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Long-term impacts of wildfire and logging on forest soils

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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 years[22]. 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 2009[8]. 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 2009[23]). 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 decades[25]. 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 (pH($CaCl_2$), 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

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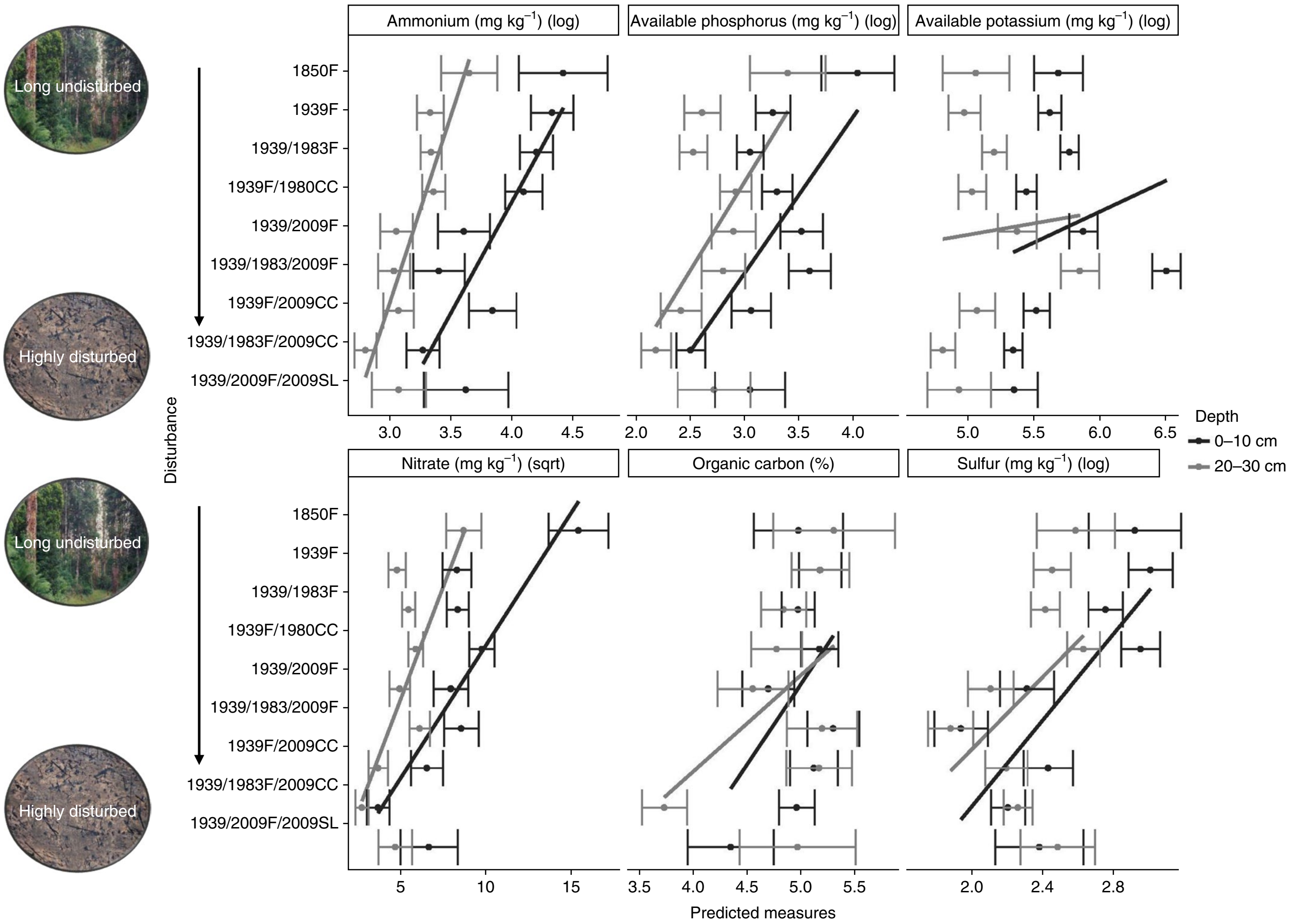

Fig. 1 | Disturbance histories influence soil measures along a multi-century chronosequence. Predicted values of vital soil measures (± standard error) in relation to disturbance history category, with trend lines. Predictions are shown for a single parent rock type (type 3: Supplementary Table 2), Australian 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

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).

