-Symbiotroph	Lichenized-Undefined Saprotroph	0	0	0	1	0	0	0
		Symbiotroph	Ectomycorrhizal	5	0	0	0	0	0	0
		Undefined	Undefined	5	0	0	4	0	1	1
RNA 0-10 cm	Ascomycota	Symbiotroph	Arbuscular Mycorrhizal	0	0	0	1	1	1	1
		Undefined	Undefined	6	1	1	3	2	1	1
		Saprotroph	Undefined Saprotroph	1	1	0	0	0	1	0
		Saprotroph	Soil Saprotroph	1	0	0	0	0	1	0
		Saprotroph	Undefined Saprotroph	0	0	0	2	0	0	1
	Basidiomycota	Undefined	Undefined	4	0	1	3	0	2	1
		Saprotroph-Pathotroph	Bryophyte Parasite-Leaf Saprotroph-Wood Saprotroph	0	0	0	1	0	0	0
		Saprotroph-Symbiotroph	Lichenized-Undefined Saprotroph	0	0	0	1	0	0	0
		Undefined	Undefined	2	0	0	4	2	0	2
		Symbiotroph	Arbuscular Mycorrhizal	0	0	0	0	0	1	0
	Glomeromycota	Undefined	Undefined	3	1	0	3	2	1	2
		Undefined	Undefined	3	1	0	3	2	1	2
		Undefined	Undefined	3	1	0	3	2	1	2
		Undefined	Undefined	3	1	0	3	2	1	2
		Undefined	Undefined	3	1	0	3	2	1	2

Chapter 4

Wildfires and logging alter the forest soil microbiome

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Abstract

Billions of microorganisms perform critical below-ground functions in all terrestrial ecosystems. While largely invisible to the naked eye, they support all higher lifeforms, form symbiotic relationships, stabilize soils, and facilitate decomposition and biogeochemical cycles. Climate change and increases in the frequency of wildfires and anthropogenic disturbances are driving major changes to global forest ecosystems. These changes can alter the composition and diversity of biological communities and shift ecosystems into states where key functions are compromised. Disturbance responses of below-ground microorganisms are poorly understood relative to those above-ground, despite the integral functions they provide. Here, we explore the diverse soil microbiome of the Mountain Ash forests in south-eastern Australia. Across a multi-decadal chronosequence in these forests we also quantify the impacts of wildfires and anthropogenic disturbances on microbial diversity and community composition. We identified 26,256 unique microbial operational taxonomic units (OTUs) across 80 sites sampled at two soil depths (0-10 cm and 20-30 cm). Using this extensive dataset, we provide evidence that wildfires, clearcut logging and salvage logging reduce the alpha diversity of microbial communities and alter their composition. Specifically, we show that multiple fires can result in more severe declines in the diversity of some microbial communities relative to logging, with effects more pronounced in the topsoil. Our findings also identify key environmental and edaphic indicators of these communities post-disturbance. With global environmental and climatic changes projected to increase and intensify, it is crucial that we determine the disturbance responses of below-ground microorganisms to best preserve the functional integrity of forests.

Introduction

In the current period of rapid, global, environmental change, forest ecosystems face many compounding and interacting challenges (Watson et al., 2018). These include, changing climatic conditions (Seidl et al., 2017), biological invasions (Farris et al., 2015; Ricciardi, 2007), pathogen attacks (Sturrock et al., 2011), anthropogenic disturbances (Maxwell, Fuller, Brooks, & Watson, 2016; Watson et al., 2018) and wildfires (Bradstock, Cohn, Gill, Bedward, & Lucas, 2009; Schoennagel et al., 2017; Seidl, Schelhaas, Rammer, & Verkerk, 2014). In recent years, global disturbance patterns in forests have been characterized by an increase in the frequency and intensity of wildfires, largely driven by climatic changes and anthropogenic disturbances (Cochrane and Laurance, 2008; Bowman *et al.*, 2011; Seidl *et al.*, 2014; Taylor, McCarthy and Lindenmayer, 2014; Abatzoglou and Williams, 2016). While natural disturbances, such as wildfire, play key functional roles in forests (Bond, Woodward, & Midgley, 2005; Bowman et al., 2009), novel wildfire intensities and frequencies, in combination with anthropogenic disturbances, can shift ecosystems into functionally compromised states (Bowman, Murphy, Neyland, Williamson, & Prior, 2014; Lindenmayer, Hobbs, Likens, Krebs, & Banks, 2011). The impact of anthropogenic disturbance (logging) and natural (wildfire) disturbance on above-ground plant and animal communities in forests have been subject to extensive study (Blair, McBurney, Blanchard, Banks, & Lindenmayer, 2016; Enright, Fontaine, Bowman, Bradstock, & Williams, 2015; Lindenmayer, Blanchard, Blair, Westgate, & Scheele, 2019; Taboada, Fernández-García, Marcos, & Calvo, 2018). However, how soil microbial communities are impacted by the same perturbations remains comparatively poorly-understood (Barnes et al., 2017; Wardle et al., 2004).

Billions of hyper-diverse and highly-cryptic microorganisms dominate the surface of the earth, yet our knowledge of this “unseen majority” is limited (Bardgett & Van Der Putten, 2014; Cavicchioli et al., 2019). Despite this, microorganisms (fungi, bacteria, archaea), collectively known as the ‘microbiome’, mediate critical ecological functions throughout ecosystems, and underpin many above-ground processes (Bardgett & Van Der Putten, 2014; Cavicchioli et al., 2019). These include, **(a)** forming symbiotic mycorrhizal relationships with >80% of terrestrial plant species (Martin, Kohler, Murat, Veneault-Fourrey, & Hobbett, 2016; van der Heijden, Martin, Selosse, & Sanders, 2015), **(b)** nutrient cycling (Deluca, Zackrisson, Gundale, & Nilsson, 2008; Philippot et al., 2013; van der Heijden et al., 2015), **(c)** decomposition (Crowther et al., 2019), **(d)** carbon storage and climate change mitigation

(Averill, Turner, & Finzi, 2014; Jansson & Hofmockel, 2019), and **(e)** regulating plant productivity and diversity (van der Heijden, Bardgett, & van Straalen, 2008).

Advances in DNA sequencing technology have facilitated the exploration of microbial communities, and in turn, elevated the understanding of their diversity, functions and multi-trophic interactions (Bálint et al., 2016; Barnes et al., 2017; Fierer, 2017). Due to their extremely high abundance and diversity, microbial communities are often thought to have high levels of functional redundancy, and therefore have high levels of resistance and resilience to disturbances (Allison & Martiny, 2008). However, recent research suggests that functional redundancy in microbial communities has been previously overstated, and therefore the impact of disturbances on these communities and the functions they provide may have been underestimated (Delgado-Baquerizo et al., 2016).

Natural disturbances, such as wildfire, and anthropogenic disturbances like clearcut logging, can alter the composition, diversity and abundance of forest microbial communities (Dooley & Treseder, 2012; Hartmann et al., 2012; Holden, Berhe, & Treseder, 2015). These disturbance impacts can be direct, or indirect, mediated through changes in edaphic properties and plant communities (Cutler et al., 2017; Hartmann et al., 2014; Holden, Berhe, & Treseder, 2015), and can differ between individual microbial communities or functional subgroups (Hartmann et al., 2014). Changes in the composition of microbial communities and declines in microbial diversity can have functional consequences in ecosystems (Delgado-Baquerizo et al., 2016, 2015). These include impacts on decomposition rates, nutrient cycling, soil fertility (Hartmann et al., 2014; Trivedi et al., 2019), symbiotic relationships (Hartmann et al., 2014; Holden et al., 2015), and specialized ecological functions such as nitrogen fixation (Philippot et al., 2013; Singh et al., 2014). The individual responses of microbial communities to disturbances such as wildfire and logging have previously been described independently of one another in other ecosystems (Dooley & Treseder, 2012; Hartmann et al., 2012, 2014; Holden & Treseder, 2013). However, little is known about how whole soil microbiomes are influenced by altered disturbance regimes of wildfires and logging, and the respective influence of environmental conditions post-disturbance.

Here, we investigate the effects of ecological disturbances (wildfire and logging) and soil properties on forest soil microbial communities. To do this, we used a multi-decadal chronosequence of disturbance histories in the tall and carbon-dense Mountain Ash (*Eucalyptus regnans*) forests of the Victorian Central Highlands, in south-eastern Australia.

Specifically, we describe the soil microbiome of these forests, and quantify the responses of individual microbial communities (fungi, archaea and bacteria) and total microbial diversity to: **(a)** major wildfires (of differing frequency), and **(b)** clearcut logging, and post-fire (salvage) logging events. We also investigated how environmental and edaphic variables influence the diversity and composition of these communities post-disturbance. To do this, we used DNA metabarcoding across two depths of forest soil at 80 field sites to answer two key research questions:

1. What is the impact of the number of fires and clearcut logging and salvage logging events on the community composition and diversity of the Mountain Ash forest soil microbiome?
2. What are the key drivers of changes in the composition and diversity of microbial communities post-disturbance in these forests?

To the best of our knowledge, this study is one of the first to simultaneously describe the impact of different frequencies of wildfire, and clearcut and salvage logging events on the soil microbiome (archaea, bacteria, fungi) of a temperate forest. This research also contributes to the understanding of the critically endangered Mountain Ash forest ecosystem, which has been degraded by the impacts of wildfire and logging on ecological functions (Burns et al., 2015).

Methods

Site description

We conducted this study in the temperate, wet-sclerophyll Mountain Ash forests of the Victorian Central Highlands in south-eastern Australia (Appendix Figure 1). These high elevation and high rainfall forests are dominated by the world's tallest flowering plant, *Eucalyptus regnans* (Mountain Ash), and have a midstorey consisting of *Acacia* and other scattered trees, and an understorey rich in broad-leaved shrubs, tree-ferns and mesophytic herb and fern species (Ashton, 1981; Blair, McBurney, Blanchard, Banks, & Lindenmayer, 2016; Bowd, Lindenmayer, Banks, & Blair, 2018). Mountain Ash forests typically experience cool and humid climatic conditions, receiving >1000 mm of rainfall annually (Ashton & Attiwill, 1994). However, periods of hot and dry conditions and wildfires have increased in recent decades (Bowman et al. 2014; Taylor, McCarthy, and Lindenmayer 2014).

Mountain Ash forest landscapes are characterised by a mosaic of natural and anthropogenic disturbance histories. The majority (80%) of these forests are broadly designated for timber

harvesting and pulp production, with the remaining (20%) located in national parks and water catchments (Burns et al., 2015; Langford, 1976). Since the 1970s, Mountain Ash forests have been extensively clearcut logged and salvage (post-wildfire) logged (Flint & Fagg, 2007; Florence, 1996). These practices involve the clearing of all vegetation within an area of 15-40 ha, removal of target tree species (*Eucalyptus regnans*), post-logging slash burning of remaining vegetative debris and aerial seeding of the target tree species (Chambers & Attiwill, 1994; Flint & Fagg, 2007; Lindenmayer et al., 2011).

Mountain Ash forests have co-evolved with the occurrence of high-severity wildfires every 75-150 years, which typically produces a new cohort of the dominant obligate seeder, *Eucalyptus regnans* (Ashton 1981; Lindenmayer et al. 2012; McCarthy, Gill, and Lindenmayer 1999). However, in recent decades the frequency of fires has increased, with major fires occurring in 1926, 1932, 1939, 1983, 2009 and most recently in 2019 (Lindenmayer et al. 2011). Collectively, multiple wildfires and widespread clearcut and salvage (post-wildfire) logging has led to the landscape being dominated by regrowth forest, with just 1.16% of the original extent of old growth forest remaining (Lindenmayer et al. 2012).

Study design

We designed our study to capture the diversity of disturbance histories in Mountain Ash forests. Specifically, we chose nine disturbance history types: five experienced fire-only and the remaining four were clearcut or salvage logged. Fire-only sites were: forests long-undisturbed (unburnt since 1850s n=4), burnt once (1939 fire n=10), burnt twice (1939/1983 n=10 and 1939/2009 n=11) or burnt three times (1939/1983/2009 n=6). Logged sites were those which regenerated after fire in 1939 and were then clearcut between 1980-1985 (n=10) or 2008-2010 (n=10). We also included sites which experienced multiple fires and clearcut logging, including those burnt in 1939 and 1983 (n=10) and clearcut in 2008-10 (n=9), and those burnt in 1939 and 2009 and salvage logged in 2009-10 (n=10). Our 80 field sites were characterized by a predominantly southerly aspect, were located at an elevation of ~600-900 meters, experienced an annual precipitation of between 1300-1800 mm, and were positioned away from drainage lines and ridges.

Data collection

We undertook field sampling of microbial communities and soil between December 2016 - March 2017 as documented in Bowd et al., 2019 (Bowd et al., 2019), and Bowd et al., 2020

(unpublished)(Bowd et al., 2020). Samples were collected to contribute to the BASE (Biomes of Australian Soil Environments) project and followed the BASE sampling protocol (Bissett et al., 2016). Specifically, at each of our 80 sites, we collected nine, 10 cm x 30 cm soil cores along the perimeter and in the centre of 25 x 25 m quadrats and stratified, pooled and mixed each soil sample by depth (0-10 cm and 20-30 cm). From the 0-10 cm and 20-30 cm composite soil samples for each site, we collected subsamples of soil (approximately 100 grams per sample) and stored them at -20°C for later DNA analysis of microbial communities. We air-dried and sieved remaining soil using a 2 mm sieve prior to analysis.

Soil chemistry

Soil chemical tests were conducted by CSBP Laboratories, as described in (Bissett et al., 2016). In brief, measures of ammonium and nitrate nitrogen were determined colorimetrically, following extraction with 2 M potassium chloride (25 °C) (Fertilisers, 2015; Rayment, 1992). Available phosphorus and potassium were measured using the Colwell method (Colwell, 1965; Rayment, 1992). Organic carbon was measured using the Walkley–Black method (Walkley, 1934). The concentrations of soluble salts were estimated by measuring electrical conductivity based on (EC 1:5). pH (CaCl₂) was measured from the same soil/water extracts, producing pH measures based on 1:5 soil/0.01 M CaCl₂ (Fertilisers, 2015; Rayment, 1992). DTPA extractable trace elements (Cu, Fe, Mn, Zn) were determined by atomic absorption spectroscopy following extraction with DTPA (Fertilisers, 2015; Rayment, 1992). Soil exchangeable cations were determined using ICP spectroscopy using a 1:5 soil:water extraction (Fertilisers, 2015; Rayment, 1992).

Genomics

DNA extraction and sequencing were undertaken by the BASE project, according to the methods described by Bissett et al., (2016). Briefly, DNA was extracted in triplicate (3 x 0.25g) using MO BIO power soil kits and extractions combined. Microbial communities were profiled by sequencing amplicons targeting the fungal ITS region (primers: ITS1F (Gardes & Bruns, 1993) and ITS4 (White, Bruns, Lee, & Taylor, 1990), bacterial 16S rRNA genes (primers: 27f (Lane, 1991) and 519r (Lane et al., 1985)) or archaeal 16S rRNA genes (primers: A2F (Reysenbach, Pace, In., Robb, & Place, 1995) and 519r (Lane et al., 1985)) using the Illumina MiSEQ platform to generate 300 base pair, paired end reads for each sample (Bissett et al., 2016).

Sequence analyses for DNA samples were conducted as per Bissett et al., (2016). Briefly, for fungal amplicon, the ITS1 region was extracted from R1 reads using ITSx v1.0.11 (Bengtsson-Palme et al., 2013), operational taxonomic units (OTUs) were clustered at 97% sequence similarity using USEARCH (v9.0.2132, 64-bit) (-cluster_otus -minsize 4) and sequences were mapped back to OTUs to generate abundances (-usearch_global -strand plus -id 0.97 -maxaccepts 56 -top_hit_only -maxrejects 256). For bacterial and archaeal 16S rRNA sequences, OTUs were clustered at 97% similarity using USEARCH as above. We assigned taxonomy to each OTU using the RDP naïve Bayesian classifier (Wang, Garrity, Tiedje, & Cole, 2007) as employed by MOTHUR (v1.39.1) (Schloss et al., 2009) against the UNITE v6 species hypothesis database (Abarenkov et al., 2010) for fungi, and Greengenes (DeSantis et al., 2006) for bacteria and archaea using a probability cutoff of 60% (Cutler et al. 2017; Hartmann et al. 2012; Wang et al. 2007). Any bacterial, fungal and archaeal OTUs unassigned to phylum were discarded.

Soil fertility and biodiversity indices

We used multiple soil measures including organic carbon, macronutrients: ammonium, nitrate, phosphorus, potassium and micronutrients: exc. magnesium, exc. copper, exc. sodium, exc. aluminum, DTPA iron, DTPA manganese and DTPA zinc as a proxy for soil fertility (Delgado-Baquerizo et al., 2017). To do this, we used z-score transformations on each soil measure and calculated the mean of all soil measures (z transformed) to obtain a single soil fertility metric for the 0-10 cm depth of soil and the 20-30 cm depth of soil, as described by Delgado-Baquerizo et al., 2017 and Maestre et al., 2012. We used the same method on the Shannon's Diversity index of bacteria, archaea and fungi for each depth of soil to serve as a proxy for 'total microbial diversity' (also as described by Delgado-Baquerizo et al., 2017). This consolidated approach allowed us to quantify relationships between soil fertility, microbial biodiversity and disturbance.

Statistical Analyses

We rarefied the abundance of each OTU to the lowest number of reads for each microbial community for each respective soil depth (Bacteria: 0-10 cm = 21,545, 20-30 cm = 37,255; Archaea: 0-10 cm = 12, 270, 20-30 cm = 31, 068; Fungi: 0-10 cm = 19,940, 20-30 cm = 24,382) using the '*rarefy_even_depth*' function in the '*phyloseq*' package (McMurdie & Holmes, 2013) to account for the uneven library sizes between samples (McKnight et al., 2019; Weiss et al., 2015). We completed all downstream analyses using rarefied abundances (Appendix Figure 2).

We calculated the Shannon's Diversity index for each microbial community at each depth in the soil profile using the 'DIVERSE' function in Primer v7, and used generalized linear models (GLM) to quantify the influence of component disturbances ('0 fires (since 1850s)', '1 fire', '2 fires', '3 fires', 'clearcut logging', 'salvage logging') on the diversity of each microbial community and 'total microbial diversity' for each soil depth. To account for the potential influence of environmental factors (which may influence the diversity of these communities), we included the 'time since last disturbance', 'elevation', 'slope' and 'soil fertility' at each of the 80 sites as a covariate in all models (Appendix Table 2). Further, eight of our logged sites, had experienced historical thinning or other silviculture treatments 30-40 years prior to clearcut and salvage logging events in 1980-1985 or 2008-2010. We accounted for their potential effects by including them as additional factors in our models. We used the 'dredge' function in the 'MuMin' package in R (Bartoń, 2013) (parameters: disturbance variables= fixed factors; rank= AIC) to select the combination of factors with the lowest Akaike Information Criterion (AIC) for each respective model. We also used Analysis of Variance (ANOVA) analyses to quantify differences between disturbance history types on total microbial diversity and soil fertility across both soil depths.

To explore the influence of component disturbances ('Number of fires', 'Clearcut logging', 'Salvage logging'), time since disturbance, and soil fertility on the community composition of microbial communities — for each soil depth (0-10 cm and 20-30 cm), we used permutational multivariate analysis of variance (PERMANOVA) based on a bray-curtis dissimilarity matrix of square-root transformed data using the 'adonis' and 'vegdist' functions in the 'vegan' package in R (Oksanen, Kindt, Legendre, O'Hara, & Stevens, 2013).

