Received: 24 October 2021 | Accepted: 10 March 2022

DOI: 10.1111/1365-2664.14172

RESEARCH ARTICLE

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

Temporal dynamics in biotic and functional recovery following mining

David J. Eldridge[1] | Ian Oliver[2] | Jeff R. Powell[3] | Josh Dorrough[4] | Yolima Carrillo[3] | Uffe N. Nielsen[3] | Catriona A. Macdonald[3] | Brian Wilson[5] | Christine Fyfe[6] | Apsara Amarasinghe[6] | Laura Kuginis[7] | Travis Peake[8] | Trish Robinson[8] | Belinda Howe[8] | Manuel Delgado-Baquerizo[9,10]

[1]Department of Planning and Environment c/- Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW, Australia; [2]Department of Planning and Environment, Lisarow, NSW, Australia; [3]Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW, Australia; [4]Department of Planning and Environment, Merimbula, NSW, Australia; [5]Department of Planning and Environment c/- School of Environmental and Rural Science, University of New England, Armidale, NSW, Australia; [6]School of Environmental and Rural Science, University of New England, Armidale, NSW, Australia; [7]Department of Planning and Environment, Newcastle, NSW, Australia; [8]Umwelt (Australia) Pty Limited, Teralba, NSW, Australia; [9]Laboratorio de Biodiversidad y Funcionamiento Ecosistémico, Instituto de Recursos Naturales y Agrobiología de Sevilla (IRNAS), Sevilla, Spain and [10]Unidad Asociada CSIC-UPO (BioFun), Universidad Pablo de Olavide, Sevilla, Spain

Correspondence
David J. Eldridge
Email: d.eldridge@unsw.edu.au

Funding information
Australian Coal Research Limited, Grant/Award Number: C27038; British Ecological Society, Grant/Award Number: LRA17\1193, MUSGONET; H2020 Marie Skłodowska-Curie Actions, Grant/Award Number: 702057; NSW Environment Trust, Grant/Award Number: 2017/RD/0095; Environmental Laboratory; University of New England; Junta de Andalucía; Spanish Ministry of Science and Innovation; Department of Planning and Environment; University of New South Wales

Handling Editor: Nubia Marques

Abstract

1. Human-induced disturbance has substantially influenced the structure and function of terrestrial ecosystems globally. However, the extent to which multiple ecosystem functions (multifunctionality) recover following anthropogenic disturbance (ecosystem recovery) remains poorly understood.
2. We report on the first study examining the temporal dynamics in recovery of multifunctionality from 3 to 12 years after the commencement of rehabilitation following mining-induced disturbance, and relate this information to changes in biota. We examined changes in 57 biotic (plants, microbial) and functional (soil) attributes associated with biodiversity and ecosystem services at four open-cut coal mines in eastern Australia.
3. Increasing time since commencement of rehabilitation was associated with increases in overall multifunctionality, soil microbial abundance, plant productivity, plant structure and soil stability, but not nutrient cycling, soil carbon sequestration nor soil nutrients. However, the temporal responses of individual ecosystem properties varied widely, from strongly positive (e.g. litter cover, fine and coarse frass, seed biomass, microbial and fungal biomass) to strongly negative (groundstorey foliage cover). We also show that sites with more developed biota tended to have greater ecosystem multifunctionality. Moreover, recovery of plant litter was closely associated with recovery of most microbial components, soil integrity and soil respiration. Overall, however, rehabilitated

sites still differed from reference ecosystems a decade after commencement of rehabilitation.

4. *Synthesis and applications*. The dominant role of plant and soil biota and litter cover in relation to functions associated with soil respiration, microbial function, soil integrity and C and N pools suggests that recovering biodiversity is a critically important priority in rehabilitation programs. Nonetheless, the slow recovery of most functions after a decade indicates that rehabilitation after open-cut mining is likely to protracted.

KEYWORDS
degradation, ecosystem recovery, functional attributes, mine site rehabilitation, mining, plant structure, soil nutrients

1 | INTRODUCTION

Human-induced disturbance is altering the rates and stocks of multiple structural and functional properties of ecosystem globally (e.g. Doley & Audet, 2013 in the context of mine site rehabilitation). Many of these ecosystem disturbances arise from intensive local activities such as mining that occur within a defined timeframe. Following disturbance, ecosystem properties enter a period of recovery, often supported by a range of restoration or rehabilitation measures designed to accelerate this recovery. Investigating how and why ecosystem properties recover following disturbance is critical if we are to improve the effectiveness of various rehabilitation practices.

A rich literature illustrates how ecosystem properties change in response to anthropogenic disturbance. Yet much less is known about how structural and functional components of ecosystems recover following disturbance. Ecosystem rehabilitation following mining provides an excellent model system in which to investigate how structural and functional recovery are related, and evolve, following disturbance. Above-ground mining operations create considerable physical disturbance involved in resource extraction such as topsoil removal, mixing of the regolith and stockpiling (Bell, 2001; Loch & Orange, 1997; Ngugi & Neldner, 2015). Rehabilitation techniques attempt to restore pre-mining conditions but often create novel ecosystems where biological activity is low, landscapes are unstable, and biotic structure and activity are altered or suppressed (Doley & Audet, 2013; Erskine & Fletcher, 2013; Gould, 2012; Holl, 2002). Examining how different ecosystem components change in these substantially altered and simplified post-mining ecosystems gives us insights into the trajectories of ecosystem development at time-scales over which factors affecting landscapes are likely to develop.