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($CaCl_2$) 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($CaCl_2$) 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).

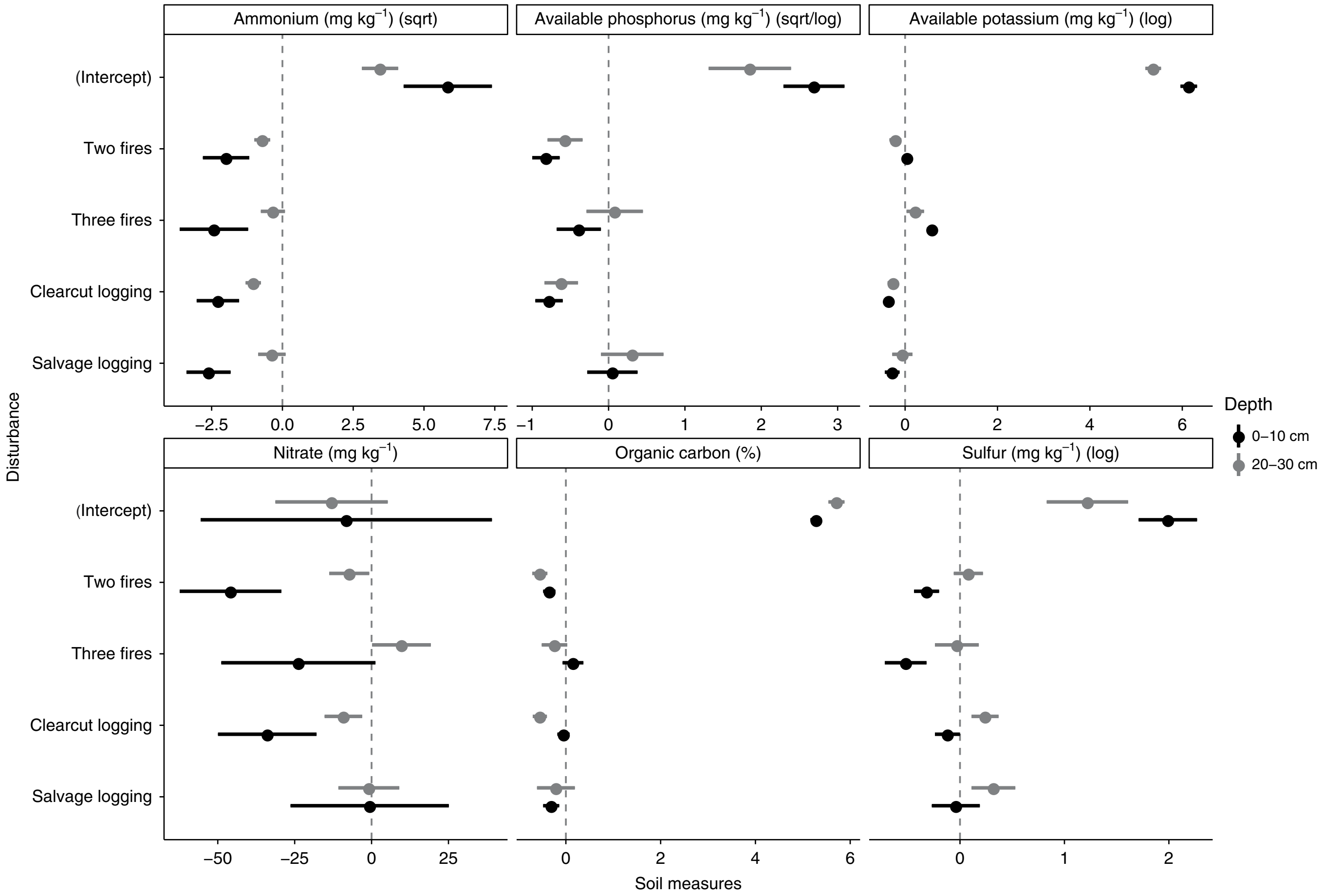

Fig. 2 | The pervasive impacts of multiple fires and logging on soil measures. Coefficients from generalized linear models of each soil measure with respect to disturbance type, parent rock and Australian soil classification, elevation, slope and the abundance of dominant plant life forms (parent rock 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).