We used canonical correspondence analysis (CCA) to quantify the influence of individual environmental variables and edaphic properties (organic carbon, macronutrients: ammonium, nitrate, phosphorus, potassium and micronutrients: exc. magnesium, exc. copper, exc. sodium, exc. aluminum, DTPA iron, DTPA manganese and DTPA zinc, and soil pH (CaCl₂), elevation and slope) on the composition of microbial communities, and visualize differences between disturbances, using the 'cca' function in the 'vegan' package in R. We standardized environmental variables using z score transformations, and square-root transformed rarefied microbial community abundance matrices to account for disproportionately high/low abundances, following the completion of sensitivity analyses (Borcard, Gillet, Legendre, 2011; Legendre & Gallagher, 2001). For each CCA, we removed colinear variables as indicated by variance inflation (VIF) scores (>10), and selected environmental variables

using step-based forward selection against 999 permutations using the ‘*ordistep*’ function in the ‘*vegan*’ package in R.

We also used the ‘*vegetarian*’ R package, and ‘*H*’ function to quantify partitioned standard diversity indices (alpha, beta, gamma) for each microbial community and respective soil depth (Charney & Record, 2009; Jost, 2007).

We generated variograms using model residuals (bins= min. and max. distance between sites) for each response variable to test for spatial auto-correlation using the ‘*geoR*’ (Ribeiro, Jr. & Diggle, 2001) package in R. We found no evidence of spatial auto-correlation in any of our response variables (Appendix figure 3). All statistical analyses were conducted using R v. 3.6.3.

Results

The Mountain Ash forest soil microbiome

We identified 26,256 microbial 97% operational taxonomic units (OTUs) from 11,718,800 DNA sequences from rarefied samples across 80 sites and two soil depths (0-10 cm and 20-30 cm) in the Mountain Ash forests. Specifically, we found 7886 fungal, 649 archaeal and 17,721 bacterial OTUs across both soil depths. Microbes in the 0-10 cm depth of soil had the highest OTU richness (23,301 OTUs), relative to those in the 20-30 cm depth of soil (19,025 OTUs). Bacteria had the highest OTU richness and diversity across both soil depths relative to communities of fungi and archaea. In contrast, archaea had the lowest OTU richness and diversity relative to communities of fungi and bacteria (Figure 1). The diversity of fungi and bacteria was highest in the 0-10 cm depth of soil, but archaea were more diverse in the 20-30 cm depth of soil (Figure 1). Further, beta diversity was highest in fungal communities, and alpha diversity highest in bacterial communities (Appendix Table 1; Appendix Figure 4).

We generated rarefaction curves using the observed species richness for each microbial community and respective soil depth. These curves indicated that, at the 97% OTU level, we did not capture the full diversity of fungal, microbial and archaeal OTUs across the disturbance history and sample types. This suggests that an increase in future survey effort at the 97% OTU level (number of sequences derived from each site) would result in a higher count of microbial OTUs (Appendix 1: Figure 2).

Archaea

We found 528 archaeal OTUs from 981,600 16S rRNA sequences from the 0-10 cm depth of soil, and 609 archaea OTUs from 2,485,440 16S rRNA sequences from the 20-30 cm depth

of soil. Almost all archaeal OTUs were assigned to the dominant phylum: Crenarchaeota (>0.99% OTU sequences), with the majority of remaining OTUs assigned to the phylum Euryarchaeota (Figure 2). Dominant archaeal families included: Nitrososphaeraceae (48% OTU sequences) and SAGMA-X (22% OTU sequences) in the 0-10 cm depth of soil, and Halobacteriaceae (33% OTU sequences) and SAGMA-X (19% OTU sequences) in the 20-30 cm depth of soil.

Bacteria

We found 16,162 bacterial OTUs from 1,723,600 16S rRNA sequences in the 0-10 cm depth of soil, and 13,737 bacterial OTUs from 2,980,400 16S rRNA sequences from the 20-30 cm depth of soil. OTUs were assigned to 36 different phyla and 200 different families across both depths of soil. The bacterial phyla Proteobacteria (38% and 26% OTU sequences in the 0-10 cm and 20-30 cm depths of soil respectively) and Acidobacteria (30% and 10% OTU sequences in the 0-10 cm and 20-30 cm depths of soil respectively) were the most dominant across samples (Figure 2).

Fungi

We found 6611 fungal OTUs from 1,595,200 ITS1 sequences in the 0-10 cm depth of soil, and 4679 fungal OTUs from 1,950,560 ITS1 sequences from the 20-30 cm depth of soil. The fungal phyla: Ascomycota (43% and 23% ITS1 sequences from the 0-10 cm and 20-30 cm depth of soil respectively) and Basidiomycota (50% and 68% ITS1 sequences from the 0-10 cm and 20-30 cm depth of soil respectively) were the most abundant and species rich across both soil depths (Figure 2).

Disturbance impacts on microbial communities

Diversity

The number of fires and clearcut and salvage logging had significant impacts on below-ground microbial diversity, with effects more pronounced in the topsoil (0-10 cm) and with the number of fires, controlling for time since fire and environmental variables (Figure 3, Table 1, Appendix Table 2). One, two and three fires (post-1850s) reduced the diversity of bacteria, archaea and total microbial diversity in the 0-10 cm depth of soil ($p=0.00-0.05$), relative to unburnt and unlogged sites (Figure 3, Table 1, Appendix Table 2). Clearcut logging also reduced the diversity of bacteria in the 0-10 cm depth of soil ($p=0.01$). In contrast, salvage (post-fire) logging increased the diversity of bacteria in the 20-30 cm depth

of soil, however, reduced the diversity of archaea across both soil depths (Figure 3, Table 1, Appendix Table 2).

Total microbial diversity did not exhibit any clear trends with respect to disturbance history type at either soil depth ($p > 0.05$) (Appendix Table 2). In contrast, soil fertility declined significantly with increasing number of disturbances across both soil depths ($p < 0.05$) (Figure 4). Microbial diversity increased slightly with increasing soil fertility in the 20-30 cm depth of soil, however, this effect was not significant ($p > 0.05$) (Figure 5). This indicates that other direct and indirect disturbance impacts not associated with soil fertility may be driving changes in total microbial diversity.

Community composition

PERMANOVA analyses indicated that the composition of all microbial communities at both soil depths differed with different disturbance types (Appendix Table 3). Specifically, the number of fires ($p = 0.001$), salvage logging ($p = 0.001$), clearcut logging ($p = 0.001-0.03$) and time since disturbance ($p = 0.001-0.004$) significantly influenced the composition of fungal, bacterial and archaeal communities across both soil depths. Soil fertility also influenced the composition of bacteria and archaea across both soil depths, and fungi in the 0-10 cm depth of soil ($0.007-0.04$) (Appendix Table 3).

Indicators of microbial community composition

Canonical correspondence analyses (CCA) identified edaphic and environmental variables which partially explained differences in the composition of microbial communities across both soil depths (Figure 6). Clustering patterns of sites in CCA plots also suggested differences in the composition of microbial communities with different disturbance origins (fire, and clearcut and salvage logging) within the ordination space. These differences were driven by different environmental and edaphic variables. For instance, the composition of fungal and bacterial communities in the 0-10 cm of soil that experienced fire-only were driven predominantly by changes to edaphic properties, whereas the composition of fungal communities that were logged were partially explained by elevation, but largely were unexplained (Appendix Table 4).

Bacteria

Differences in the composition of bacterial communities in the 0-10 cm depth of soil were partially (26% of total variation) explained by measures of exc. aluminum (Al), exc. magnesium (Mg), exc. sodium (Na), nitrate (NO_3^-), potassium (K), organic carbon (C), phosphorus (P), elevation, DTPA iron (Fe), DTPA manganese (Mn) and DTPA zinc (Zn) ($X^2=0.32$, $F=1.5$, $p=0.001$); and differences in the 20-30 cm depth of soil were partially (25% of total variation) explained by measures of DTPA iron (Fe), DTPA manganese (Mn), DTPA zinc (Zn), exc. magnesium (Mg), nitrate (NO_3^-), phosphorus (P), ammonium (NH_4^+), pH (CaCl_2) and elevation ($X^2=0.64$, $F=2.62$, $p=0.001$).

Fungi

Differences in the composition of fungal communities in the 0-10 cm depth of soil were partially (12% of total variation) explained by measures of exc. aluminum (Al), phosphorus (P), potassium (K), DTPA iron (Fe), DTPA manganese (Mn) and elevation ($X^2=1.50$, $F=1.58$, $p=0.001$); and differences in the 20-30 cm depth of soil were partially (11% of total variation) explained by measures of pH (CaCl_2), nitrate (NO_3^-), carbon (C), elevation, DTPA iron (Fe) and DTPA manganese (Mn) ($X^2=1.5$, $F=1.55$, $p=0.001$).

Archaea

Differences in the composition of archaeal communities at 0-10 cm depth were partially (22% of total variation) explained by measures of DTPA iron (Fe), DTPA manganese (Mn), exc. magnesium (Mg), exc. aluminum (Al), elevation, nitrate (NO_3^-) and organic carbon (C) ($X^2=0.46$, $F=2.91$, $p=0.001$). Differences in the 20-30 cm depth of soil were partially (32% of total variation) explained by measures of DTPA iron (Fe), DTPA manganese (Mn), DTPA zinc (Zn), elevation, pH (CaCl_2), exc. magnesium (Mg), nitrate (NO_3^-), ammonium (NH_4^+) and phosphorus (P) ($X^2=0.36$, $F=3.60$, $p=0.001$).

Discussion

Using an extensive dataset of over 11 million DNA sequences, and 26,256 microbial OTUs, we have shown that the number of wildfires and clearcut and salvage logging has major impacts on the soil microbiome. Specifically, we found that these disturbances altered the composition and reduced the diversity of microbial communities. Our findings also suggest that wildfire and logging alter the composition of microbial communities, which were partially explained by environmental and edaphic properties. Wildfires had the most consistent negative impacts on the diversity of individual microbial communities relative to other disturbance types. Diversity declines and changes in the composition of microbial communities can have functional implications in forest ecosystems (Delgado-Baquerizo et al., 2016, 2015), and influence soil fertility and processes (Hartmann et al., 2014; Trivedi et al., 2019), symbiotic relationships (Hartmann et al., 2014; Holden et al., 2015), and specialized ecological functions (Philippot et al., 2013; Singh et al., 2014). To the best of our knowledge, our study is one of the first to compare the responses of multiple microbial communities to different disturbances across a multi-decadal chronosequence in a temperate forest. Our findings provide a timely insight into the disturbance responses of microbial communities, which may have widespread implications in forests.

Disturbance impacts on the soil microbiome

Disturbances are key drivers of ecological change in forests and can have multi-decadal effects that influence above and below-ground trophic levels, and their respective interactions. For instance, wildfires can alter the composition and structure of plant communities (Blair et al., 2016; Bowman et al., 2014; Donato, Fontaine, Robinson, Kauffman, & Law, 2009), and edaphic properties (Bowd, Banks, Strong, & Lindenmayer, 2019; Certini, 2005; Hume, Chen, & Taylor, 2018; Jennings et al., 2011). Disturbance impacts on microbial communities, while less-understood, can be short or long-term (Fichtner et al. 2014; Holden and Treseder 2013), and direct or indirect through environmental changes and multi-trophic interactions (Barnes et al., 2017; van der Putten et al., 2013). While we did not explicitly quantify temporal differences in microbial communities with disturbances, our results suggest that wildfire and clearcut and salvage logging can alter the composition and diversity of microbial communities for at least eight years.

Microbial communities that occupy different soil depths can respond differently to disturbances, with those in the topsoil typically more vulnerable to direct disturbance impacts (Liu et al. 2012). For instance, wildfire and post-logging slash burning can heat soil temperatures to over 500 °C, which can combust soil organic matter, volatilize nutrient pools, and kill soil microbes, with impacts more severe in the topsoil (Certini 2005; Hume, Chen, and Taylor 2018; Liu et al. 2012; Neary et al. 1999; Walker et al. 2019). This may explain why we found pronounced disturbance impacts on the diversity of microbial communities in the 0-10 cm depth of soil, relative to the 20-30 cm depth of soil. However, we also observed declines in the diversity of archaea in deeper soil depths, which likely reflect compositional changes to soils, such as erosion and nutrient leaching (Certini, 2005; Malvar et al., 2017; Wilson, 1999).

Edaphic properties including soil pH (Lauber, Hamady, Knight, & Fierer, 2009), organic carbon and nutrient composition (Delgado-Baquerizo et al., 2017; Tedersoo et al., 2014) are key drivers of microbial communities. Disturbances including wildfire and clearcut and salvage logging can alter these edaphic properties, and lead to declines in organic carbon and soil nutrients (Bowd et al. 2019; Hume, Chen, and Taylor 2018; Kishchuk et al. 2015). Here, we provide evidence of disturbance-induced declines in soil fertility, which influenced the composition of some microbial communities. Further, we highlight individual edaphic properties that were key drivers of the post-disturbance composition of microbial communities, including soil pH, organic carbon, macronutrients: nitrate, ammonium and, available phosphorus and potassium, and micronutrients: exc. magnesium, exc. sodium, DTPA manganese and DTPA iron. Similar drivers of microbial communities have been observed in other global forest ecosystems (Bahram et al., 2018; Holden & Treseder, 2013; Lladó, López-Mondéjar, & Baldrian, 2018; Tedersoo et al., 2014). Identifying the influence of various edaphic properties on microbial communities enhances the ability to predict and manage their responses to environmental changes and disturbances. However, future research efforts are required to quantify how these interactions influence respective ecological functions.

Environmental and edaphic indicators of the composition of microbial communities post-disturbance differed between disturbance types (fire-only, clearcut logging, and post-fire salvage logging) and individual microbial communities. For instance, individual soil properties explained more of the variation in the community composition of bacteria and archaea (24-32 %), than fungi (11-12%). Edaphic properties were key indicators of bacterial

and fungal communities post-fire, whereas differences in the composition of these organisms post-clearcut and post-salvage logging were largely unexplained by the variables we measured. This result is typical of similar microbial ecological studies where most of the total variance in the composition of microbial communities is unexplained by soil or site-based characteristics (Fierer, 2017). Unexplained compositional changes in microbial communities post-disturbance could be attributed to factors including soil heating (Neary et al., 1999), differences in plant communities (Urbanová, Šnajdr, & Baldrian, 2015) and structural soil changes, including post-logging soil compaction, erosion and nutrient leaching (Cambi, Certini, Neri, & Marchi, 2015; Certini, 2005; Hartmann et al., 2012; Wilson, 1999). Future investigations on the influence of these variables are warranted, given the large proportion of unexplained variance we observed across microbial communities.

Wildfires and clearcut and post-fire salvage logging significantly influenced the diversity and composition of microbial communities in our study. Consistent with the results of research in boreal forests (Wardle & Jonsson, 2014), we found the impacts of wildfires were more extensive on the diversity of bacteria than on fungi. However, salvage-logging reduced the diversity of archaea only, and clearcut logging reduced the diversity of bacteria only. Differences in the responses of individual microbial communities to disturbances may reflect differing levels of resistance and resilience, which can vary between individual microorganisms or functional sub-groups (Hartmann et al. 2014; Sun et al. 2017). For instance, compositional shifts in microbial communities can simultaneously reflect declines in the abundance of sensitive microorganisms, such as symbionts (Hartmann et al., 2014; Holden & Treseder, 2013), and increases in early successional species (Sun et al. 2015), or those that benefit from post-disturbance environmental changes including saprotrophic and pathotrophic microorganisms (Hartmann et al., 2014; Mushinski et al., 2018; Varenium et al., 2016). Differences in the disturbance responses of microbial communities also may indicate differences in the recolonization potential of individual microorganisms, and subsequently, dispersal mechanisms (Pressler, Moore, and Cotrufo 2018; Sun et al. 2017), availability of inoculum sources (Glassman et al., 2016) and physiological differences (Schmidt et al. 2014; Sun et al. 2017). Our findings highlight the importance of quantifying the disturbance responses of individual microbial communities, which can differ from one another (Schmidt 2014).

Microbial diversity simultaneously drives multiple ecological functions ('multifunctionality') (Delgado-Baquerizo et al., 2015), and regulates vital soil processes in ecosystems (Maron et al., 2018; Philippot et al., 2013; Trivedi et al., 2019). Declines in microbial diversity have previously been underestimated, but they can have widespread functional implications in ecosystems (Delgado-Baquerizo et al., 2016). Specifically, diversity declines could produce adverse impacts on decomposition rates, nutrient cycling and soil fertility (Hartmann et al., 2014; Trivedi et al., 2019, Maron et al., 2018), symbiotic relationships (Hartmann et al., 2014; Holden et al., 2015), and specialized ecological functions such as nitrogen fixation (Philippot et al., 2013; Singh et al., 2014). Losses in the diversity of species which have specialised functions, such as nitrogen fixation, may be disproportionately impacted by disturbances (Singh et al., 2014). However, functional complementarity also can exist in microbial communities, where more resilient species occupy post-disturbance environments and fulfil functional requirements (Jones et al., 2010). While we did not investigate the direct functional implications of disturbance impacts on microbial communities, the confounding linkages between microbial communities and multifunctionality (Delgado-Baquerizo et al., 2015) suggests our findings may have functional implications in forests. However, future research efforts are required to quantify the direct impacts of disturbances on the key functions microbial communities have in forest ecosystems including decomposition, symbiotic relationships and nitrogen fixation. Specifically, there is a need to move beyond community-based approaches and consider the responses of individual organisms that have these important functional roles (Bissett, Brown, Siciliano, & Thrall, 2013).

Conclusions

Global forest ecosystems face a myriad of compounding challenges, the effects of which may have widespread functional consequences above and below-ground (Barnes et al., 2017; Wardle et al., 2004). Globally, millions of hectares of forests are disturbed by wildfires and logging annually (Cohen et al., 2016; Hansen, Stehman, & Potapov, 2010). Collectively these disturbances have altered the structure and function of forests, with intact patches of undisturbed forest in rapid decline (Watson et al., 2018). In recent years, the relationship between microbial communities and climate change, and their capacity to act as either as a source or sink of CO₂ has received considerable attention (Cavicchioli et al., 2019; Eisenhauer, Cesarz, Koller, Worm, & Reich, 2012; Jansson & Hofmockel, 2019). However, the response of microbial communities to the consequences of changing climatic conditions, including altered disturbance regimes, remains limited. We have demonstrated that individual

components of altered disturbance regimes: the number of fires, clearcut logging, and post-fire salvage logging can influence the composition and reduce the diversity of the soil microbiome of Mountain Ash forests for at least eight years. Further, we have identified disturbance driven declines in soil fertility, and key environmental drivers of the community composition of microbial communities post-disturbance.

Management Implications

Millions of highly-diverse, yet highly-cryptic microorganisms are yet to be formally described across terrestrial ecosystems (Fierer, 2017; Hawksworth & Lücking, 2017). Further, the functional implications of changes in microbial communities are poorly understood at the ecosystem level (Bissett et al., 2013). As a result of these limitations, microbial communities are poorly represented in conservation efforts and strategies for ecosystem management (Griffith, 2012; Heilmann-Clausen et al., 2015). Indeed, traditional above-ground focused approaches to land management often use plant communities as a proxy for microbial communities, despite potential differences in post-disturbance trajectories (Fierer, 2017; Lamb et al., 2011; May & McMullan-Fisher, 2012). Given their diverse and integral functional roles, neglecting microbial communities in conservation, policies, and management could compromise the functional integrity of ecosystems in the event of major disturbances (Cavicchioli et al., 2019; Heilmann-Clausen et al., 2015).