Ecosystem functioning is associated with multiple ecosystem processes that occur simultaneously (multifunctionality). Relatively little is known about the temporal dynamics of the recovery of ecosystem multifunctionality following human-induced disturbances, although recent meta-analyses suggest that when single measures or attributes are used to guide the success of restoration efforts, only a part of lost functions and biodiversity may recover (Moreno-Mateos et al., 2020). Thus, restricting any assessment of recovery to single attributes hinders our ability to examine ecosystem-wide changes in recovery where synergies and trade-offs among different ecosystem attributes combine to provide a whole-of-system view of recovery. Similarly, we have a relatively poor understanding of how the recovery of soil biota, a major driver of ecosystem functioning, evolves after disturbance. A critical consideration is that there are different types of recovery, for example, recovery of plants and microbes (biotic recovery) and recovery of functions (functional recovery). These different components of recovery provide different insights into the nature of the recovery process. Most studies have tended to focus on the recovery of the structure of biotic communities, simply because these are conceptually and often technically easier to assess (König et al., 2017). Structural recovery of the biota describes the extent to which the biological building blocks of ecosystems recover from disturbance, and functional recovery how quickly essential processes and tasks are restored or move towards what we would expect in analogous but undisturbed environments. Structural recovery might describe, for example, how the physical arrangement of tree and shrub cover, or microbial biomass improves over time. These different types of recovery likely vary over different time-scales so that recovery of biotic structure might precede functional recovery or vice versa (Scheffer et al., 2015). For example, post-rehabilitation increases in soil microbial biomass might be expected to occur at a faster rate (greater recovery) than processes that rely on the production of plant material that takes longer (e.g. measures of coarse woody debris). Furthermore, the recovery of these functional processes likely varies with the type of function (Berga et al., 2012). It is critical, therefore, that any studies of the recovery process consider both biotic structure and functional forms of recovery in an assessment of change, allowing us to demonstrate the interconnectedness of different attributes and functions as ecosystems recover from disturbance.

Herein, we describe a study of the temporal dynamics in the recovery of multifunctionality from 3 to 12 years after the commencement of rehabilitation following open-cut mining. Our study includes 57 soil, plant and microbial ecosystem properties associated with biodiversity and ecosystem services. We considered ecosystem properties including the attributes of the structure of the biotic community that are typically regarded as ecosystem building blocks such as microbial richness and biomass, plant and litter cover. Our functional attributes were proxies of processes such as the mineralisation of organic matter, decomposition of organic material and plant biomass production. We expected that the recovery of multiple biotic structural and functional properties would increase with increasing time from the commencement of rehabilitation, but that functional changes would precede structural changes. Our study is important because it can provide important insights into the relative importance of the recovery of different elements of biotic structure and function following major disturbance. This is important for guiding rehabilitation processes following major landscape disturbance and provides important insights into the natural processes of ecosystem development following disturbance.

2 | MATERIALS AND METHODS

2.1 | Study area and mine selection

The study was conducted at four open-cut coal mines (hereafter Mines 1 to 4) across a distance of about 70 km in the Hunter Valley, eastern Australia (−32.25 and −32.74 to 151.97 and 151.47). There were 90 sites in total: 42 that were in various states of rehabilitation (from 3 to 12 years) and 48 reference sites spread across the four mines. Sites were chosen on each of the mines in order to get the widest possible gradient in time since rehabilitation. We attempted to select sites of different ages across the four mines in order to avoid confounding mine location with time since rehabilitation. This was possible for three of the four mines, but due to a lack of suitable rehabilitation sites, older sites tended to be found at Mine 3 only.

Climate in the study area is predominantly temperate, mean annual rainfall ranges from 570 to 700 mm (Bureau of Meteorology, 2019), and is weakly summer dominant with about 50% more rain in the six warmer months (October to March) than the six cooler months. The geomorphology is predominantly Quaternary sandy and clayey calcareous sediments occurring on level to slightly undulating plains with slopes to 1%, often interspersed by areas of aligned west–east trending dunes of low relief (<4 m). The geology is a mixture of Quaternary Colluvium from the Narrabeen Group and the Singleton Coal Measures (comprising sandstones, shales, mudstones). The soils derived from these materials are red and yellow Chromosols and Sodosols (Australian Soil Classification; Isbell, 1996) or Acrisols (World Reference Base; IUSS, 2006) and are characterised by abrupt changes in texture from the loamy and sandy loam surfaces to clay loams and clays at depth.