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 post-fire 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 forests[10]. 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 floor[18], compact the soil[32], volatilize soil nutrients[28] and redistribute organic matter[28,33], resulting in the release of large amounts of CO_2 into the atmosphere (Fig. 4)[33]. These impacts can alter plant–soil–microbial

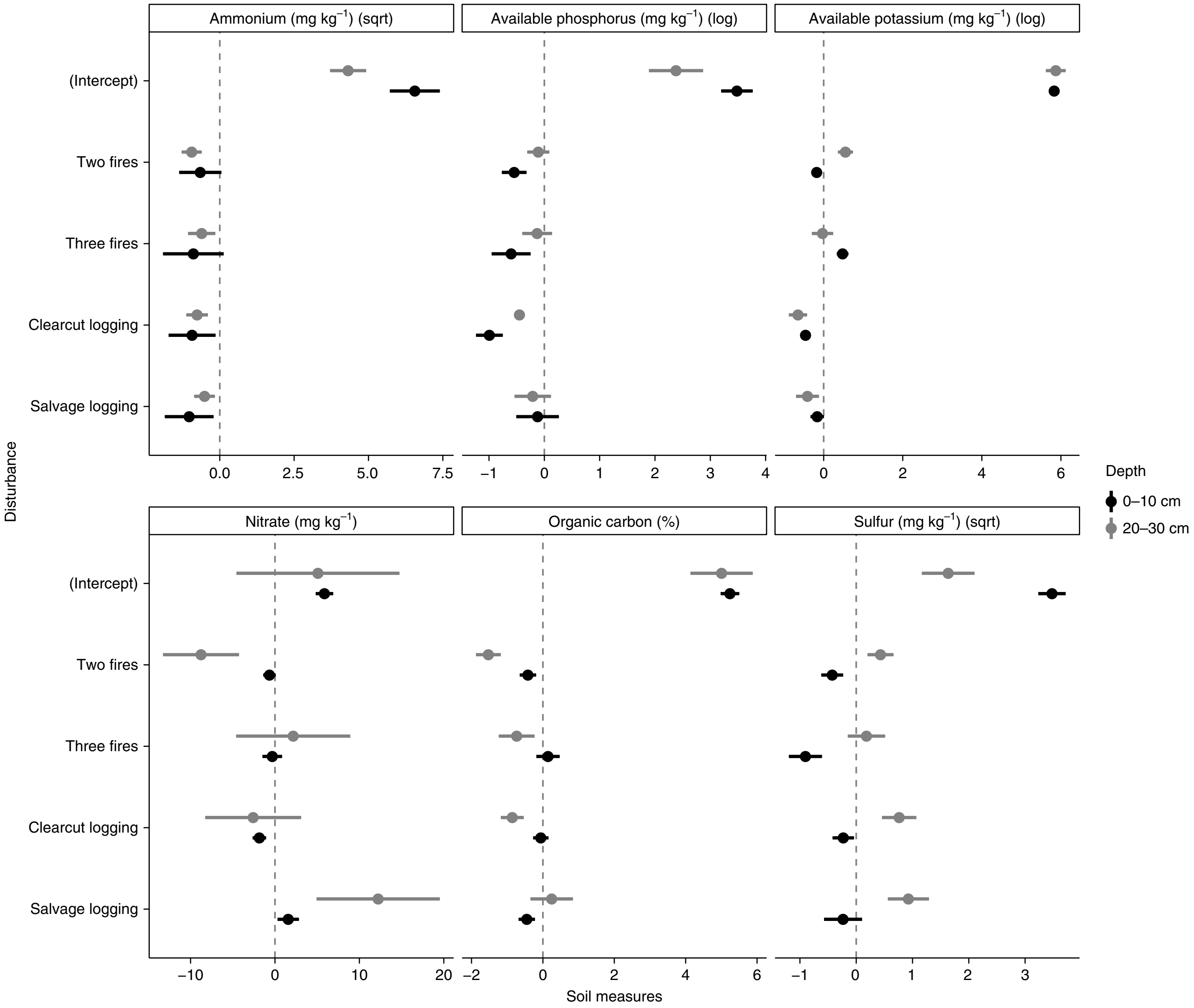

Fig. 3 | The impact of fire and logging in similarly aged forests on soil measures. Coefficients from generalized linear models of each soil measure in similarly aged sites (last disturbed in 2009) with respect to disturbance type, parent rock and Australian soil classification, elevation, slope and 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.

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 composition[33].

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 rec over[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 implications[3].

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 deposits[38]. Further inputs of these key nutrients are a product of self-thinning and litterfall[39], microbial activity[40] and above-ground biological fixation from species such as *Acacia*s, which can dominate post-disturbance regrowth and offset losses in nitrogen within nine years post-disturbance[41]. 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 ecosystems[42]. However, when controlling for successional stage, we found unlogged sites burnt in 2009 consistently had

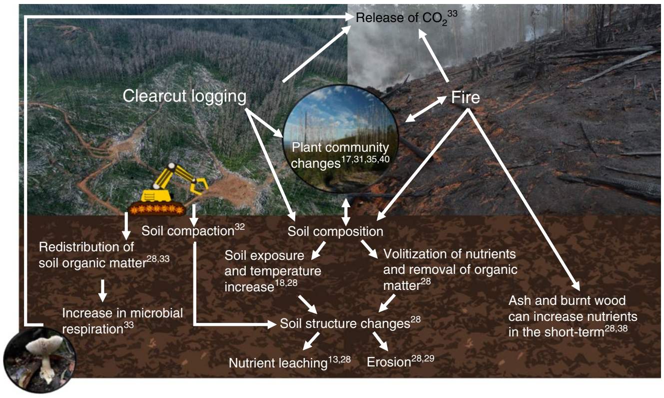

Fig. 4 | Post-disturbance processes and pathways that influence and impact abiotic soil environments. White arrows indicate influential relationships and flow-on effects associated with disturbance in soil environments. For example, fire and clearcut logging can alter the structural integrity of soils, 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

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 years[22]) 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 disturbance[48]. Our findings suggest that below-ground abiotic soil environments may take a similar amount of time to recover.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, statements of data availability and associated accession codes are available at https://doi.org/10.1038/s41561-018-0294-2.