Predicted increases in the frequency of wildfires across terrestrial ecosystems in the coming decades (Abatzoglou and Williams 2016; Bradstock et al. 2009; Jolly et al. 2015; Taylor, McCarthy, and Lindenmayer 2014) will likely amplify diversity declines and compositional shifts in microbial communities both directly, and indirectly through changes in edaphic properties (Bowd et al. 2019). Given the influence of edaphic properties, including available phosphorus, nitrate and organic carbon on microbial communities, we suggest that land-management monitor these variables, which may predict changes in diversity measures, especially in the event of future perturbations.

Compositional shifts and diversity declines in microbial communities can impact multifunctionality in ecosystems (Delgado-Baquerizo et al., 2016, 2015), and have adverse impacts on decomposition, nutrient cycling (Hartmann et al., 2014; Philippot et al., 2013; Singh et al., 2014; Trivedi et al., 2019) and symbiotic relationships (Hartmann et al., 2014; Holden et al., 2015). To best maintain the vital functions microbial communities have in forests, there is a critical need to incorporate microbial ecology into ecological models, and

subsequently into the development of policy and management decisions (Cavicchioli et al., 2019; Griffith, 2012; Treseder et al., 2012). Further, forests should be managed to maintain the full suite of microbial diversity (Maron et al., 2018), and limit further diversity declines by excluding perturbations where possible, especially in forests subject to recent disturbances to limit compounding impacts.

Acknowledgments

We thank the Mycological Society of America, The Paddy Pallin Foundation, The Ecological Society of Australia's: Holsworth Wildlife Fund and the Centre of Biodiversity Analysis, who funded this project. We also thank the volunteers who assisted in data collection for their support, and contributions to this study.

We acknowledge the contribution of the BASE project partners (DOI: 10.4227/71/561c9bc670099), an initiative supported by Bioplatforms Australia with funds provided by the Australian Commonwealth Government through the National Collaborative Research Infrastructure Strategy.

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Data Accessibility

rDNA sequence reads have been submitted to the NCBI SRA under bioproject PRJNA317932 and biosample accessions SAMN11293827- SAMN11294174. Data available from corresponding author on reasonable request.

Author contributions

E.J.B. conducted data collection and statistical analyses, and led the writing of the manuscript and experimental design of this study.

D.B.L. contributed to the experimental design of this study and manuscript editing.

S.C.B. contributed to the experimental design of this study and manuscript editing.

T.M. contributed to the experimental design of this study and manuscript editing.

A.B. contributed to the methodological design of this study, manuscript editing and conducted the bioinformatics analyses underpinning microbial data.

Tables and Figures

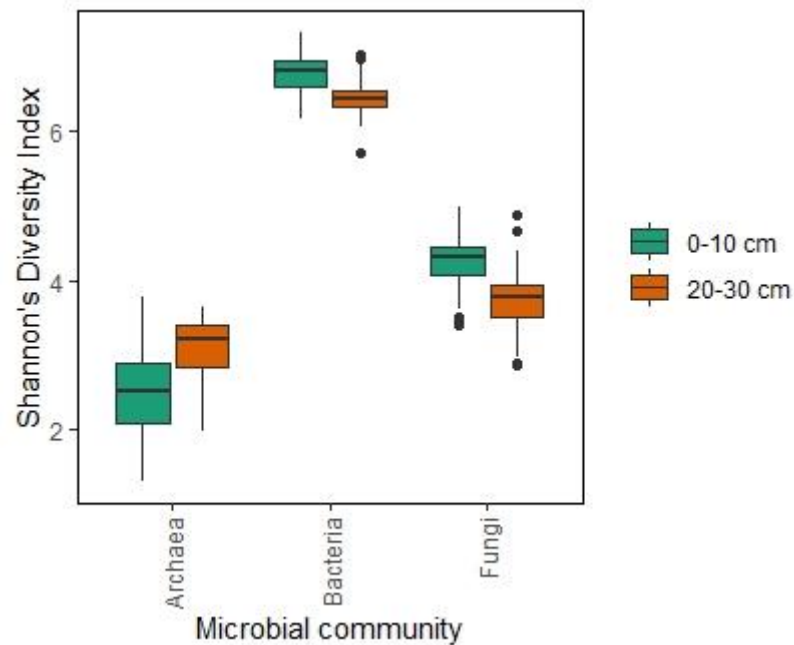


Figure 1. Box plot of the Shannon's diversity index and richness of microbial communities at different soil depths (0-10 cm and 20- 30 cm). Boxes represent the interquartile range (IQR) between the first and third quartiles (25th and 75th percentiles, respectively), and the horizontal line inside the box defines the median. Whiskers represent the lowest and highest values within 1.5 times the IQR from the first and third quartiles, respectively.

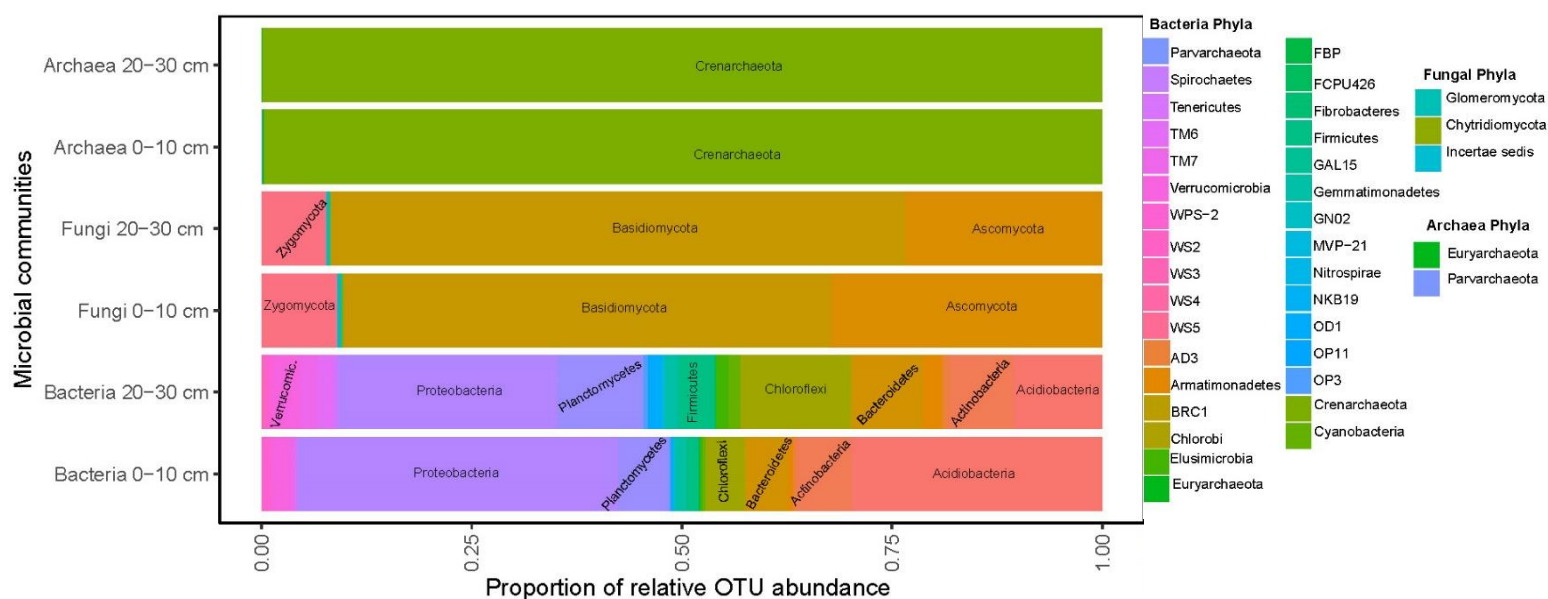


Figure 2. Cumulative abundance (proportion) of fungal, archaeal and bacterial phyla across 80 sites and two soil depths (0-10 cm and 20-30 cm). The legend describes phyla not labeled in the figure.

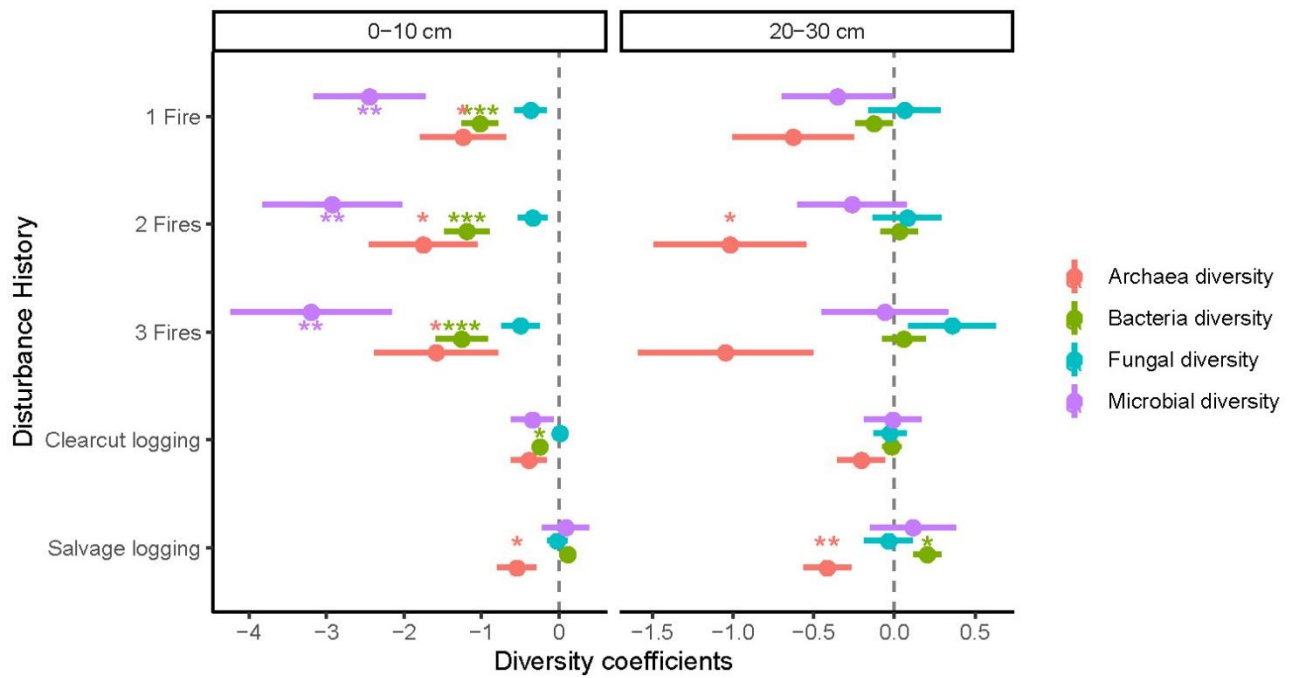


Figure 3. Coefficients from generalized linear models of the diversity of each microbial communities and total microbial diversity across both soil depths (0-10 cm and 20-30 cm) in response to disturbance. A complete list of the influence of the factors and covariates generated using these models is shown in Appendix Table 2.

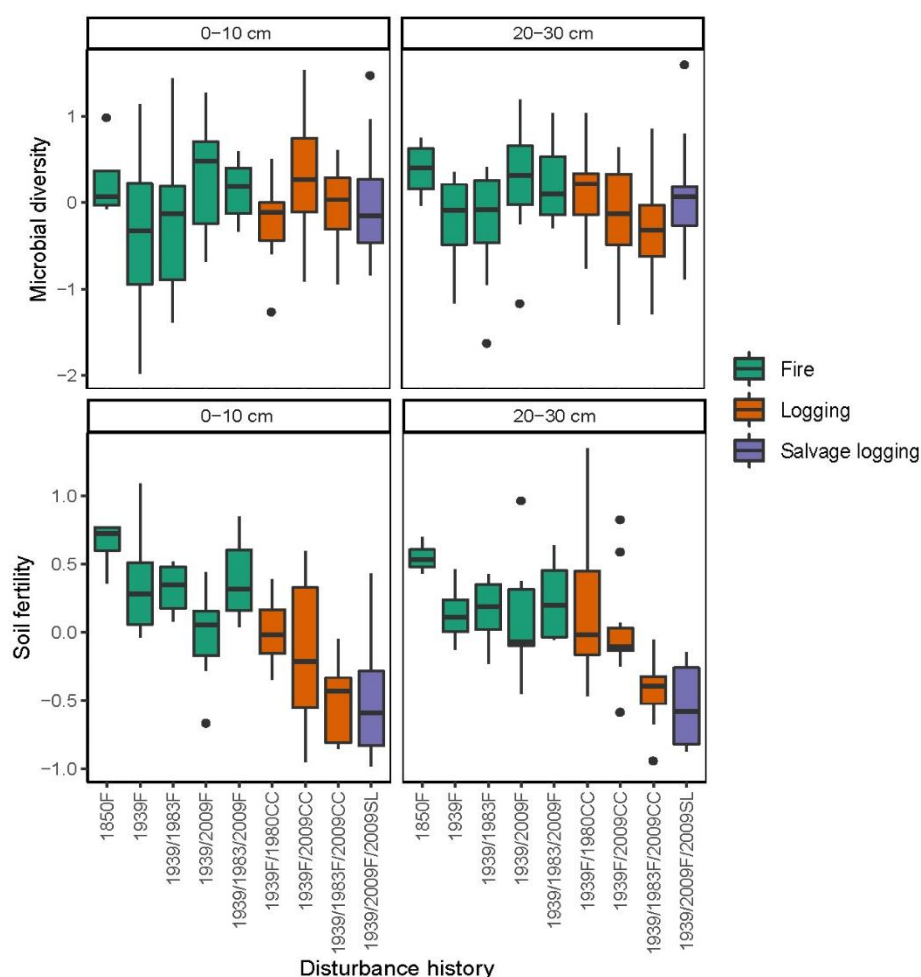


Figure 4. Box plot of the total microbial diversity and soil fertility and disturbance histories arranged from least disturbed (long-undisturbed forest ‘1850F’) to most disturbed (Salvage logged forest ‘1939F/2009F/2009SL’) across all sites and both soil depths (0-10 cm and 20-30 cm). Disturbance history labels are indicative of the disturbance origin ‘F’=fire, ‘CC’=clearcut logged, ‘SL’= salvage logged and the corresponding year of disturbance. Grey shading = confidence intervals. Boxes represent the interquartile range (IQR) between the first and third quartiles (25th and 75th percentiles, respectively), and the horizontal line inside the box defines the median. Whiskers represent the lowest and highest values within 1.5 times the IQR from the first and third quartiles, respectively.

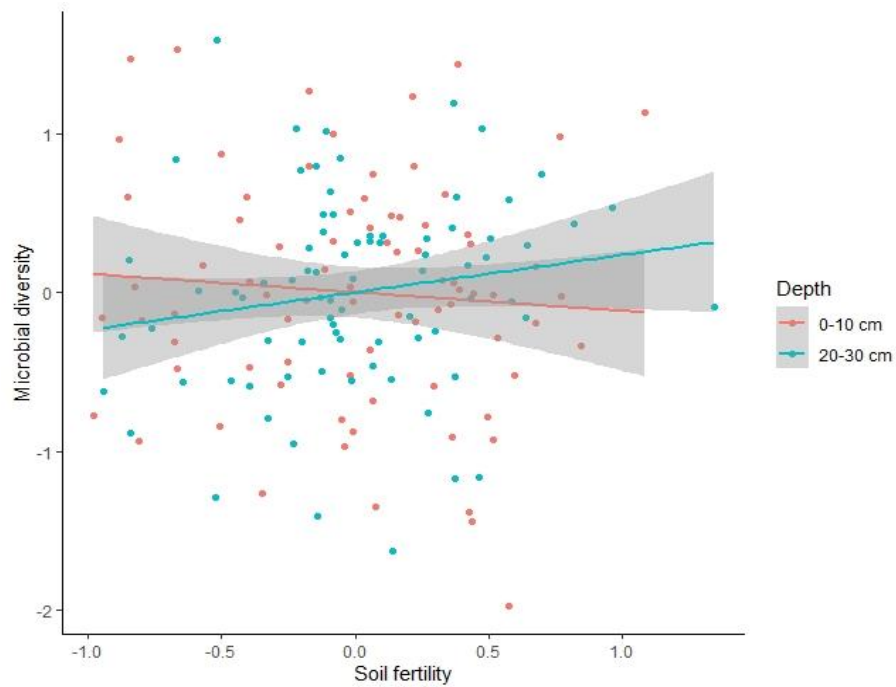


Figure 5. Scatter plot of microbial diversity and soil fertility across all sites and both soil depths (0-10 cm and 20-30 cm). Grey shading = confidence intervals.