2.2 | Minesite rehabilitation practices

Rehabilitation practices were similar among the four mines, although there were some differences in plant species sown. In general, prior to mining, topsoil was removed and stockpiled, for short periods of up to 6 months. Mined surfaces and dumps were reshaped, including backfilling of any open-cut voids, and surfaces ripped, to 600 mm deep, depending on slope. Large rocks were then formed into piles and removed. Following surface reshaping, stockpiled topsoil was spread to depths of 100 to 200 mm, and gypsum added, where appropriate, at 5 t/ha to assist in soil remediation. A mixture of tree, shrub, grass and forb seed, representative of the natural vegetation types in the area (Table S1) was direct seeded into the newly formed topsoils, without fertiliser, sometimes using a hydroseeding procedure. Structurally, the natural vegetation communities can be characterised as dry sclerophyll open forest and woodland and were dominated by *Eucalyptus* spp. or *Corymbia maculata* trees with a grassy understorey (Appendix S1).

2.3 | Plant and soil sampling

Within a 20 m by 20 m Biodiversity Assessment Method (BAM; DPIE, 2020) floristics plot we recorded the foliage cover of all native and exotic vascular plant species, the length of logs (>0.1 m diameter), the cover of litter (detached leaves, sticks, bark) and characteristics of the soil surface. Within each BAM plot we also established eight 25 × 25 cm quadrats; four beneath trees and four in the open. All litter was collected from each quadrat and pooled to obtain one tree and one open sample per plot. Litter was air dried and sorted in the laboratory into the following categories: sticks and bark, tree and shrub leaves, grass and forb leaves, coarse frass (>4 mm diameter and <40 mm long), fine frass (litter fragments <4 mm but >2 mm diameter), reproductive material (seeds/seedpods, fruits and flowers), woody material (woodchips and mulch) and vertebrate dung. Following litter collection, a single soil sample (0–5 cm depth) was collected from the centre of each of the eight quadrats and pooled by quadrat type (beneath trees or open) to obtain one composite sample of each type. For each composite sample, a small subsample was immediately separated and frozen (−18°C) and later freeze-dried for DNA- and phospholipid-based microbial analyses.

We used a field-based protocol (Landscape Function Analysis, hereafter 'LFA' Tongway, 1995) to assess the characteristics of the soil surface within the BAM plot. Within the plot we measured 12 surface attributes: surface roughness, crust resistance, crust brokenness, surface stability, surface integrity (cover of uneroded surface), cover of deposited materials, biocrust cover, plant foliage cover, plant basal cover, litter cover, litter origin and the degree of litter incorporation (Appendix S2). These 12 surface features provide a measure of the health of the soil surface. Indices derived from these measures have been shown to be highly correlated with ecosystem functions related to soil stability, nutrient cycling and infiltration (Maestre & Puche, 2009; Eldridge et al., 2019; Appendix S2).

2.4 | Soil chemical and microbial analyses

Extractable phosphorus (Colwell-P) and pH (1:5 soil water extract) were determined following standard procedures (Rayment & Lyons, 2011). Total nitrogen and soil carbon fractions (total organic carbon, particulate organic carbon, humic organic carbon, resistant organic carbon) were estimated using mid-infrared (MIR) spectroscopy techniques (Baldock et al., 2013; Baldock et al., 2014; Appendix S3).

DNA was extracted from 0.25 g of freeze-dried soil using the DNeasy PowerSoil Kit (Qiagen) according to the manufacturer's instructions. Amplicons targeting the bacterial 16S rRNA gene (341F-805R; Herlemann et al., 2011) and the fungal ITS region (FITS7-ITS4R; Ihrmark et al., 2012) were sequenced at the Ramaciotti Centre for Genomics, University of New South Wales (Sydney, Australia), on the Illumina MiSeq platform (Appendix S4). Raw sequencing data can be accessed at the NCBI Sequence Read Archive under BioProject PRJNA817003. DNA sequence processing methods, including assignment of DNA sequencing reads to operational taxonomic units (OTUs) are described in Appendix S4. The OTU abundance tables were rarefied to an even number of sequences per sample (6,677 and 9,073 sequences for bacteria and fungi, respectively; the minimum number of sequences observed). Alpha diversity metrics were then calculated using the 'VEGAN' package (Oksanen et al., 2019) in R statistical software.

Three methods were used to derive proxies of microbial activity: (a) potential soil enzyme activity, (b) soil respiration and (c) phospholipid-derived fatty acids (which is a surrogate of active microbial biomass). We measured the potential activity of six enzymes (Appendix S5, Table S5) as proxies for carbon, nitrogen and phosphorus degradation using fluorometry with, as described in Bell et al. (2013) with some modifications (Appendix S5). The MicroResp™ technique was used to determine substrate-induced respiration rates using seven substrates: fructose, glucose, maltose, raffinose, sucrose, threonine and xylose. Basal respiration was assessed with filtered sterile deionised water. Thirty microlitres each of filtered sterile substrate and deionised water were added to the pre-incubated soil in deep-well plates. Absorbance was measured at 570 nm immediately before and after the 24 hr incubation period using a microplate reader (SpectraMax M2^e) (Burton et al., 2007; Campbell et al., 2003). The rate of CO_2 respiration per gram of dry soil was calculated according to the formula as described in MicroResp™ manual (MicroResp™, James Hutton Ltd). Microbial phospholipid fatty acids (PLFAs) were assessed as indicators of total microbial biomass in soil and the relative abundance of general microbial functional groups such as bacteria (gram negative, gram positive), Actinobacteria, fungi, mycorrhizae, as well as of protists, which are soil microfauna (Appendix S6).