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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 statistical analysis, experimental design and manuscript editing. C.L.S. contributed to manuscript editing.

Competing interests

The authors declare no competing interests.

Additional information

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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 industry[24]. The 2009 fires burnt 53,500 ha of *Eucalyptus regnans* forest, with a large proportion being regrowth from the 1939 fires[23]. This has resulted in an abundant young, dense, fire-prone regrowth landscape with limited structural diversity[26].

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 fire[54]. This practice follows standard clearcut logging methods, with the exception that there is no slash burn if the regeneration from the initial wildfire is adequate[49].

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 Planning[56]. 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 additional, 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 2014[57])[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–February 2017. Using 1 ha long-term monitoring and newly established plots, we measured quadrats of 25 m × 25 m at least 20 m away from the roadside to account for edge effects[58]. 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 (H_2O_2) and one drop of acetic acid and then heated them to remove organic matter. We added an additional 5 ml of H_2O_2 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 content[60]. 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 method[64]. Organic carbon was measured using the Walkley–Black method[65]. The concentrations of soluble salts were estimated by measuring electrical conductivity based on a 1:5 soil/water extract (EC 1:5). pH ($CaCl_2$) 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 $CaCl_2$[61,62]. DTPA-extractable trace elements (Cu, Fe, Mn, Zn) were determined by atomic absorption spectroscopy following extraction with DPTA[61,62]. Boron was measured using inductively couple plasma (ICP) spectroscopy after $CaCl_2$ 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', 'Ground-fern', 'Tree-fern', 'Shrub', 'Tree'), as described by Bowd and colleagues[31], 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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