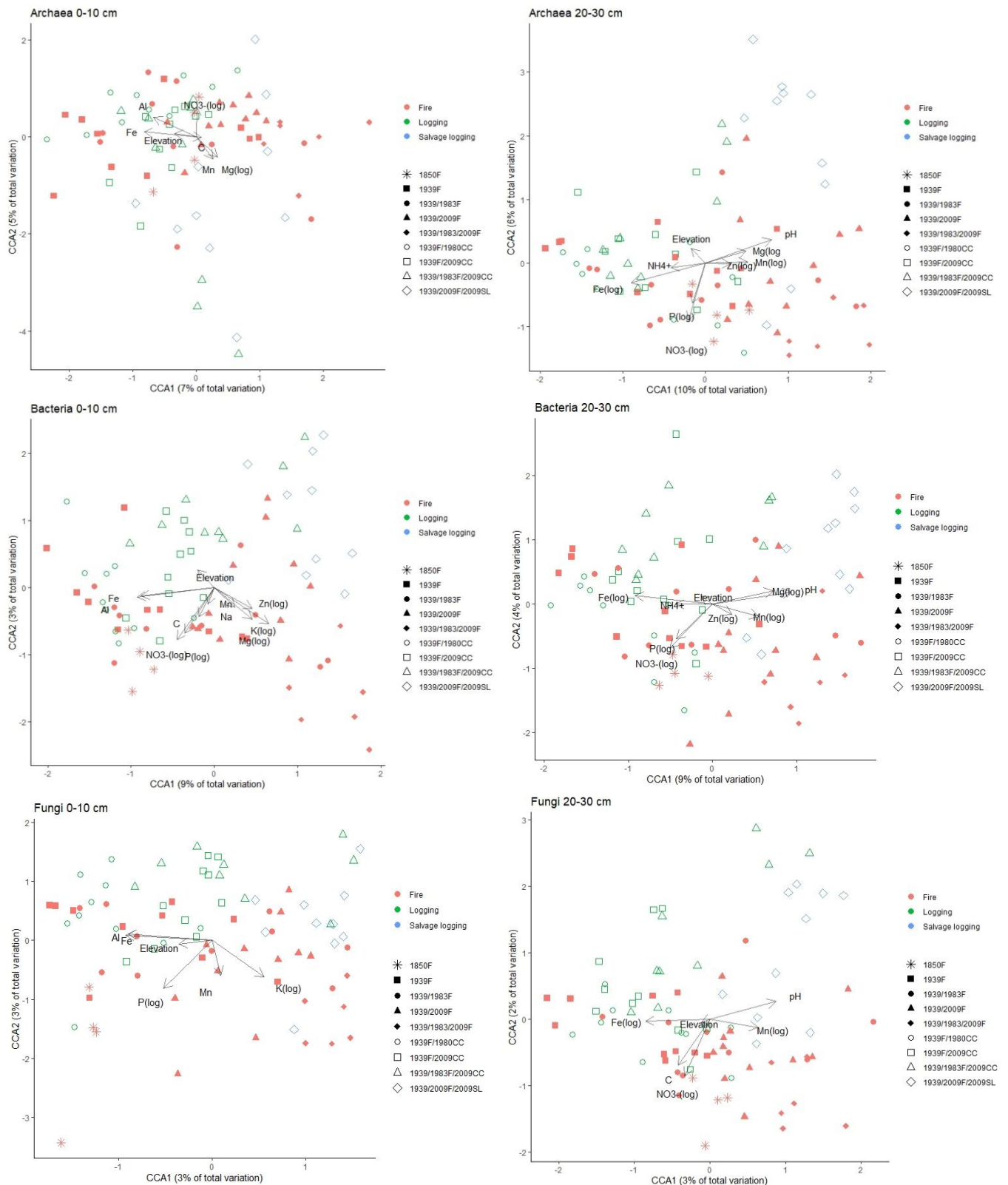
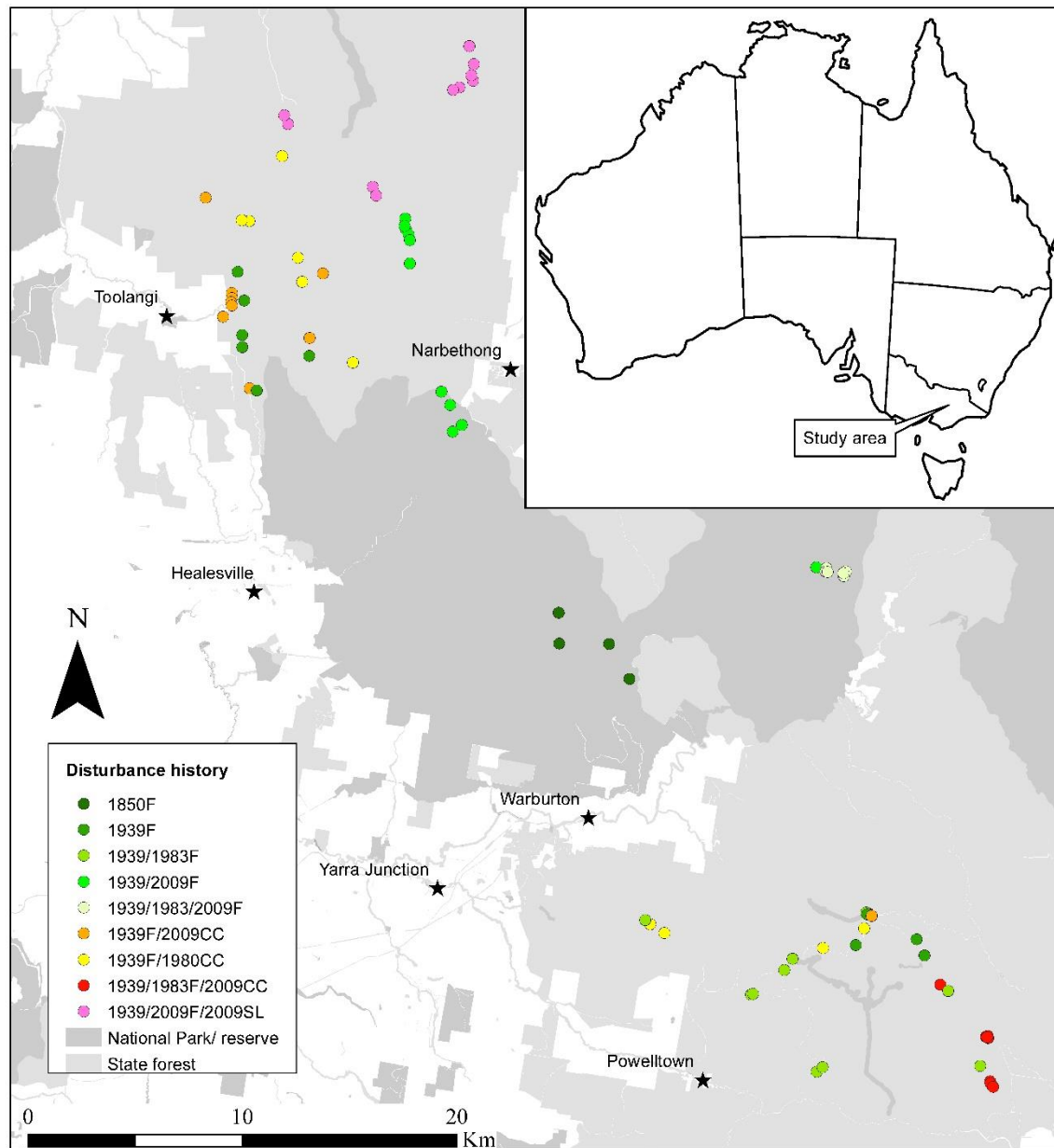


Figure 6. Canonical correspondence analysis (CCA) of each microbial community and soil depth, across nine disturbance history types and various environmental and edaphic properties. Linear combination (LC) site scores are plotted

Table 1. Coefficients from generalized linear models on the influence of component disturbances on the diversity of individual microbial communities, and total microbial diversity. Red bold text = significant negative result; green underlined text = significant positive result. The influence of other environmental variables included in each model are located in Appendix Table 2.

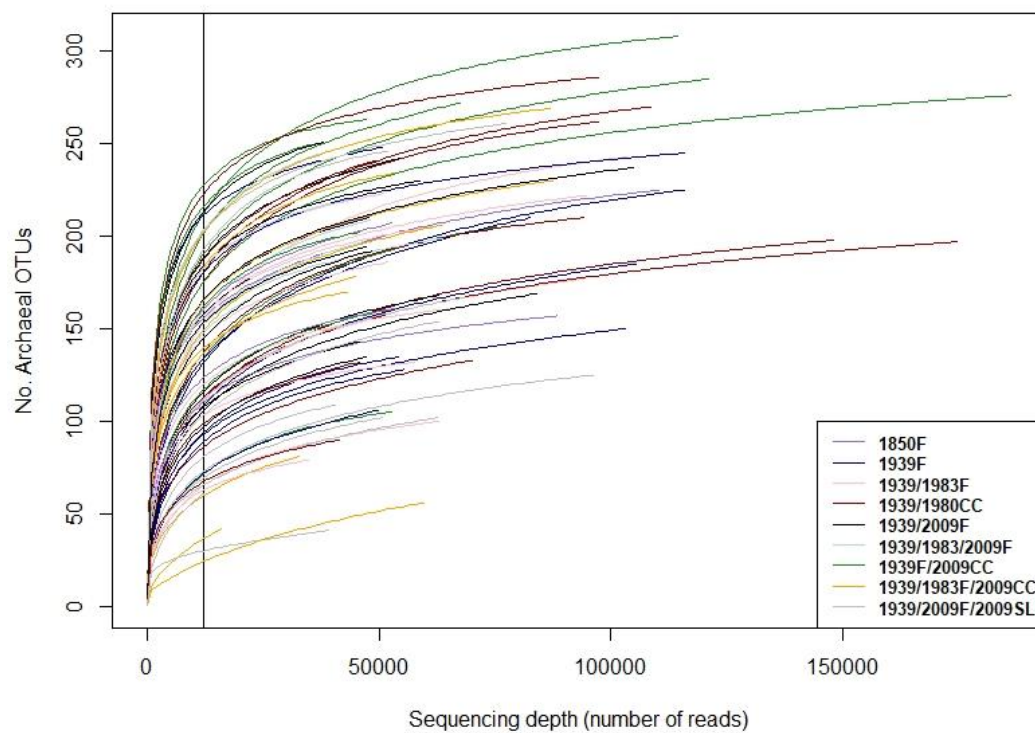
	Depth		(± Intercept)	1 Fire	2 Fires	3 Fires	Clearcut logging	Salvage logging
Bacteria diversity	0-10 cm	Estimate	8.43 (± 0.39)	-1.02 (± 0.23)	-1.19 (± 0.29)	-1.26 (± 0.33)	-0.25 (± 0.09)	0.11 (± 0.10)
		p	< 2e-16	0.00	0.00	0.00	0.01	0.29
	20-30 cm	Estimate	6.46 (± 0.11)	-0.13 (± 0.12)	0.03 (± 0.12)	0.06 (± 0.13)	-0.02 (± 0.06)	<u>0.20 (± 0.09)</u>
		p	<2e-16	0.28	0.78	0.67	0.79	<u>0.02</u>
Fungal diversity	0-10 cm	Estimate	5.04 (± 0.37)	-0.37 (± 0.20)	-0.34 (± 0.19)	-0.50 (± 0.25)	0.01 (± 0.09)	-0.03 (± 0.13)
		p	<2e-16	0.08	0.08	0.05	0.92	0.84
	20-30 cm	Estimate	2.92 (± 0.42)	0.06 (± 0.22)	0.08 (± 0.21)	0.36 (± 0.27)	-0.03 (± 0.10)	-0.04 (± 0.15)
		p	0.00	0.78	0.70	0.19	0.78	0.82
Archaea diversity	0-10 cm	Estimate	4.19 (± 0.80)	-1.24 (± 0.55)	-1.75 (± 0.70)	-1.59 (± 0.80)	-0.39 (± 0.23)	-0.55 (± 0.25)
		p	0.00	0.03	0.01	0.05	0.09	0.03
	20-30 cm	Estimate	4.16 (± 0.55)	-0.63 (± 0.38)	-1.02 (± 0.47)	-1.05 (± 0.54)	-0.21 (± 0.15)	-0.42 (± 0.15)
		p	0.00	0.10	0.03	0.06	0.16	0.01
Microbial diversity	0-10 cm	Estimate	4.03 (± 1.21)	-2.45 (± 0.72)	-2.93 (± 0.90)	-3.20 (± 1.04)	-0.35 (± 0.28)	0.08 (± 0.30)
		p	0.00	0.00	0.00	0.00	0.22	0.78
	20-30 cm	Estimate	0.23 (± 0.32)	-0.35 (± 0.34)	-0.26 (± 0.34)	-0.06 (± 0.39)	-0.01 (± 0.18)	0.11 (± 0.27)
		p	0.48	0.31	0.44	0.88	0.96	0.67

Appendices

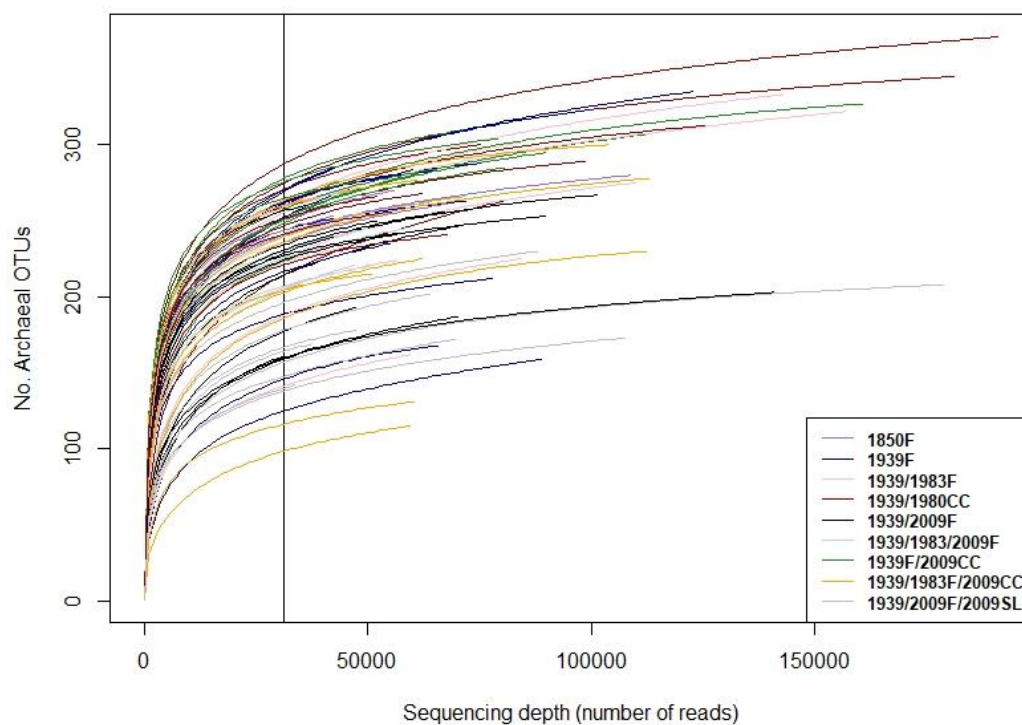


Appendix Figure 1. Map of sampled sites across the Mountain Ash forests of south-eastern Australia. Different coloured points are indicative of different disturbance histories: F= fire; CC=clearcut logging; SL=salvage logging.