2.5 | Statistical analyses

Here we report on the recovery of 57 attributes described above for 90 sites (Appendix S7). Of the 90 sites, 42 ranged in time since the commencement of rehabilitation treatments from 3 to 12 years (hereafter 'Rehabilitated'), and 48 were largely intact communities that may have been altered slightly but represent highly functional (hereafter 'Reference') sites that showed various levels of disturbance or change typical of the remaining remnants for these vegetation communities (Table S1.2). Our attributes were classified as either biotic structural attributes (n = 22), that is, they represent biological components such as the plant cover or microbes, or functional (n = 35), that is, they contributed to resource and/or energy flows, for example, soil respiration (Table S7.1). We also had information on pH, which we used to explore downstream relationships with microbial biomass and diversity. Prior to statistical analyses, we scaled all quadrat-level data to the plot level using the relative cover of trees at each site.

First we standardised (z-transformed) the value of each attribute, for each of the 42 rehabilitation sites, and arranged the 57 biotic/functional attributes into seven categories (soil carbon sequestration, decomposition, microbes, plant productivity, plant structure, soil stability and soil nutrients, Appendix S7). The multifunctionality values for the seven categories were calculated as the mean standardised value for those attributes within a given category. The multifunctionality approach allows us to compare attributes that might vary markedly in their mean and range by bringing the value of all attributes to a common scale with a mean = 0 and SD = 1. For example, the soil stability multifunctionality index was calculated as the mean standardised values of six attributes (soil brokenness, deposited materials, soil integrity, surface resistance, soil surface roughness and crust stability). This is possible because increasing values of each attribute represent increasing function. We then explored whether the multifunctionality index of the seven categories changed in relation to time since rehabilitation.

Next, we allocated the seven categories to either a biotic or functional category and averaged the functional attributes (soil carbon, decomposition, nutrients, plant productivity and soil stability) to form an average value of ecosystem multifunctionality and did the same for the microbes and plant structure to create an average measure of biotic structure. This averaging is possible because the values are standardised and therefore bounded. The relationship between biotic structure and multifunctionality allowed us to explore whether rehabilitation of the average functional effect was associated with changes in the average biotic effect.

We then used a relative interaction intensity (RII) index (Armas et al., 2004) to explore how the raw values of the 57 individual attributes changed with time since restoration after accounting for values at their relevant reference (control) site. The RII index is calculated as $(X_R - X_C)/(X_R + X_C)$, where X is the value of the attribute, R = Rehabilitated and C = Control (Reference). This relativisation process results in an index that is bounded by −1 and 1, with RII values >0 indicating relatively greater values in rehabilitated sites. The control (reference) sites used in this index were those from the same mine. The significance of any relationships between biota structure and multifunctionality, time since commencement of rehabilitation or RII and any individual attributes was tested using linear and nonlinear (quadratic) regressions, with mine identity as a random effect. Akaike's information criterion (AIC) was used to decide the model that provided the best fit in each case. We then visualised Pearson's correlation, among the 22 relativised biotic attributes and the 35 relativised functional attributes in a heat map.

3 | RESULTS

3.1 | Coupled recovery of biota and ecosystem functions

Our study provides evidence that increases in biotic structure and ecosystem multifunctionality are significantly positively related, and tend to increase with increasing time since commencement of rehabilitation (Figure 1). We also detected evidence of coupling among certain plant and microbial biota and specific aspects of ecosystem functioning (Appendix S8, Figure S8.1). For example, the recovery of carbon pools, biomass of fine litter fractions (e.g. frass and seeds) and soil respiration was associated with microbial recovery, particularly bacterial biomass and plant litter cover (Figure S8.1). The recovery of arbuscular mycorrhizal fungal (AMF) biomass was strongly positively associated with recovery of all carbon sources. Despite the many weak negative correlations among different attributes, few were strongly negative. Notable, however, was that the recovery of groundstorey plant cover was negatively correlated with the recovery of coarse litter fractions. Similarly, a greater degree of soil surface cracking (surface brokenness) and surface roughness was negatively correlated with most measures of biotic recovery, except groundstorey plant cover (Figure S8.1).

3.2 | Temporal dynamics in biota structure and ecosystem functioning after disturbance

Overall multifunctionality tended to increase with increasing time since commencement of rehabilitation (Figure 2a). For individual ecosystem categories, increasing time since rehabilitation was associated with linear increases in decomposition (Figure 2b), microbial biomass (Figure 2c), plant productivity (Figure 2d) and plant structure (Figure 2e), but there were no significant changes in soil stability, carbon or nutrient pools (Figures 2f–h). We also found some strong positive relationships among our biotic measures. In particular, the recovery of different measures of microbial biomass (total microbial biomass, Gram+ biomass, bacterial biomass and AMF biomass) was strongly positively correlated with increases in both the cover ($p < 0.002$, $R^2 = 0.19–0.24$, $n = 42$) and incorporation ($p < 0.002$, $R^2 = 0.26–0.40$, $n = 42$) of litter (Figure S8.2).