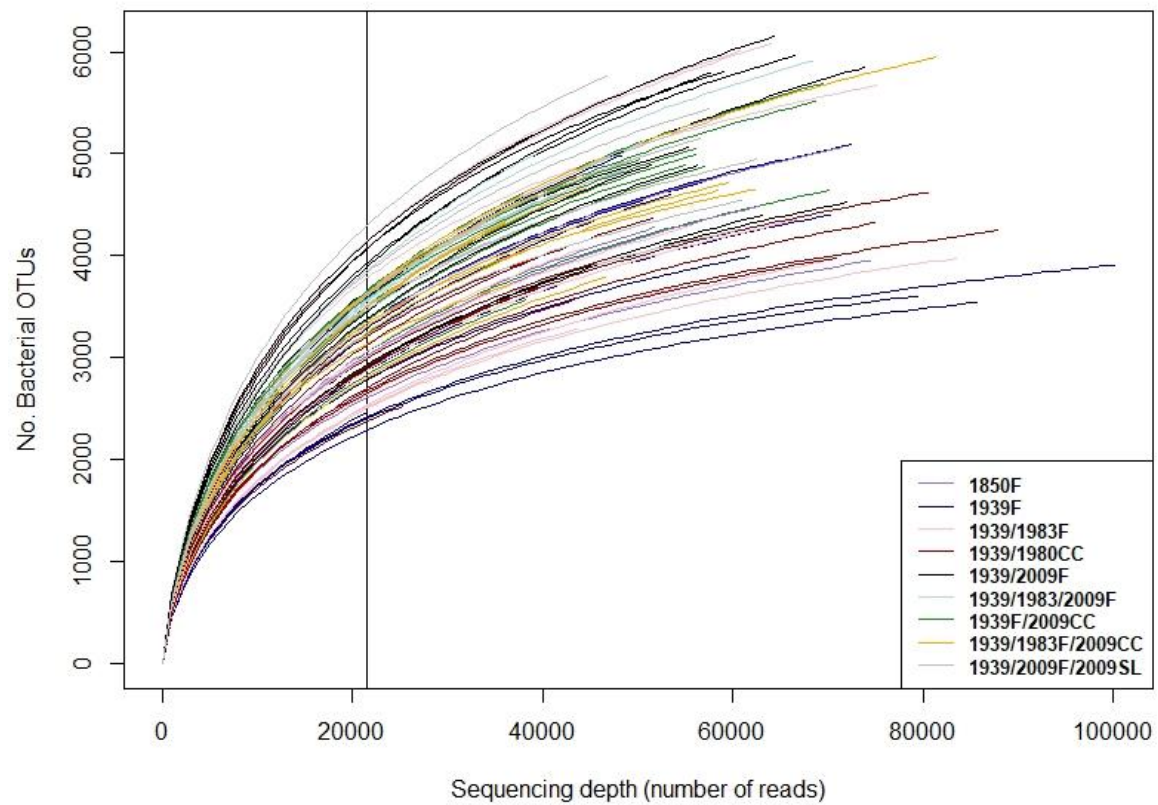
Archaea 0-10 cm samples



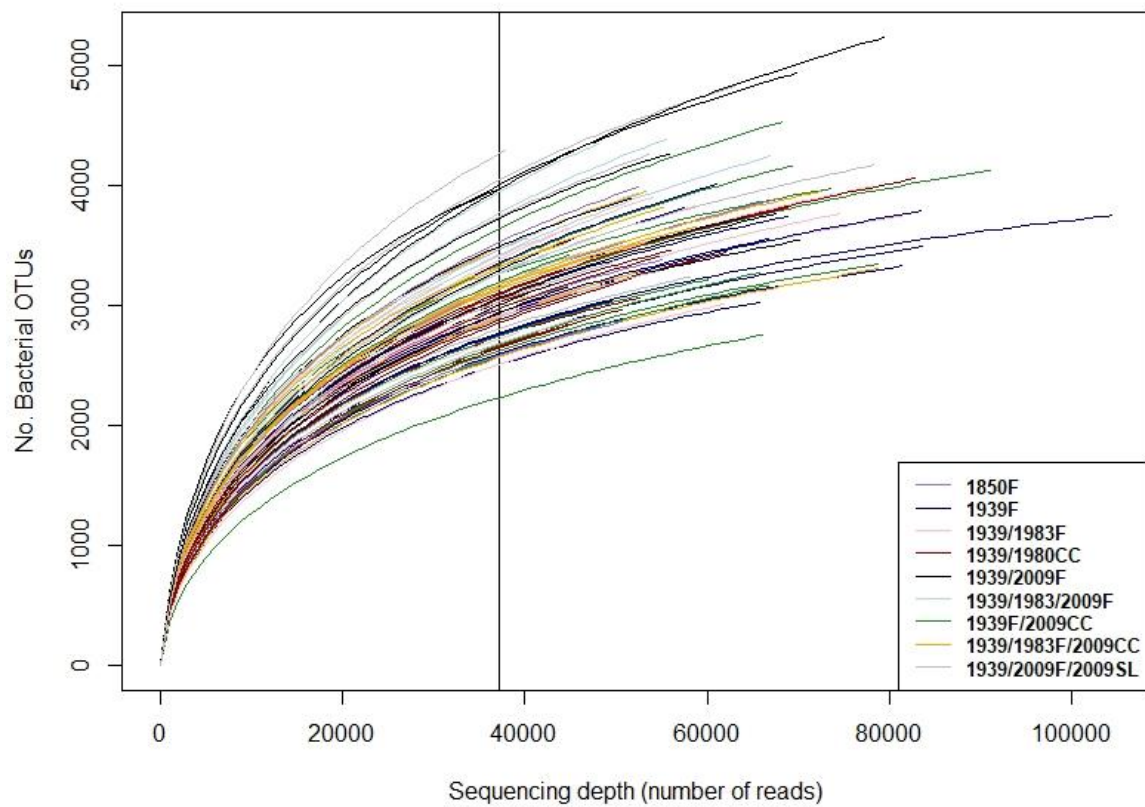
Archaea 20-30 cm samples

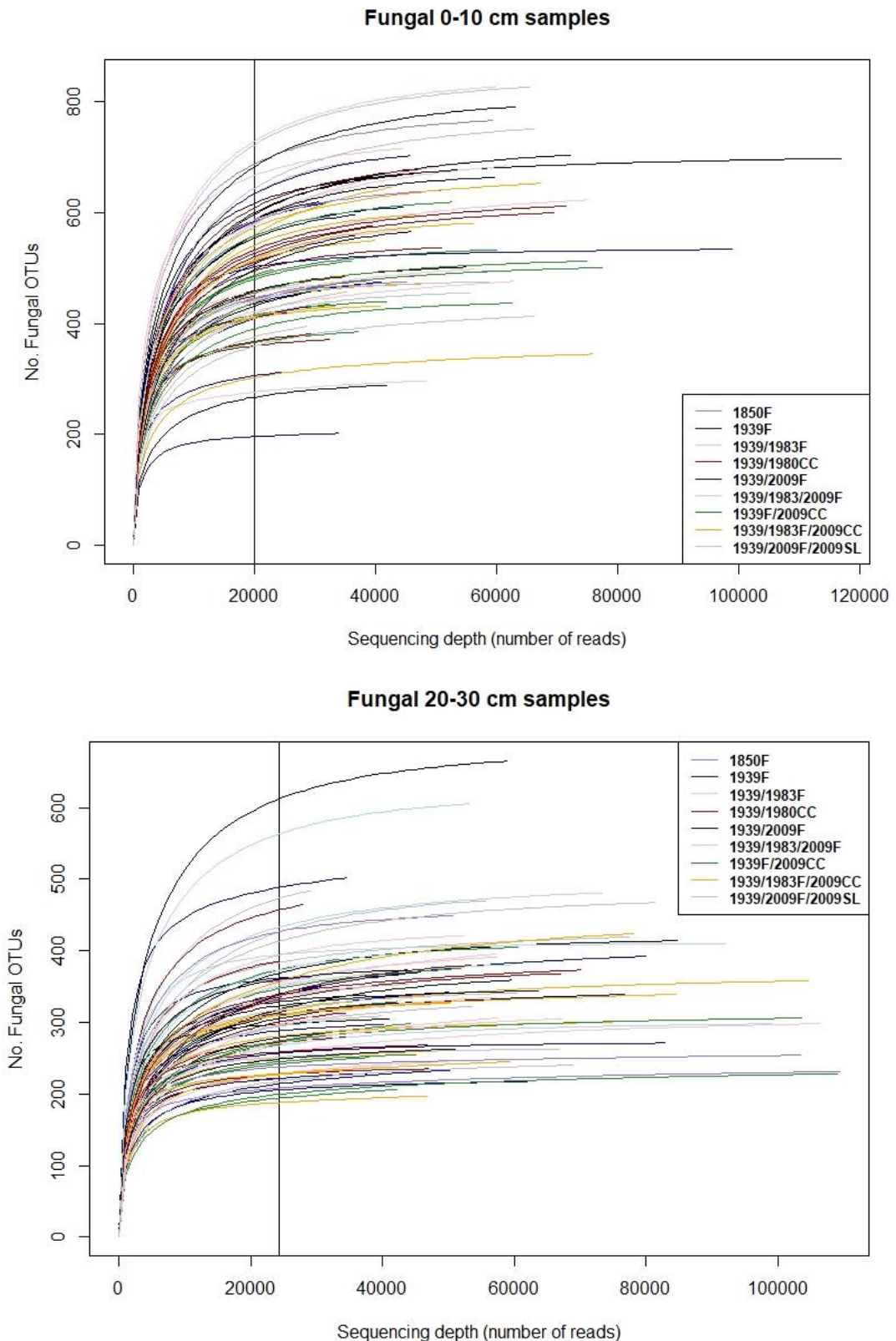


Bacterial 0-10 cm samples

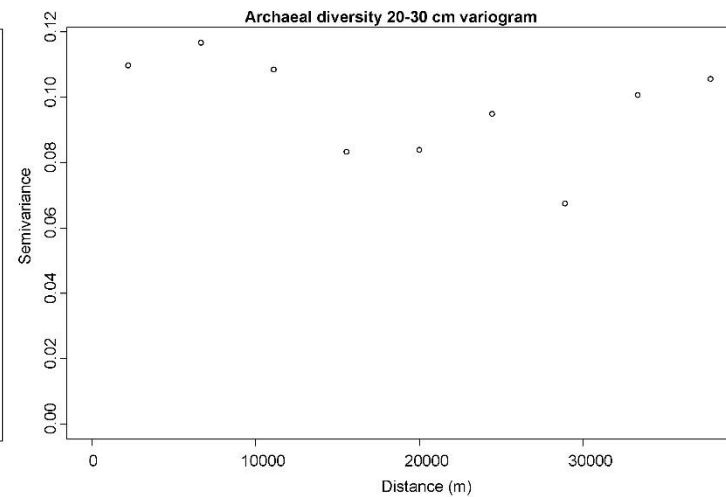
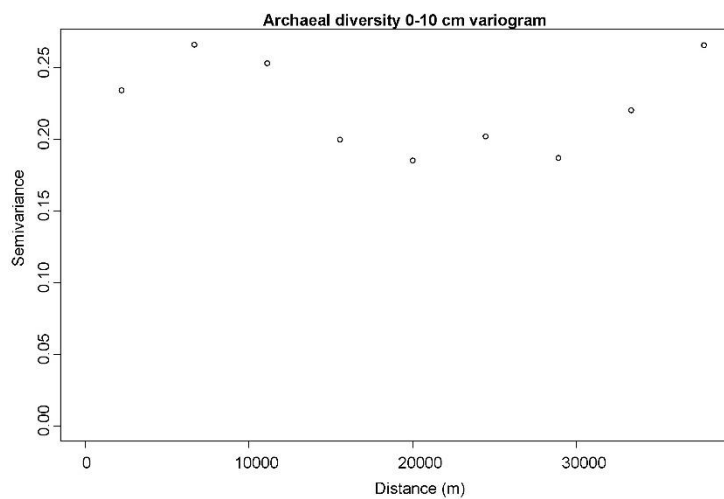
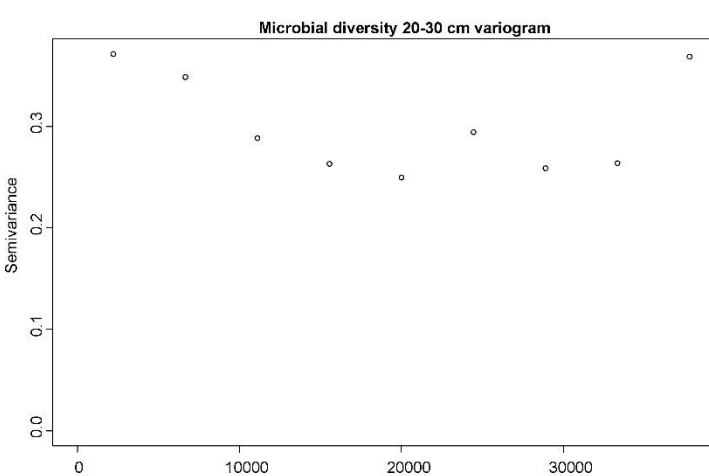
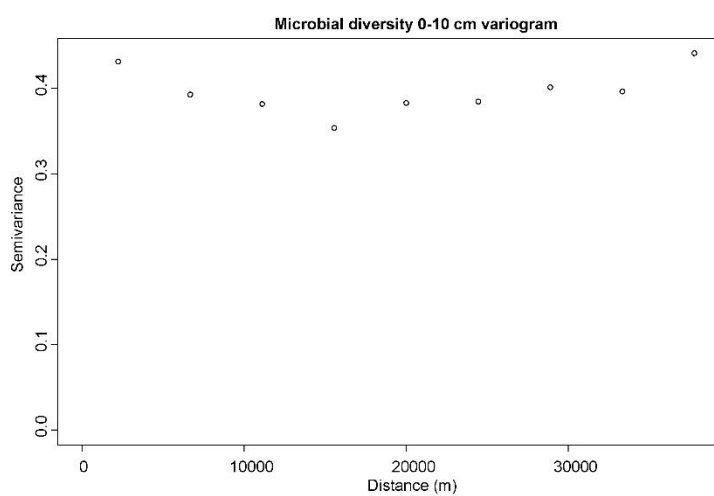
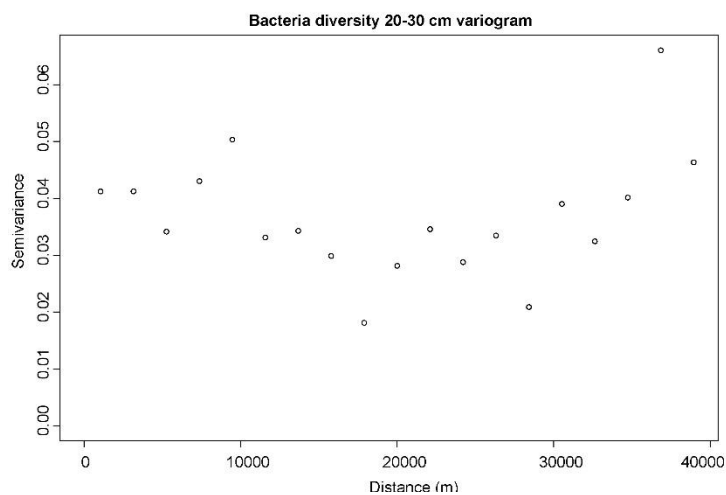
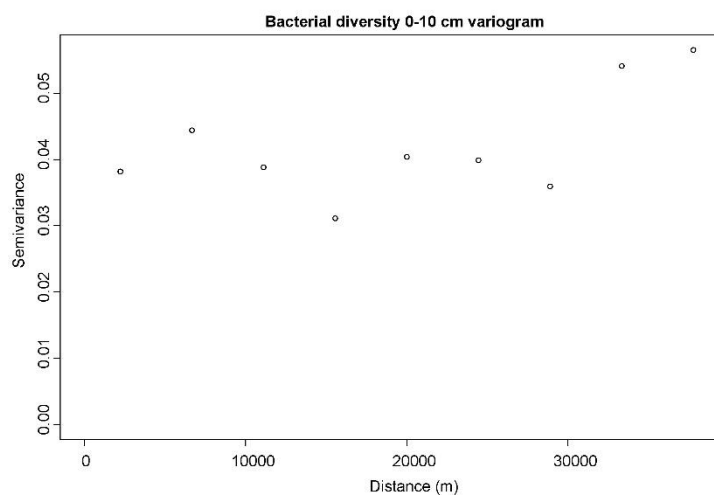


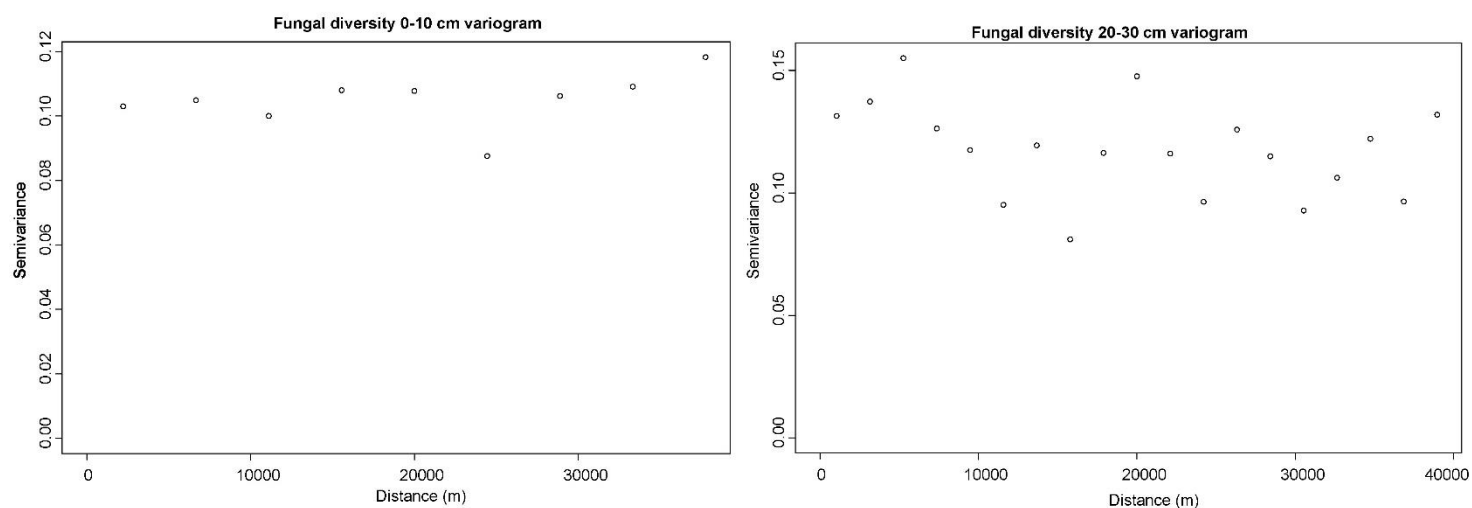
Bacterial 20-30 cm samples



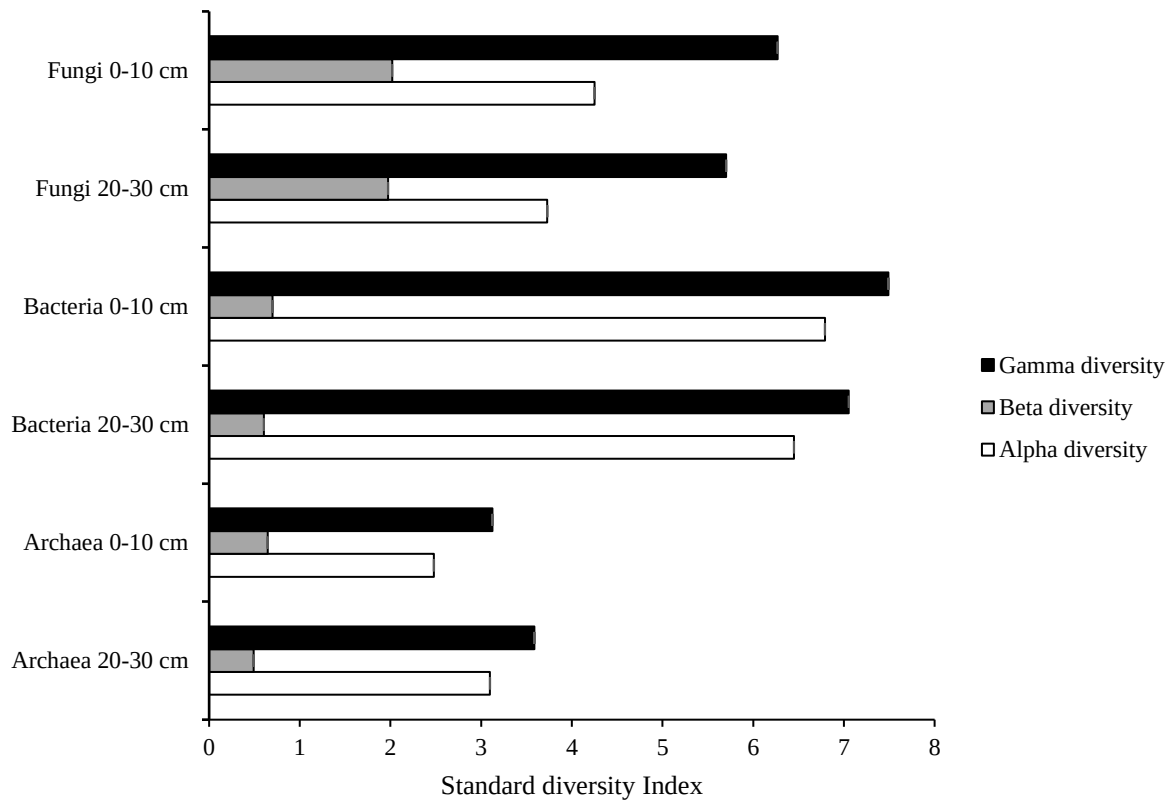


Appendix Figure 2. Rarefaction curves for each sample within each microbial community, with respect to sampled soil depth and disturbance history types. The vertical lines are indicative of the sequencing depth that was used in each rarefaction.





Appendix Figure 3. Variograms generated using residual values from each generalized linear regression model for all response variables (Diversity (Shannon’s diversity) of fungal, bacterial and archaeal OTUs and total microbial diversity across both soil depths (DNA 0-10 cm, DNA 20-30 cm).



Appendix Figure 4. Partitioned Standard Shannon's Diversity Indices for alpha, beta and gamma diversity across microbial communities.

Appendix Table 1. Partitioned Standard Shannon's Diversity Indices for alpha, beta and gamma diversity across microbial communities.

	Depth	Alpha diversity	Beta diversity	Gamma diversity
Archaea	<i>0-10 cm</i>	2.48 ± 0.00	0.65 ± 0.00	3.12 ± 0.00
	<i>20-30 cm</i>	3.10 ± 0.00	0.49 ± 0.00	3.59 ± 0.00
Fungi	<i>0-10 cm</i>	4.25 ± 0.00	2.02 ± 0.00	6.27 ± 0.00
	<i>20-30 cm</i>	3.73 ± 0.00	1.97 ± 0.00	5.70 ± 0.00
Bacteria	<i>0-10 cm</i>	6.79 ± 0.00	0.70 ± 0.00	7.49 ± 0.00
	<i>20-30 cm</i>	6.45 ± 0.00	0.60 ± 0.00	7.05 ± 0.00

Appendix Table 2. Coefficients describing the influence of environmental variables on microbial communities across two soil depths generated using generalized linear models (GLMS) (with respect to full model). Coefficients describing the influence of disturbance variables which were included in the full model are located in Table 1 in the main text. TSD = time since disturbance. Red bold text indicates significant negative association and green underlined text indicated significant positive associations.

	Depth	Elevation	Slope	TSD	Soil fertility	Historical thinning	Historical silviculture
Bacteria diversity	0-10 cm	<u>0.00 (± 0.00)</u>	<u>0.01 (± 0.00)</u>	-0.01 (± 0.00)	-0.13 (± 0.07)		
		<u>0.03</u>	<u>0.01</u>	0.00	0.08		
	20-30 cm				0.10 (± 0.07)		
					0.13		
Fungal diversity	0-10 cm	0.00 (± 0.00)					
		0.09					
	20-30 cm	<u>0.00 (± 0.00)</u>					0.38 (± 0.24)
		<u>0.02</u>					0.12
Archaea diversity	0-10 cm		0.02 (± 0.01)	-0.01 (± 0.00)	-0.29 (± 0.17)	0.38 (± 0.21)	
			0.09	0.06	0.10	0.08	
	20-30 cm			0.00 (± 0.00)		0.42 (± 0.14)	
				0.12		0.01	
Microbial diversity	0-10 cm	<u>0.00 (± 0.00)</u>	<u>0.03 (± 0.01)</u>	-0.02 (± 0.01)			
		<u>0.04</u>	<u>0.03</u>	0.01			
	20-30 cm				0.28 (± 0.20)		0.79 (± 0.38)
					0.17		0.04

Appendix Table 3. PERMANOVA analysis output, indicated the influence of disturbance, soil fertility and time since disturbance (TSD) on the composition of fungal, bacterial and archaeal communities in the 0-10 cm and 20-30 cm depths of soil.

			No. fires	Clearfell logging	Salvage logging	Soil fertility	TSD	Residual	Total
Fungi	0-10 cm	Df	3	1	1	1	1	72	79
		Sum Sq	2.4317	0.7317	0.8265	0.378	0.6354	19.137	24.1403
		F	3.0496	2.7529	3.1098	1.4222	2.3905	0.79274	
		R ²	0.10073	0.03031	0.03424	0.01566	0.02632		
		p	0.001	0.001	0.001	0.033	0.001		
	20-30 cm	Df	3	1	1	1	1	72	79
		Sum Sq	2.1368	0.7106	0.5717	0.4082	0.5458	18.79	23.163
		F	2.7293	2.723	2.1906	1.5641	2.0913		
		R ²	0.09225	0.03068	0.02468	0.01762	0.02356	0.81121	1
		p	0.001	0.001	0.001	0.009	0.001		
Bacteria	0-10 cm	Df	3	1	1	1	1	72	79
		Sum Sq	1.9897	0.2651	0.5751	0.2675	0.3376	7.9484	11.3834
		F	6.0078	2.4017	5.2099	2.4228	3.0583	0.69824	
		R ²	0.17479	0.02329	0.05052	0.0235	0.02966		
		p	0.001	0.005	0.001	0.007	0.001		
	20-30 cm	Df	3	1	1	1	1	72	79
		Sum Sq	1.4092	0.2554	0.4892	0.2361	0.3225	6.7821	9.4946
		F	4.9869	2.7114	5.1939	2.5068	3.4238		
		R ²	0.14843	0.0269	0.05153	0.02487	0.03397	0.71431	1
		p	0.001	0.005	0.001	0.007	0.004		
Archaea	0-10 cm	Df	3	1	1	1	1	72	79
		Sum Sq	1.2763	0.2358	0.595	0.2178	0.3609	7.6945	10.3804
		F	3.981	2.2069	5.568	2.0384	3.3772	0.74125	
		R ²	0.12295	0.02272	0.05732	0.02099	0.03477		
		p	0.001	0.029	0.001	0.037	0.004		
	20-30 cm	Df	3	1	1	1	1	72	79
		Sum Sq	0.8776	0.1749	0.4205	0.1574	0.4082	4.9613	6.9998
		F	4.2452	2.5387	6.1027	2.2841	5.9238		
		R ²	0.12537	0.02499	0.06008	0.02248	0.05831	0.70877	1
		p	0.001	0.014	0.001	0.025	0.001		

Appendix Table 4. Edaphic and environmental variables which explained some of the variation in microbial communities post-disturbance.

	Archaea		Fungi		Bacteria	
	<i>0-10 cm</i>	<i>20-30 cm</i>	<i>0-10 cm</i>	<i>20-30 cm</i>	<i>0-10 cm</i>	<i>20-30 cm</i>
Phosphorus		✓	✓		✓	✓
Potassium			✓		✓	
Nitrate	✓	✓		✓	✓	✓
Ammonium		✓				✓
Organic carbon	✓			✓	✓	
Exc. Sodium					✓	
Exc. Aluminium	✓		✓		✓	
Exc. Magnesium	✓	✓			✓	✓
DTPA Iron	✓	✓	✓	✓	✓	✓
DTPA Manganese	✓	✓	✓	✓	✓	✓
DTPA Zinc		✓			✓	✓
pH				✓		✓
Elevation	✓	✓	✓	✓	✓	✓
Variation explained	22%	32%	12%	11%	26%	25%
adjR²	0.14	0.23	0.04	0.04	0.19	0.16
p =	0.001	0.001	0.001	0.001	0.001	0.001

Chapter 5

Direct and indirect disturbance impacts in forests

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D.B.L. contributed to the experimental design of this study and manuscript editing.

S.C.B. contributed to the experimental design of this study and manuscript editing.

T.M. contributed to the experimental design of this study and manuscript editing.

A.B. contributed to manuscript editing and conducted the bioinformatics analyses underpinning microbial data.

Abstract

Climate change, coupled with increases in human and natural disturbances, is driving major changes to the structure and function of global forest ecosystems. Yet, the direct and indirect mechanisms which underpin these changes remain poorly understood at the ecosystem level. Here, using structural equation modelling across a 150+ year chronosequence, we disentangle the multifaceted direct and indirect effects of major natural and human disturbances on biotic (plant and microbial) and abiotic (soil) components in a temperate forest ecosystem. Specifically, we show that wildfires, logging and post-fire (salvage) logging can simultaneously impact plant and microbial communities, and abiotic soil properties both directly and indirectly through plant-soil-microbial interactions. We quantified 68 direct and indirect disturbance impacts across these abiotic and biotic components, with the majority resulting in ecosystem-wide adverse effects. Indirect disturbance effects accounted for 43% of total disturbance impacts, with some amplifying or partially mitigating direct disturbance impacts. Overall, human disturbances were associated with more negative effects than natural disturbances, suggesting logging results in adverse effects in forest ecosystems. This is likely because of the compounding nature of logging disturbances which involve mechanical clearing and post-logging slash burning. Our analyses provide novel insights into the complex and multifaceted dynamics of natural and human disturbances and the mechanisms which underpin their relative impacts.

Introduction

Forests are among the world's most productive, diverse and functionally-critical ecosystems. They constitute large, high-quality water-catchments ¹, store vast amounts of carbon crucial for climate change mitigation ², and support a substantial proportion of the earth's biodiversity ³. Natural wildfire regimes, characterised by distinct patterns of intensity, severity and frequency, are key ecological processes in forests, and influence biodiversity ^{4,5}. In recent decades, extensive human perturbation and an increase in natural disturbances, such as wildfires now characterise disturbance regimes in forests worldwide ^{4,6,7}. The compounding impacts of these novel and frequent disturbances may threaten forest ecosystems directly or indirectly through interactions and feedbacks.

Across all terrestrial ecosystems, above and below-ground biological communities and abiotic properties form interactions and feedbacks that underpin critical ecological functions, including plant productivity ^{8,9}, decomposition, nutrient cycling, and carbon storage ^{8,10–12}. For instance, microbial communities can influence the availability of soil nutrients by decomposing organic matter ^{11,13,14}, which can subsequently influence plant growth and survival ^{15,16}. Ecological research has traditionally focused on above-ground disturbance responses, with little consideration of the interactions between them ^{17,18}. However, perturbations that seemingly influence individual ecological components can have ecosystem-wide implications through their interactions, thereby relaying indirect disturbance effects ^{18–20}.

Extensive research on the pervasive impacts of clearcut logging and post-fire salvage logging on individual ecological components have been demonstrated across forest ecosystems globally ²¹. For instance, these compounding disturbances (mechanical clearing and post-logging burning) can alter plant ^{22,23}, mammal ²⁴, microbial ²⁵ and bird communities²⁶, alter soil properties ^{27,28}, and remove key structural elements of habitat, such as hollow-bearing trees ²⁴.

While direct and interactive responses of ecological components to climatic changes and land-use conversion have been previously explored independently of one another, how they simultaneously respond to major natural and human disturbances in forest ecosystems remains poorly documented ^{8,18–20}. This limits understanding of the full-extent to which disturbances impact forest ecosystems, and the factors that influence taxon-specific disturbance responses.

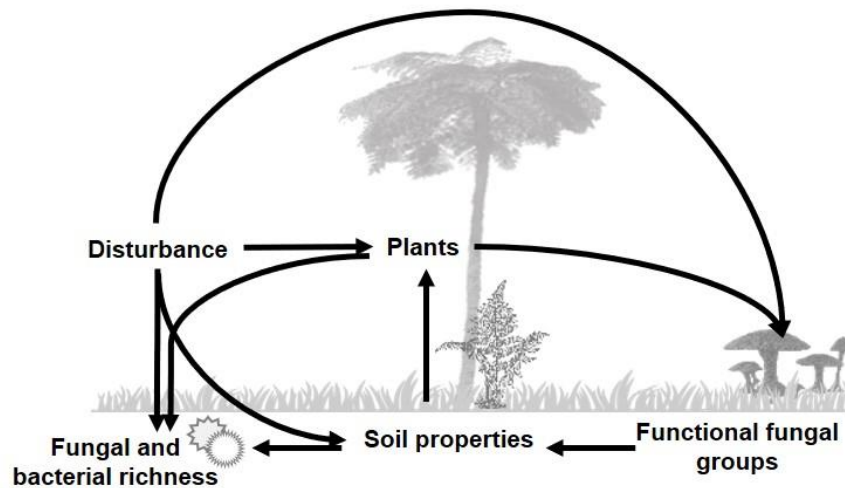
In a period of global climatic and environmental change, with disturbances predicted to increase and intensify ^{29–31}, it is critical to quantify abiotic and biotic disturbance responses and the interactive mechanisms which underpin them, to best preserve the functional integrity of forests. This understanding also provides for a multi-faceted approach to land-management, which traditionally has been biased toward above-ground biodiversity ⁸. In this study we quantified the direct and indirect impacts of fire frequency, clearcut logging and salvage logging on above and below-ground ecological components. We also quantified differences between disturbance types and the respective responses of individual ecological components. We hypothesised that ecological interactions would mediate indirect disturbance impacts throughout the ecosystem, above and below-ground. This is because of the well-known interactions between above and below-ground ecological components in forests^{11,13,15,18}. Further, we anticipated disturbance impacts may differ between different disturbance types that vary in their intensity. For instance, clearcut logging practices involve the combination of both mechanical clearing and post-logging burning, which are further compounded in salvage-logging operations which occur immediately following a natural wildfire ³²

Here, we quantify the impacts of natural disturbances (wildfire) and human disturbances (logging) across a 150+ year-chronosequence in the iconic Mountain Ash (*Eucalyptus regnans*) forests in south-eastern Australia, supporting the world's tallest flowering plants. These forests are well adapted to wildfires, which occur within a historical average fire-return period of 75-150 years ³³. However, like other global forest ecosystems, Mountain Ash forests have experienced climatic changes and increases in the frequency of wildfires and anthropogenic disturbances in recent decades ³.

Across 80 sites, stratified by different disturbance histories, we gathered a series of key datasets to quantify the direct and indirect disturbance impacts of, and interactions between, major abiotic and biotic components in Mountain Ash forests. Specifically, we investigated: **(1)** the abundance (percentage cover) of above-ground dominant plant lifeforms (*Acacia*, *Eucalyptus*, tree (exclusive of *Eucalyptus* and *Acacia*), treefern, shrub); and **(2)** the richness (Chao1 estimates) of soil microbial communities: bacteria and fungi, including fungal functional groups (symbiotrophic, saprotrophic); and **(3)** key soil measures: organic carbon, nitrate, available phosphorus, available potassium and pH (CaCl₂), across two depths of forest soils (0-10 cm and 20-30 cm). To do this, we used a single multi-level structural equation model (SEM) ³⁴ to quantify the relative impacts of wildfire frequency (1, 2 and 3

fires in recorded history since 1850s (1939, 1983 and 2009 wildfires) and clearcut logging (in 1980s and 2007-2011) and salvage logging (2009-2011) on these ecological components, relative to undisturbed forest, and identify ecologically-meaningful interactions between response variables (Figure 1). We designed our model based on a *priori* model with hypothesized causal pathways (Figure 1), controlling for time since disturbance and other environmental site-conditions (elevation, slope) (Table S1). This enabled us to quantify direct disturbance impacts and calculate indirect disturbance effects mediated through plant-soil-microbial interactions using multiplicative path tracing of standardised coefficients (by “relevant range”)^{18,35} (Figure 1). We also identified non-causal correlations within and between abiotic and biotic components that are likely influenced by a shared underlying driver or may represent ecological feedbacks³⁴(Table S2).

a)



b)

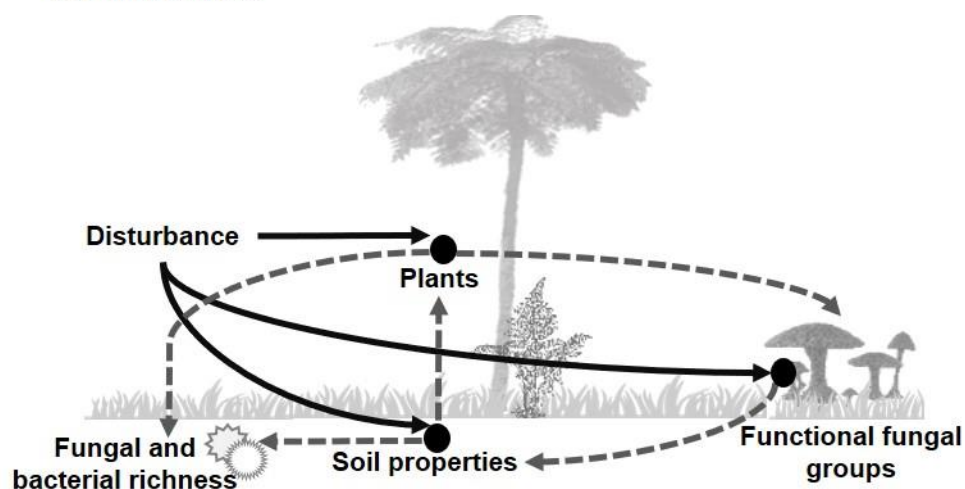


Figure 1. Causal paths investigated using a structural equation model (SEM)

a) Hypothesised causal pathways of direct (solid lines) disturbance impacts and plant-soil-microbial interactions investigated using structural equation modelling 34.

b) Hypothesised causal pathways of indirect disturbance effects (dashed lines) mediated through plant-soil-microbial interactions (black dots). In the context of this figure, plants = abundance (%) of dominant plant lifeforms (Acacia, tree, Eucalyptus, treefern, shrub), fungal and bacterial richness = Chao1 estimates, functional groups of fungi= saprotrophic and symbiotrophic fungal richness (Chao1 estimates), disturbance = number of wildfires post-1850s (1, 2, 3), and clearcut and salvage logging. Table S1 details the rationale for the hypothesised causal direction of each path in the SEM.

Disturbances simultaneously impact abiotic and biotic components in forests

Our analysis revealed widespread disturbance impacts on plants, soil microbes and edaphic properties across two soil depths (Fisher's $C = 350.458$; $p=1$, $df=484$) (Figure 2; Table 1; Table S3,S4). These impacts included both positive effects (associated with increases in ecological measures) and negative effects (associated with declines in ecological measures), and differed between abiotic and biotic components and disturbance types (Figure 2; Table 1). For instance, forests burnt twice and three times (post-1850s) were characterized by a lower richness of bacteria in the 0-10 cm depth of soil, and an increased abundance of eucalypt, shrub and treefern species, relative to long-unburnt forest. Similarly, relative to long-unburnt forests, forests burnt once had a higher abundance of shrub and tree lifeforms, but had lower nitrate concentrations in both soil depths. Further, forests burnt twice were associated with lower concentrations of available phosphorus in surface soil (0-10 cm), relative to long-unburnt forest. In contrast, relative to long-unburnt forest, forests burnt three times had increased concentrations of available potassium and a higher richness of saprotrophic fungi and total fungal richness in the 20-30 cm depth of soil (Figure 2; Table 1; Table S3).

Negative disturbance impacts (measured by negative effect sizes of wildfire and logging) were most severe in logged forests, relative to those burnt by wildfire alone (Figure 2; Table 1; Table S3). Specifically, clearcut logging reduced measures of organic carbon in the 20-30 cm depth of soil, available potassium and symbiotrophic fungal richness across both soil depths, and available phosphorus and the richness of bacteria in the 0-10 cm depth of soil, relative to unlogged forest. Similarly, salvage logging reduced the richness of bacteria in the 0-10 cm depth of soil, concentrations of nitrate and available phosphorus across both soil depths, and organic carbon in the 20-30 cm depth of soil, relative to unlogged forest (Figure 2; Table S2). Further, forests subject to clearcutting and salvage logging had an increased abundance of *Acacia* species, but salvage logging also reduced the abundance of tree, treefern and shrub species (Figure 2; Table S2).

Plant-soil-microbial interactions mediate indirect disturbance effects

From the SEM, we identified several positive and negative plant-soil-microbial interactions that mediated indirect disturbance effects between corresponding response variables (Fisher's $C = 350.458$; $p=1$, $df=484$) (Table S4). Collectively, these effects accounted for 43 % of disturbance impacts identified in this study (68 total). Several of these, either partially

mitigated or amplified disturbance impacts, however net disturbance impacts reflected direct impacts (Figure 2,3; Table S4,S5).

Plant-microbial interactions mediated negative indirect disturbance effects in forests that were burnt twice, three times and those that were clearcut or salvage logged. Specifically, declines in the abundance of tree species in forests that were salvage logged, reduced the richness of symbiotrophic fungi in the 0-10 cm depth of soil. In contrast, increases in the abundance of *Eucalyptus* species in forests burnt twice, burnt three times, and salvage logged reduced the richness of saprotrophic fungi in the 20-30 cm depth of soil (Figure 2,3; Table S4,S5).

Soil-microbial and soil-plant interactions mediated the largest number of indirect disturbance effects, with the vast majority being negative (Figure 2,3; Table S4,S5). For instance, in forests burnt once and salvage-logged, reduced concentrations of nitrate, resulted in declines in the richness of fungi across both soil depths. Declines in available phosphorus in the 0-10 cm depth of soil in forests burnt twice, salvage logged and clearcut logged also decreased the abundance of tree ferns. Further, clearcut logging-induced declines in available potassium decreased the abundance of trees and the richness of bacteria in the 20-30 cm depth of soil. Declines in organic carbon in the 20-30 cm depth of soil in clearcut and salvage logged forests also reduced the richness of bacteria in the 20-30 cm depth of soil and the abundance of shrub species. In contrast, in salvage logged forests, increases in soil pH in the 0-10 cm depth of soil increased the richness of bacteria in the 0-10 cm depth of soil, and increases soil pH in the 20-30 cm depth of soil decreased the abundance of *Acacia* and tree fern species. Higher concentrations of available potassium in forests burnt three times also increased the richness of bacteria in the 20-30 cm depth of soil and the abundance of tree species.

Relative to other disturbance types, salvage logging and clearcut logging had the most extensive and complex impacts on abiotic and biotic ecological components, relative to other disturbances. This was primarily due to widespread, plant-soil-microbial interactions which mediated indirect disturbance effects, accounting for 48% of total disturbance impacts in these logged forests (Figure 2,3; Table 1; Table S3,S4).