3.3 | Individual changes in ecosystem properties and biota

We also examined changes in the post-mining recovery of multiple, individual ecosystem properties and found a wide range of responses from strongly positive to strongly negative changes in ecosystem recovery with time (Figures 3–5). For example, there were strong positive temporal relationships for the recovery of native plant cover, litter cover, litter origin, litter incorporation and biocrust cover (Figure 3), the biomass of most plant components (Figure 4) and measures of bacterial and fungal biomass (Figure 5). The only significant negative relationship was related to the recovery of groundstorey plant foliage cover (Figure 3) and its biomass (groundstorey leaves; Figure 4). There were no significant changes in most soil nutrients, soil carbon or measures of soil stability (Figure S8.3) and measures of decomposition (respiration and soil enzymes (Figure S8.4) with time since rehabilitation.

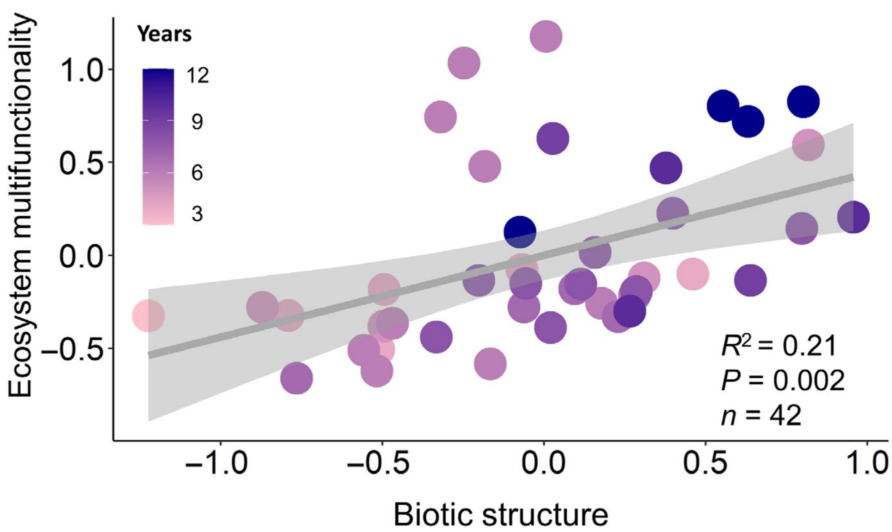

FIGURE 1 Relationship between biota and ecosystem multifunctionality for 42 sites ranging in 3–12 years since commencement of rehabilitation. The multifunctionality value for biota is calculated as the average standardised values for the 11 microbial categories and the 11 plant structural categories

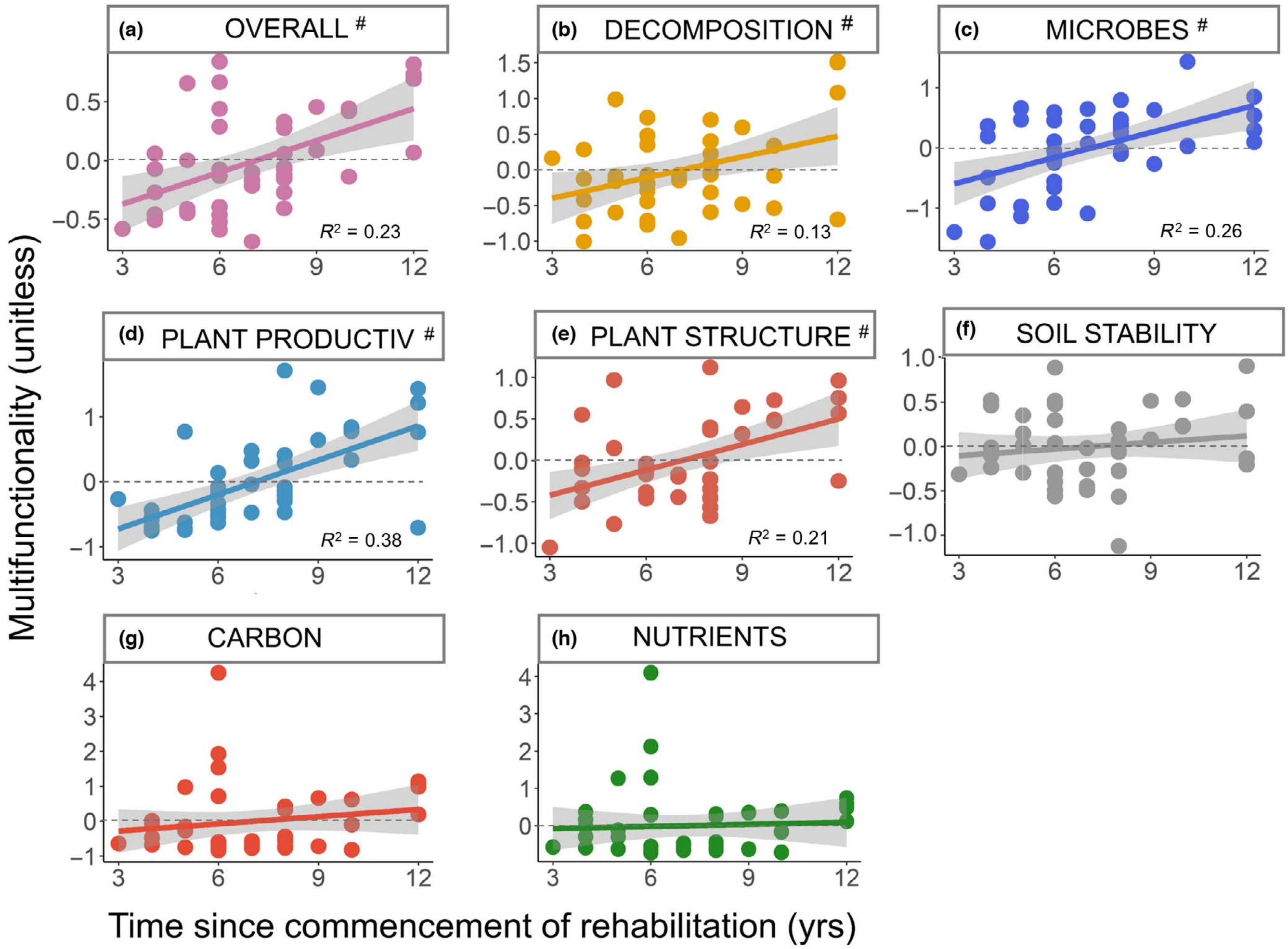

FIGURE 2 Relationship between (a) average multifunctionality, and multifunctionality of (b) decomposition, (c) microbial biota, (d) plant productivity, (e) plant structure, (f) soil stability, (g) soil carbon sequestration and (h) nutrients, in relation to time since the commencement of rehabilitation. # indicates linear model significant at $p < 0.05$. Points refer to 42 sites ranging in 3–12 years since commencement of rehabilitation

4 | DISCUSSION

Our study provides novel insights into the temporal dynamics of ecosystem recovery following human-induced disturbance, using mining as a model system. We found that the recovery of multifunctionality increased with time since the commencement of rehabilitation (Figure 2), but ecosystem properties showed contrasting rates of recovery. These results apply specifically to rehabilitation in a temperate environment following open-cut mining associated with extensive landscape disturbance, surface reshaping, ripping and topsoil amendment. Furthermore, the relationships between the recovery of biotic structure and that of functional components, and time since the commencement of restoration, were always positive or neutral, but there was no evidence that recovery of the biota structure preceded functional recovery. Even so, our analyses, using the relative interaction index, permitted direct comparisons with reference ecosystems, and suggested that our ecosystems are still markedly different from the reference state, at least in the initial 6–9 years following commencement of rehabilitation. Overall, our results demonstrate the complex changes in biotic and functional measures of recovery using mining as a suitable model. By linking multiple biota and multifunctional approaches, they illustrate the complex trajectories of change in biotic and abiotic ecosystem variables as they recover from substantial mining-induced disturbance.

4.1 | Recovery of ecosystem structure and function increases with rehabilitation age

Recovery of both biotic structure and function increased with time since commencement of rehabilitation, consistent with prediction. Despite the wide spectrum of functional and biotic attributes (Appendix S7) we still found a positive relationship between the structural recovery of biotic structure and its function. However, this significant correlation was relatively weak (R^2 = 0.21), with early and mid-aged sites showing a wide range of both biotic structure and multifunctionality, suggesting the importance of other unmeasured site-specific effects, and indicating that recovery of