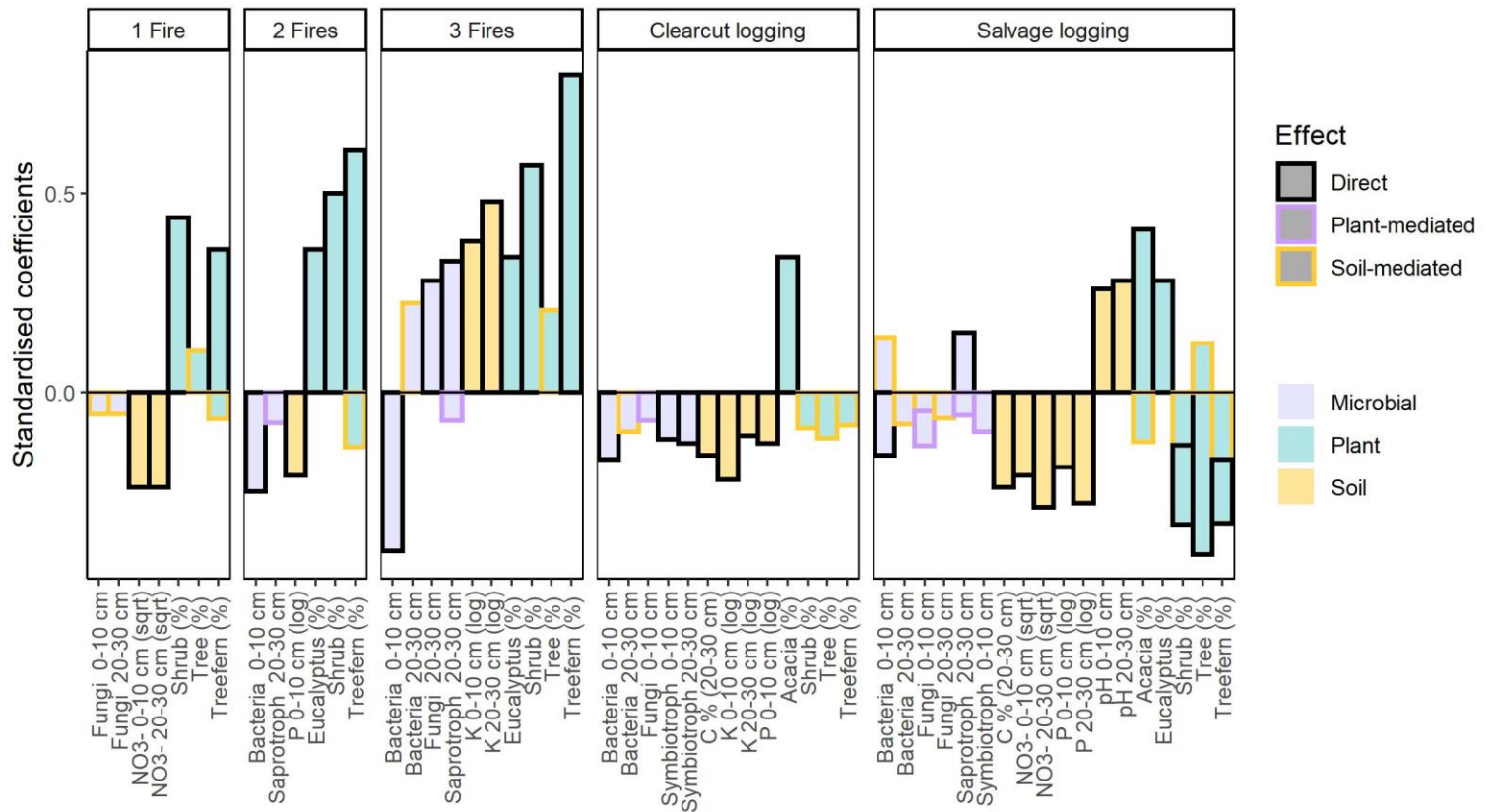
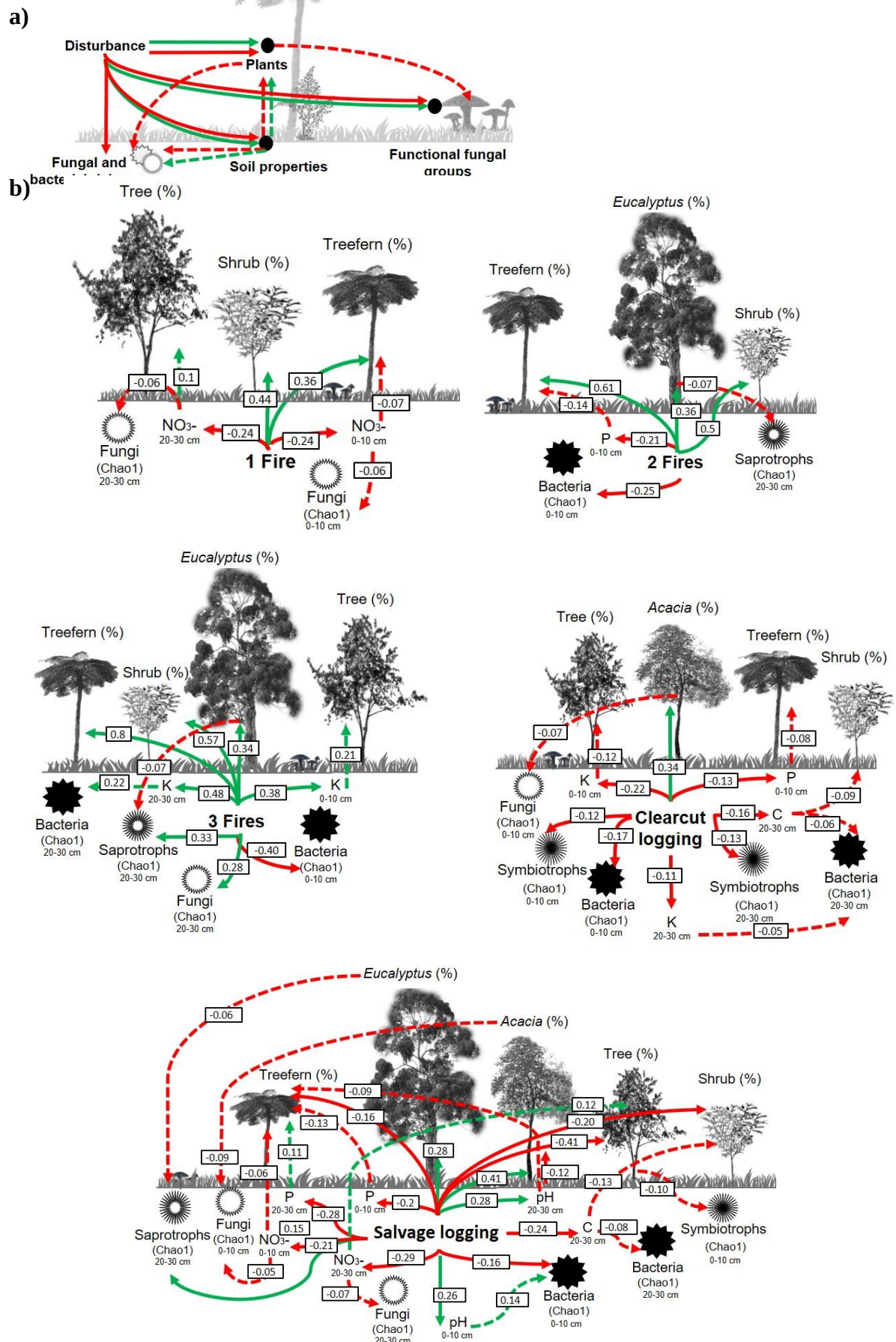


Figure 2. Direct and indirect disturbance impacts on abiotic and biotic ecological components in forests

Significant ($p < 0.05$) direct and indirect disturbance impacts on abiotic and biotic ecological components, mediated through plant-soil-microbial interactions. We calculated indirect disturbance effects using multiplicative path tracing and significant standardised (scaled by “relevant range”) coefficients of direct disturbance impacts on, and respective interactions between, response variables^{34,36} generated by the SEM (Fisher’s $C = 350.458$; $p = 1$, $df = 484$)³⁴. Relative disturbance impacts had both positive and negative effects on abiotic and biotic ecological components. Clearcut and salvage logging had the most extensive direct adverse impacts below-ground (soils and microbes), relative to unlogged forest. See Tables S3,S4 for full model details.



Fisher's C = 350.458; p=1, df=484

Figure 3. Ecosystem-wide direct and indirect disturbance impacts

a) Summary diagram of significant direct (solid line) and indirect (dashed line), positive (green) and negative (red) disturbance effects above and below-ground. Black dots indicate plant-soil-microbial interactions that mediated indirect disturbance impacts.

b) Significant direct (solid line) and indirect (dashed line) ($p < 0.05$) positive (green) and negative (red) impacts of disturbance on above-ground plant communities and below ground microbial communities and key soil components across two soil depths, generated using a SEM with standardised coefficients (scaled by “relevant ranges”) ³⁴ (Fisher’s $C = 350.458$; $p = 1$, $df = 488$). Wildfires and logging had ecosystem-wide direct and indirect impacts that spanned abiotic and biotic ecological components, above and below-ground. Salvage logging had the most complex and widespread impacts on forest ecosystems, relative to other disturbance impacts. See Table S3,S4 for full model details. Plant images were supplied by David Blair and Elle Bowd.

Table 1. Sixty-six significant ($p < 0.05$) direct, indirect and net disturbance impacts on plants, microbes and soils. Disturbance impacts (standardised coefficients) for each component disturbance are relative to long-unburnt and unlogged forest. Red text = negative disturbance effect (negative coefficient), green cells = positive disturbance effect (positive coefficient). See Table S3,S4 for full model details.

Response	Depth	No. Fires (1)			No. Fires (2)			No. Fires (3)		
		Direct	Indirect	Net	Direct	Indirect	Net	Direct	Indirect	Net
	NO ₃ - (sqrt)	0-10 cm	-0.24							
		20-30 cm	-0.24							
	K (log)	0-10 cm						0.38		
		20-30 cm						0.48		
	P (log)	0-10 cm			-0.21					
	Bacterial richness (Chao1)	0-10 cm			-0.25			-0.40		
		20-30 cm							0.22	
	Saprotrophic fungal richness (Chao1)	0-10 cm								
		20-30 cm				-0.08		0.33	-0.07	
	Fungal richness (Chao1)	0-10 cm	-0.06							
		20-30 cm	-0.06					0.28		
	Shrub %(probit)		0.44		0.50			0.57		
	Tree %(probit)		0.10						0.19	
			Clearcut logging		Salvage logging			0.80		
Response		Direct	Indirect	Net	Direct	Indirect	Net	0.34		
	NO ₃ - (sqrt)	0-10 cm			-0.21					
		20-30 cm			-0.29					
	K (log)	0-10 cm	-0.22							
		20-30 cm	-0.11							
	P (log)	0-10 cm	-0.13		-0.19					
		20-30 cm			-0.28					
	pH (CaCl ₂)	0-10 cm			0.26					
		20-30 cm			0.28					
	C	20-30 cm	-0.16		-0.24					
	Bacterial richness (Chao1)	0-10 cm	-0.17		-0.16	0.14	-0.02			
		20-30 cm		-0.10		-0.08				
	Saprotrophic fungal richness (Chao1)	0-10 cm								
		20-30 cm			0.15	-0.06	0.10			
	Fungal richness (Chao1)	0-10 cm		-0.07		-0.14				
		20-30 cm				-0.07				
	Symbiotrophic fungal richness (Chao1)	0-10 cm	-0.12			-0.10				
		20-30 cm	-0.13							
	Eucalyptus %(probit)				0.28					
	Acacia %(probit)		0.34		0.41	-0.12	0.29			
	Shrub %(probit)			-0.09	-0.20	-0.13	-0.34			
	Tree %(probit)			-0.12	-0.41	0.12	-0.29			
	Treefern %(probit)			-0.08	-0.16	-0.17	-0.33			

Implications of widespread direct and indirect disturbance impacts

We provide compelling empirical evidence that wildfire, clearcut logging and post-fire (salvage) logging have widespread impacts on forest ecosystems that span major abiotic and biotic ecological components, above and below-ground. These impacts manifest both directly and indirectly, mediated through plant-soil-microbial interactions. Disturbance impacts increased with the number of wildfires and clearcut and salvage logging. However, across all abiotic and biotic ecological components, clearcut and salvage logging had the most widespread, complex and adverse disturbance impacts. Our findings disentangle the multifaceted effects of disturbances in forest ecosystems and demonstrate differences between disturbance responses across major abiotic and biotic ecological components, above and below-ground. Further, by quantifying both direct and indirect disturbance impacts, we provide novel insights into the mechanisms through which plant-soil-microbial interactions can mediate disturbance impacts throughout forest ecosystems^{17–20}.

Wildfires, and clearcut and salvage logging in forests affected abiotic and biotic ecological components below-ground. Specifically, these disturbances had primarily negative direct impacts on key soil properties, which relayed negative indirect impacts on the richness of microbial communities, and the abundance of some plant lifeforms. However, disturbance impacts on the topsoil (0–10 cm) and subsoil (20–30 cm) varied with disturbance types. For instance, potassium measures across both depths increased with three fires, but declined with clearcut logging. Further, logging produced the highest number of adverse impacts across both soil depths, with were most pronounced with salvage logging. This may be explained by the compounding nature of logging disturbances which involve both mechanical disturbances that can compact soils and alter their composition²⁸, and wildfire (and post-logging burning) which can heat soil above 500°C resulting in long-term losses of soil nutrients, organic carbon and organic matter through volatilization and post-fire erosion^{27,37,38}.

The interval between wildfires also may influence below-ground soil properties. For instance, multiple wildfires within short fire return intervals can deplete carbon stores via the combustion of “legacy carbon”³⁹. In the short-term, soil surface ash-deposits can also temporarily increase nitrogen and phosphorus and facilitate the rapid post-disturbance regeneration of vegetation^{40,41}. However, despite biochemical inputs and plant-soil-microbial interactions, our findings indicate that disturbances are major drivers of declines in key soil properties, which have indirect effects on plant and microbial communities. Similar multi-

decadal, direct disturbance impacts on soil properties have been observed across boreal forest ecosystems^{38,42}.

Consistent with other studies, we identified top-down and bottom-up interactions between major abiotic and biotic ecological components, which mediated indirect disturbance effects throughout the entire ecosystem^{18–20,43}. Soil-plant interactions are likely explained by plant uptake rates of available nutrients⁴⁴, which can increase plant growth and survival^{15,16}. Soil-microbial and plant-microbial interactions are likely explained by taxon-specific environmental requirements^{45,46}, including the availability of organic compounds, decaying plant matter, carbon-allocation to roots¹⁴ and habitat availability, which may be host-specific^{46,47}. Interactions between microbial communities and soils also reflect saprotrophic and symbiotrophic ecological functions including decomposition⁴⁸ and nutrient cycling^{45,49} which can influence nutrient availability and soil composition.

Although wildfire and logging produced some similar impacts on abiotic and biotic components below-ground, their direct impacts on plant communities differed. This is likely explained by the compounding nature of clearcut and salvage logging which involves high-intensity physical disturbances from mechanical clearing, and post-logging burning that consumes much of the remaining slash and debris²³. For instance, while our findings indicate that wildfire can increase the abundance of shrub and treefern lifeforms, clearcut and salvage logging reduced the abundance of these lifeforms, relative to long-unburnt forest. This may be explained by declines in resprouting plant species, that, while being resilient to fire, are sensitive to clearcut logging practices that kill, damage and expose resprouting organs⁵⁰. The most severe declines in plant lifeforms (treeferns, trees and shrubs) occurred in salvage logged forests, which mediated indirect effects on microbial communities.

Root-system damage, soil compaction and post-logging burning can directly influence microbial communities for multiple decades by destroying microbial biomass and inoculum sources^{51,52}, altering the availability of saprotrophic fungal habitat⁵³, and soil nutrient and/or plant community composition, which can impact host-specific microbes including symbionts^{47,52}. However, some microbial species, including saprotrophic fungi are more resistant to the impacts of disturbance and likely benefit from changes to the physical environment associated with wildfire and logging such as exposed organic matter, vegetation dieback, physical breakdown of soil aggregates, and an increase in micro-habitat heterogeneity due to

varying disturbance intensities across small scales ⁵². These factors could explain the increase in these species with three wildfires that we observed in our study.

Similar to studies in other forest ecosystems, we identified several plant-soil-microbial interactions that either partially mitigated ⁵⁴, or amplified disturbance impacts ¹⁸. However, as net disturbance impacts reflected direct disturbance impacts, particularly in logged sites, our findings strongly indicate that despite these interactions, disturbances are major direct drivers of above and below-ground ecological components in forests.

Our analyses allowed for the separation of component disturbances from different disturbance histories, but we did not quantify the effect of interactions between them (e.g. clearcut logging * wildfire). However, because forest stands frequently experience both wildfires and clearcut logging, our findings suggest that the compounding influence of these disturbances would amplify respective impacts across above and below-ground trophic levels. Further, given the multi-decadal legacy that these disturbances have on individual above and below-ground ecological components, we suggest the impacts documented here will be just as long-term ²⁷. While we investigated the effects of different wildfire frequencies on ecological variables, we did not explore the impacts of different wildfire intensities. Additional research is required to quantify these limitations.

We identified interactions between key abiotic and biotic, above and below-ground ecological components in forests, which collectively explained 40% of disturbance impacts. The causal direction of these interactions (A -> B; and not B -> A) indicated in the *priori* model of hypothesised causal pathways (Figure 1) was determined using prior subject knowledge and consultation with the literature (Table S1). However, this limited our ability to analyse all possible bottom-up and top-down interactions, which can be bidirectional, cyclic, or may follow alternative causal paths. Future research efforts are required to further examine these complex interactions.

Another caveat associated with this study is that we did not measure climatic variables, fuel loads and fuel moisture prior to wildfire events, which can influence the impacts of wildfire in an ecosystem ⁵⁵. Further, we did not have pre-fire or pre-logging data, so are unable to quantify site-specific differences pre and post disturbance. While these unmeasured variables may explain some variability in our findings, we have attempted to control for the potential effects of site-based variation in disturbance impacts in site selection and analysis by including environmental variables, time since disturbance, and checking for spatial

autocorrelation. Future research efforts should seek to quantify these potential sources of variation in site-specific disturbance impacts, as well as measuring total soil nutrient pools and microbial and plant biomass to compliment our findings.

Management implications

Wildfire and clearcut and salvage logging have major impacts on above and below-ground forest ecosystems, both directly, and indirectly through plant-soil-microbial interactions, that likely last for multiple decades. By quantifying 68 direct and indirect disturbance impacts across major abiotic and biotic ecological components, our findings provide novel insights into the extent to which disturbance impacts affect forests, and the mechanisms which underpin those impacts. Our findings highlight previously poorly understood, direct and indirect below-ground disturbance impacts, which were extensive in logged forests. Our results suggest that neglecting indirect disturbance effects, and below-ground forest environments, and their respective interactions with above-ground environments, traditional above-ground-focused approaches to land management may be vastly underestimating disturbance impacts on forests.

Soils constitute the largest terrestrial carbon stock on earth (more than the atmosphere and vegetation combined)⁵⁶, and influence plant growth and seedling survival^{8,9}, decomposition rates and nutrient cycling^{2,10,57}, and harbour hyper-diverse microbial communities that mediate critical ecological functions in forests^{11,12}. The effective management of soils and their communities is an integral part of addressing global disturbance threats including climate change¹¹, wildfire and logging.

While forests are adapted to specific disturbance regimes, our research contributes to a growing body of literature on how altered disturbance regimes can affect the functional integrity of ecosystems^{58,59}. Predicted global increases in high fire-risk conditions will likely increase the frequency of large, stand-replacing fires in the next few decades across terrestrial ecosystems^{29–31}. The resulting young, dense wildfire regrowth is at increased risk of repeated burning at high-severity, precluding species for reaching ecological maturity and falling into a “landscape-trap” impeding key ecological functions⁶⁰. For instance, when high-severity wildfire intervals are too frequent in forest ecosystems, dominant species can be replaced by non-forests and woodlands⁶¹, severely eroding habitat suitability for an array of threatened species⁶².

The subsequent compounding impact of a rapidly changing climate and increases in post-fire salvage logging will likely amplify the direct and indirect disturbance impacts identified in this study. This suggests that our results may act as a precursor for potentially more severe shifts in forests in the future. With major functional implications likely to result from these widespread disturbance-impacts (which are yet to be directly quantified), we urge land-managers to practice sensitive management approaches that consider whole forest ecosystems and their respective plant-soil-microbial interactions.

Specifically, we recommend that future biodiversity monitoring and planning are multifaceted, and incorporate both abiotic and biotic ecological components, above and below-ground, and their respective interactions. Further, to best preserve the functional integrity of forests, where possible, older undisturbed forests should be conserved and human perturbations curtailed, especially in already disturbed locations to minimise compounding impacts.

Acknowledgements

We thank the Mycological Society of America, The Paddy Pallin Foundation, The Ecological Society of Australia's: Holsworth Wildlife Fund, the Centre of Biodiversity Analysis, and volunteers who assisted in data collection for their support, and contributions to this study.

We acknowledge the contribution of the BASE project partners (DOI: 10.4227/71/561c9bc670099), an initiative supported by Bioplatforms Australia with funds provided by the Australian Commonwealth Government through the National Collaborative Research Infrastructure Strategy.

Competing interests

The authors declare no competing interests.

Figure titles

Figure 1. Causal paths investigated using a structural equation model (SEM)

a) Hypothesised causal pathways of direct (solid lines) disturbance impacts and plant-soil-microbial interactions investigated using structural equation modelling 34.

b) Hypothesised causal pathways of indirect disturbance effects (dashed lines) mediated through plant-soil-microbial interactions (black dots). In the context of this figure, plants = abundance (%) of dominant plant lifeforms (Acacia, tree, Eucalyptus, treefern, shrub), fungal and bacterial richness = Chao1 estimates, functional groups of fungi= saprotrophic and symbiotrophic fungal richness (Chao1 estimates), disturbance = number of wildfires post-1850s (1, 2, 3), and clearcut and salvage logging. Table S1 details the rationale for the hypothesised causal direction of each path in the SEM.

Figure 2. Direct and indirect disturbance impacts on abiotic and biotic ecological components in forests

Significant ($p < 0.05$) direct and indirect disturbance impacts on abiotic and biotic ecological components, mediated through plant-soil-microbial interactions. We calculated indirect disturbance effects using multiplicative path tracing and significant standardised (scaled by “relevant range”) coefficients of direct disturbance impacts on, and respective interactions between, response variables^{34,36} generated by the SEM (Fisher’s $C = 350.458$; $p = 1$, $df = 484$)³⁴. Relative disturbance impacts had both positive and negative effects on abiotic and biotic ecological components. Clearcut and salvage logging had the most extensive direct adverse impacts below-ground (soils and microbes), relative to unlogged forest. See Tables S3, S4 for full model details.

Figure 3. Ecosystem-wide direct and indirect disturbance impacts

a) Summary diagram of significant direct (solid line) and indirect (dashed line), positive (green) and negative (red) disturbance effects above and below-ground. Black dots indicate plant-soil-microbial interactions that mediated indirect disturbance impacts.

b) Significant direct (solid line) and indirect (dashed line) ($p < 0.05$) positive (green) and negative (red) impacts of disturbance on above-ground plant communities and below ground microbial communities and key soil components across two soil depths, generated using a SEM with standardised coefficients (scaled by “relevant ranges”) ³⁴ (Fisher’s $C = 350.458$; $p = 1$, $df = 484$). Wildfires and logging had ecosystem-wide direct and indirect impacts that

spanned abiotic and biotic ecological components, above and below-ground. Salvage logging had the most complex and widespread impacts on forest ecosystems, relative to other disturbance impacts. See Table S3,S4 for full model details. Plant images were supplied by David Blair and Elle Bowd.

Methods

Site description

We conducted this study in the tall and carbon-dense (1,867 tonnes of carbon/ha)⁶³ *Eucalyptus regnans* (Mountain Ash) forests of the Victorian Central Highlands located in southeastern Australia. These high-altitude and high-rainfall forests are characterised by a tall overstory of *Eucalyptus regnans*, mid-storey of *Acacia* and other scattered trees, broad-leaved shrubs and a diverse ground-layer rich in mesophytic herb and fern species^{40,50}. Typically, Mountain Ash forests experience a cool, mild climate, with occasional periods of snow in winter months⁴⁰. However, hotter and drier summer conditions have increased in recent years, subsequently increasing the risk of wildfires²⁹.

Mountain Ash forests are well-adapted to wildfires occurring within the historical fire return period of 75-150 years, prolifically regenerating afterfire from seed or resprouting organs^{23,33}. However, the frequency of large, stand-replacing wildfires has increased in recent decades, with major wildfires occurring in 1939, 1983 and most recently in 2009. This has resulted in an abundant young, dense, fire-prone landscape, with only 1.16 % of old-growth forest remaining^{64,65}.

In addition to wildfire, Mountain Ash forests have experienced ongoing clearcut logging since the 1970s⁶⁶. These practices involve clearing and cutting of all vegetation within an area of between 15 and 40 ha, and the removal of merchantable *Eucalyptus* trees²³.

Remaining vegetative debris is then burnt at high-intensity and subsequently re-seeded with the dominant eucalypt species^{67,68}. Similarly, post-fire salvage logging entails clearcut logging that occurs immediately following a natural wildfire. In summary, salvage logging follows standard clearcut logging practices of clearing, burning and re-seeding with the exception that there is no post-logging burn if the regeneration from the natural wildfire is adequate²⁴.

We conducted comprehensive above and below-ground, multi-trophic sampling across 80 625 m² (25 m x 25 m) sites in the Mountain Ash forests in south-eastern Australia during Austral summer months (December 2016 – March 2017). Sites were characterized by a

predominantly southerly aspect, were located at an elevation of ~600-900 meters, experienced an annual precipitation of between 1300-1800 mm, and were positioned away from drainage lines and ridges. At each site, we recorded the projective foliage cover of each vascular plant species, which were later divided into respective lifeforms. We also collected nine, 10 cm x 30 cm soil cores along the perimeter and in the centre of each site and stratified, pooled and mixed each soil sample by depth (0-10 cm and 20-30 cm)⁶⁹. These 720 soil cores underpinned the three below-ground, multi-faceted datasets described in this study: (1) Key soil properties, (2) Fungal communities, (3) Bacterial communities. Detailed methods are described below for each respective dataset.

We designed our study to encompass the broad diversity of disturbance histories in Mountain Ash forests. Specifically, we selected nine disturbance history categories in total: five experienced fire-only, and the remaining four categories were clearcut or salvage logging. Fire-only sites consisted of forests, long-undisturbed (unburnt since 1850s: 4 replicates), burnt once (1939 fire: 10 replicates), twice (1939/1983: 10 replicates; and 1939/2009: 11 replicates) and three times (1939/1983/2009: 6 replicates). Logged sites were those burnt in 1939 and clearcut in 1980–85 (10 replicates) or 2008–10 (10 replicates), and salvage logged in 2009–10 (10 replicates) after a second fire in 2009. In addition, sites that experienced multiple fires and clearcut logging were those burnt in 1939/1983 and clearcut in 2008–10 (9 sites). Of those clearcut/salvage logged sites, 8 had experienced historical thinning or other silviculture events that occurred between 30-40 years prior to the most recent clearcut and salvage logging events in 1980-1985 or 2008-2010.

Microbial communities

From the 0-10 cm and 20-30 cm composite soil samples for each site, we collected subsamples of soil (approximately 100 grams per sample) and stored them at -20°C for later DNA analysis. DNA extraction and sequencing were undertaken by the BASE project, according to the methods described by Bissett et al. (2016)⁶⁹. Briefly, DNA was extracted in triplicate (3 x 0.25g) using MOBIO power soil kits and extractions combined. The fungal ITS region (primers ITS1F⁷⁰ and ITS4⁷¹), and the partial bacterial 16S rRNA genes (primers 27f⁷² and 519r⁷³) were amplified and sequenced using the Illumina MiSEQ platform to generate 300 base pair, paired end reads for each sample⁶⁹.

Sequence analyses for DNA samples were conducted as per Bissett et al., (2016)⁶⁹. In summary, for ITS the ITS1 gene region was extracted from R1 reads using ITSx v1.0.11⁷⁴,

OTUs clustered at 97% sequence similarity using USEARCH (v9.0.2132, 64-bit) (-cluster_otus -minsize 4) and sequences mapped back to OTUs to generate abundances (-usearch_global -strand plus -id 0.97 -maxaccepts 56 -top_hit_only -maxrejects 256). For Bacterial 16S sequences, OTUs were clustered at 97% similarity using USEARCH as above. We assigned taxonomy to each OTU using the RDP naïve Bayesian classifier ⁷⁵ as employed by MOTHUR (v1.39.1) ⁷⁶ against the UNITE v6 species hypothesis database ⁷⁷ for fungi, and Greengenes ⁷⁸ for bacteria using a probability cutoff of 60% ^{75,79,80}. Any fungal or bacterial OTUs unassigned to phylum were discarded from this study (56-61% of total fungal OTUs, and <1% of total bacterial).

Fungal functional groups

We used the FUNGUILD v1.0 flat database to assign fungal OTUs into functional groups based on trophic strategies: ‘symbiotroph’ and ‘saprotroph’ with a confidence rating of “highly probable” and “probable” ⁸¹. Symbiotrophic fungi exchange resources with hosts, and saprotrophic fungi receive nutrients by breaking down dead hosts ⁸¹. Fungal OTUs assigned to multiple functional groups were included in all respective groups. While FUNGUILD is widely used in fungal community research, it is important to note that given our sampling was of bulk soil, we cannot be certain that fungal OTUs assigned to functional groups were fulfilling their respective functional roles at the time of sampling. Therefore, “highly probable” and “probable” fungal OTUs assigned to functional groups should be regarded as potentially/ likely fulfilling respective functional roles within their lifecycle.

We rarefied the abundance of each OTU to the lowest number of reads for each sample type (Fungal DNA samples: 0-10 cm = 19,943 ; 20-30 cm = 24,382; Bacterial DNA samples: 0-10 cm = 21,599; 20-30 cm = 37,675 using the *rarefy_even_depth* function in the *phyloseq* package in R v 3.6.0 to account for the uneven library sizes between samples (Weiss *et al.*, 2015). Using the rarefied OTU abundance matrix, we calculated the estimated richness (Chao1) of bacteria, fungi, and saprotrophic and symbiotrophic fungi across the two soil depths using the Chao1 richness estimator function ‘*estimate_richness*’, in the *phyloseq* package. Further information on the microbial community composition of Mountain Ash forests is detailed in Bowd *et al.*, 2020 unpublished data ⁸³.

Soil properties

Remaining soil for each composite sample (0-10 cm and 20-30 cm depth of soil) was collected and sieved to 2 mm for soil chemical analyses, as described in detail by Bowd *et al.*

2019²⁷ (Table S6). We selected major components of soils that can be influenced by disturbance, and also influence microbial communities: nitrate, available phosphorus, organic carbon, pH (CaCl₂) and available potassium to include in this study. We determined nitrate content colorimetrically, following extraction with 2 M potassium chloride (25 °C)^{84,85}. We measured available phosphorus and potassium were measured using the Colwell method^{84,85}. We measured Organic carbon using the Walkley–Black method⁸⁶. The concentrations of soluble salts were estimated by measuring electrical conductivity based on a 1:5 soil/water extract (EC 1:5). We determined the pH (CaCl₂) using a 1:5 soil/0.01 M CaCl₂ solution^{84,85}.

Major Lifeforms

For each site, we recorded the projective foliage cover of vascular plant species in each quadrat on each site using the survey protocol and sample configurations developed by the Australian Department of the Environment, Land, Water and Planning⁸⁷. Projective foliage cover was used as a measure of species abundance and is hereafter referred to as ‘abundance’. each plant species using criteria defined by Bowd et al. 2018⁵⁰. In summary, each plant species was assigned a single life form, and those life forms that were dominant were used in our analysis (‘*Eucalyptus*’, ‘*Acacia*’, ‘Tree’, ‘Shrub’ and ‘Tree-fern’). For each of these dominant life forms, we calculated the total abundance for each site (sum of the abundance of each plant species in each respective life form category in each site). We separated ‘*Eucalyptus*’ and ‘*Acacia*’ species from the ‘Tree’ life form group. This was because *Eucalyptus* trees are the dominant over-storey species within these forests, whereas *Acacia* species dominate the mid-storey and have different ecological roles, such as nitrogen fixation²³. Plant lifeform abundance (projective foliage cover) was converted to proportions for analysis, constant values were added for any “0” and “1” values using the lower detection limit method.

Statistical analyses

We used a multilevel path analysis ('piecewise' structural equation modelling) to quantify disturbance impacts on above and below-ground response variables, and response/response interactions derived from a subset of gaussian linear models using the "piecewiseSEM" package in R³⁴. In each model, we included component disturbance events as factors of all sites (wildfire frequency (0 fires (since 1850s): n=4; 1 fire: n=30; 2 fires: n=40; 3 Fires: n=6) and last clearcut logging/salvage logging event (clearcut logging: n=29; salvage logging=10), and interactions between response variables (Figure 1). We also included time since disturbance and other site and environmental variables (elevation, slope, thinning) to account for any potential explained variation in all models. We employed the "dredge" function from the "MuMIn" package in R (parameters: disturbance variables= fixed factors; rank= AICc) to select the combination of factors with the lowest AICc for each respective model. We used these final models in the piecewise structural equation model. To meet the assumptions of gaussian linear models, variables were transformed (log, sqrt, probit) where appropriate. We also tested the potential of multi-collinearity in all models using the variance inflation factor (VIF), and removed any variables with a VIF>5 in the "car" package in R.

We used Shipley's tests of directed separation to test the assumption that all variables not considered in all response models were conditionally independent (Table S5)³⁴. Dependant variables identified in these tests were either included in the respective model, or discounted from the basis set of paths in the SEM, and classified as non-casual interactions or likely bidirectional correlations. Fisher's C value of 350.458, p-value = 1, df= 484 indicated an appropriate fit of the final model.

We standardised coefficients generated by the piecewise structural equation model by the "relevant range" of the data, which can be interpreted as the expected proportional shift in y (along its range) given a full shift along the range of x^{34,88}. Standardised coefficients provided relative effect sizes that could be directly compared between response variables. This also allowed us to calculate indirect disturbance effects by multiplying significant coefficients along pathways of interacting response variables ("multiplicative path-tracing") in the path model^{18,35,36}.

We generated variograms using model residuals (bins= min. and max. distance between sites) for each response variable to test for spatial auto-correlation using the "geoR"

package in R. We found no evidence of spatial auto-correlation in any of our response variables. All analyses were conducted using R 3.6.0.

Data availability

If accepted, data supporting this paper will be submitted to Dryad repository.

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Conclusions

Disturbances are major drivers of the structure and function of forests worldwide (Bowman et al., 2009; Thom & Seidl, 2016). However, novel disturbance intensities and frequencies can shift ecosystems into functionally compromised states (Bowman et al. 2014; Lindenmayer et al. 2011). Despite mediating critical ecological functions, below-ground responses to altered disturbance regimes are poorly-understood. Here, for the first time in Mountain Ash forests, my research describes how soil properties and microbial communities are influenced by altered disturbance regimes, differing in fire frequency, and clearcut and salvage logging events. My research also describes the disturbance responses of plant communities and disentangles the complex relationship between disturbances and plant-soil-microbial interactions. My research findings indicate that adverse disturbance impacts can be extensive below-ground, and result in declines in key soil nutrients and the diversity and richness of some microbial communities. These changes can have widespread implications in forest ecosystems with adverse impacts on decomposition rates, nutrient cycling and soil fertility (Hartmann et al., 2014; Maron et al., 2018; Trivedi et al., 2019), symbiotic relationships (Hartmann et al., 2014; Holden, Berhe, & Treseder, 2015), and specialized ecological functions such as nitrogen fixation (Philippot et al., 2013; Singh et al., 2014).

In **Chapter 1** entitled Logging and fire regimes alter plant communities, my findings provide evidence that disturbance impacts on plant communities were related to their respective regeneration strategies post-disturbance. Specifically, clearcut and post-fire salvage logging reduced the abundance of resprouting plant species, and multiple wildfires reduced the abundance of some onsite-seeder species. My findings suggest that resprouting plant species are more sensitive to the mechanical disturbances associated with logging than the impacts of wildfire alone. Further, some obligate-seeder species may be unable to

replenish propagules within short fire-return intervals. My research highlights the importance of limiting perturbations where possible to conserve vulnerable plant species.

Chapter 2 entitled Long-term impacts of wildfire and logging on forest soils, describes the multi-decadal adverse impacts of fire (~78 years) and clearcut logging (~34 years) on key components of forest soils across two soil depths. Specifically, these disturbances resulted in significant declines in soil nutrients including nitrate and available phosphorus, relative to long-undisturbed forests. The adverse impacts of these disturbances were more pronounced in the topsoil and were exacerbated with compounding disturbances, including multiple fires and clearcut logging. My conclusions from this paper are that disturbances can have long-lasting impacts on forest soils, which may have widespread functional implications in forests. This work highlights the importance of limiting perturbations in forests, especially in those previously disturbed, to avoid compounding impacts. Further, my research identifies the need to incorporate sustainable soil management into future forest management, monitoring and planning.

Chapter 3 entitled Fire and logging regimes alter functional communities of fungi, provides evidence of differing disturbance impacts on the composition of fungal communities and the richness and abundance of their respective functional groups across two depths of forest soils. My findings show that the composition of fungal communities may not return to pre-disturbance conditions for up to at least 34 years post-disturbance in lower soil depths. Further, while often associated with high levels of functional redundancy, my research shows that disturbance impacts on fungal communities can have functional implications in forests. For instance, relative to unlogged forests, clearcut logging reduced the richness and abundance of symbiotrophic fungi, and salvage logging increased pathotrophic and saprotrophic fungi. My research highlights the importance of managing forests to maintain the full suite of fungal diversity. Further, to best preserve the vital functions fungi have in

forests, long-undisturbed forests should be conserved, and perturbations limited where possible.

Chapter 4 entitled Wildfires and logging alter a forest soil microbiome, provides evidence that multiple wildfires, and clearcut and salvage logging can result in declines in the diversity of individual microbial communities and total microbial diversity, with effects pronounced in the topsoil. Further, my research identified soil edaphic properties which were key drivers of the composition of microbial communities. Because microbial diversity drives multi-functionality in terrestrial ecosystems, diversity declines post-disturbance may compromise ecological functions. However, functional complementarity in microbial communities does exist, and future research is required to quantify how disturbances directly influence functional roles. My research highlights the importance of managing forests to maintain microbial diversity, and therefore ecological functioning, by limiting perturbations where possible, especially in previously disturbed forests, to prevent compounding impacts.

Chapter 5 entitled Direct and indirect disturbance impacts in forests, provides evidence that that wildfires, logging and post-fire (salvage) logging can simultaneously impact plant and microbial communities, and abiotic soil properties both directly and indirectly through plant-soil-microbial interactions. Further, this paper shows that human disturbances were associated with more negative effects than natural disturbances, suggesting logging results in adverse effects in forest ecosystems. These results highlight the importance of including above and below-ground ecological components, and their respective interactions in forest management, monitoring and planning, to best preserve the functional integrity of forests.

In summary, my research findings of above and below-ground disturbance impacts provide a new insight into how Mountain Ash forests respond to disturbances over the short and long-term. Specifically, my findings suggest that by neglecting the disturbance responses

of below-ground forest environments, and their respective multi-trophic interactions, traditional above-ground-focused approaches to land management may be underestimating disturbance impacts in forests. Therefore, the effective management of soils and their communities is an integral part of addressing global disturbance threats including climate change (Cavicchioli et al., 2019), wildfire and logging. This is especially pertinent now, in the current period of rapid, global, environmental change, with predicted increases in the frequency of wildfires likely to amplify disturbance impacts above and below-ground. Bridging the gap between ecological research and policy is essential in facilitating adaptive management to conserve ecosystems during this period. To ensure the recommendations of my research reach land-management and policy, I aim to effectively communicate these findings through engagement with media, attending local and global conferences, and actively engaging in stakeholder consultation and with policy and land-management agencies directly.

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