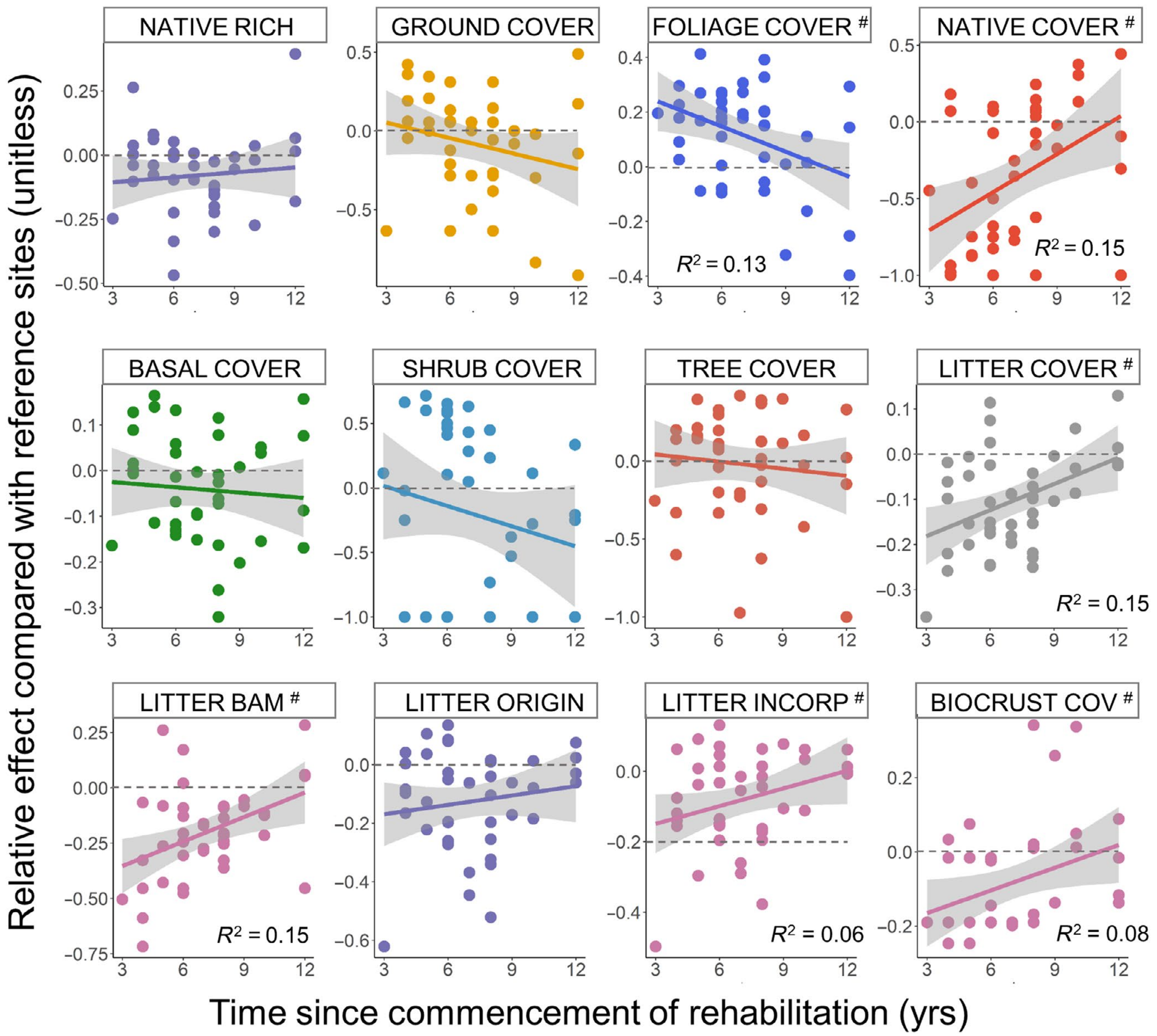

FIGURE 3 Changes in the relative effect of rehabilitated compared with the reference sites (RII) in relation to time since commencement of rehabilitation for plant cover and litter components. # indicates significant linear relationship at $p < 0.05$. Points refer to 42 sites ranging in 3–12 years since commencement of rehabilitation

one does not necessarily lead to recovery of the other. Apart from soil stability, carbon and nutrients, all categories of multifunctionality increased over time, and the response was best represented as a linear relationship. The strongest effects for functions were for plant productivity and plant structure. Individual attributes associated with the production of plant biomass (all but coarse woody debris, Figure 4) and litter cover and native plant cover (Figure 3) showed the strongest positive response to restoration age. Plant productivity reflects different biomass compartments associated with woody and groundstorey biomass, and closely parallels that of plant structure. A relatively small number of attributes responded positively to rehabilitation (i.e. rehabilitation winners: microbes, plant productivity, plant structure, decomposition) but a larger suite were rehabilitation losers (e.g. soil nutrients, carbon, soil stability) 12 years after gross landscape disturbance associated with open-cut coal mining.

Mine restoration often focusses initially on seeding and planting in order to stabilise overburden and reduce sediment movement (Ward & Koch, 1995; Feng et al., 2019). We acknowledge that similar seeding and planting practices on mines located on different substrates or under different environmental conditions will likely result in different rehabilitation outcomes, and part of these effects could have been due to different mixes or sown species. Significantly more native plant species were used in the seeding mixtures at Mine 3 (19 ± 1.3 species, $M \pm SE$) than the other mines (nine species; $F_{3,44} = 12.03$, $p = 0.001$), but this was unrelated to the number of species sown during the rehabilitation process (Table S1). Direct seeding and planting of grasses and woody

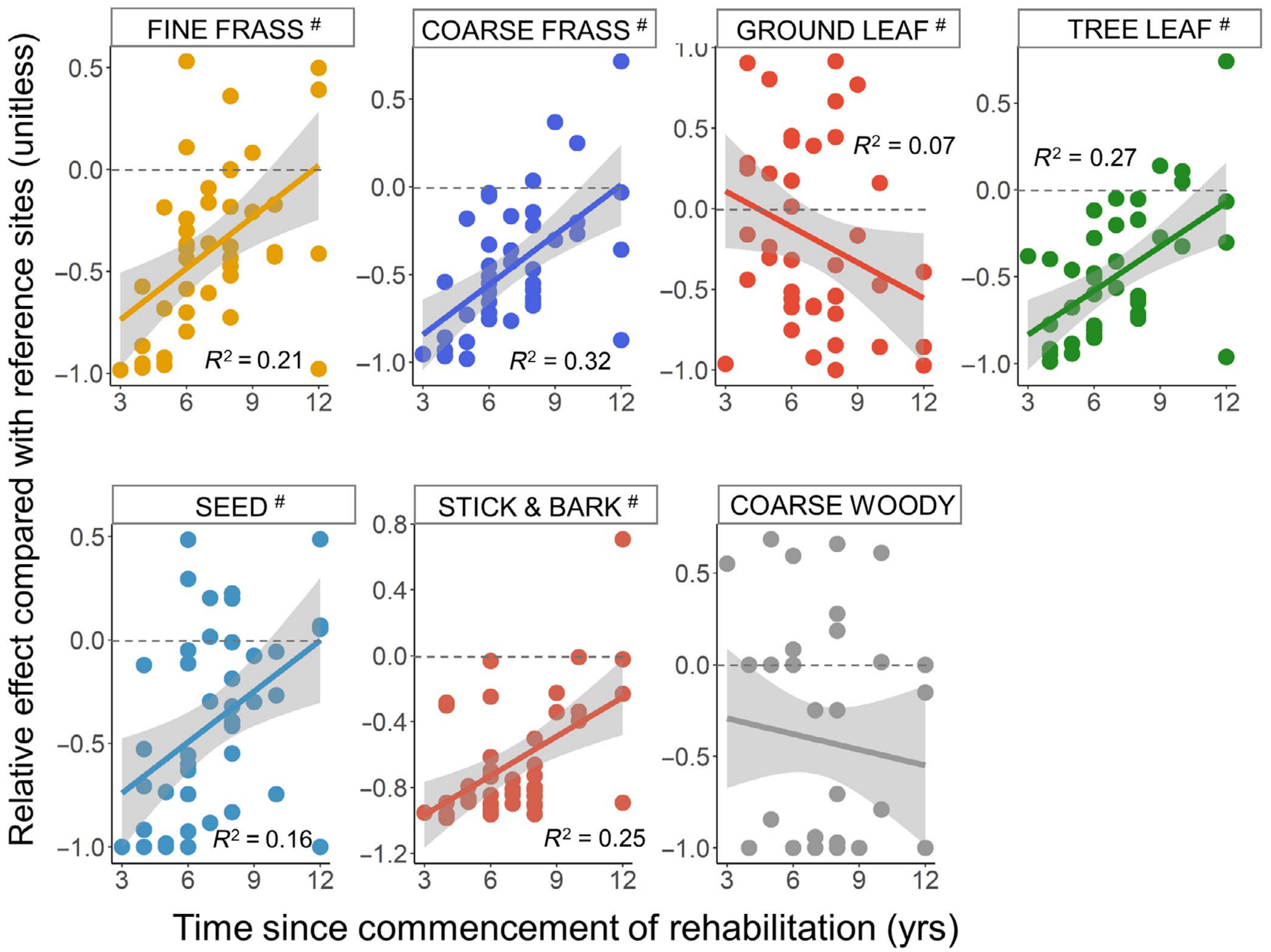

FIGURE 4 Changes in the relative effect of rehabilitated compared with the reference sites (RII) in relation to time since commencement of rehabilitation for different plant biomass components. # indicates significant linear relationship at $p < 0.05$. Points refer to 42 sites ranging in 3–12 years since commencement of rehabilitation

plants (e.g. eucalypts, acacias) for mine restoration results in rapid recovery of biotic structure (Grant, 2006), and increases in organic material (leaves, reproductive structures, woody material) associated with rapid vegetative growth (plant productivity function). These changes could help explain the rapid recovery in microbial biomass and measures of litter cover. Symbiotic nitrogen fixation by *Acacia* spp., which are early pioneering species in minesite restoration (Jasper, 2007), has marked effects on soil microbial communities and nutrient availability (Banning et al., 2011; Revillini et al., 2016). Reduced groundstorey plant cover might be responsible for the generally poor temporal response of different carbon fractions to rehabilitation. Furthermore, an extensive cover and incorporation of litter could immobilise nitrogen in microbial biomass, although this was not reflected in lower levels of total nitrogen. Differences will likely depend on whether the community is dominated by woody plants, which varied markedly among different mine sites, and therefore recalcitrant forms of carbon, or herbaceous material, where decomposition rates are much greater (Fornara & Tilman, 2008).

The accumulation of plant material is critically important for the maintenance of soil functions and services following mining-induced disturbance. While there were no clear relationships among recovery of functions and measures of the standing plant community (e.g. richness, native plant cover), we found strong relationships for different litter components. Specifically, litter cover and whether it is local or transported from elsewhere (litter origin) were strongly positively correlated with measures of soil respiration, the four carbon fractions, and to a lesser extent, total nitrogen (Figure S8.1). Strong links between litter and soil multifunctionality are not unexpected. Litter has been shown to be a strong predictor of global dryland soil multifunctionality, related specifically to carbon, nitrogen and phosphorus cycling and storage (Eldridge et al., 2019). Surface litter can reduce the loss of soil moisture by moderating variability in soil temperature (e.g. Hobbie, 2015; Montana et al., 1988; Wallwork et al., 1985). Litter also improves habitat for litter-active micro-microfauna (Cepeda-Pizarro & Whitford, 1989), thus resulting in greater soil multifunctionality (Eldridge et al., 2019).

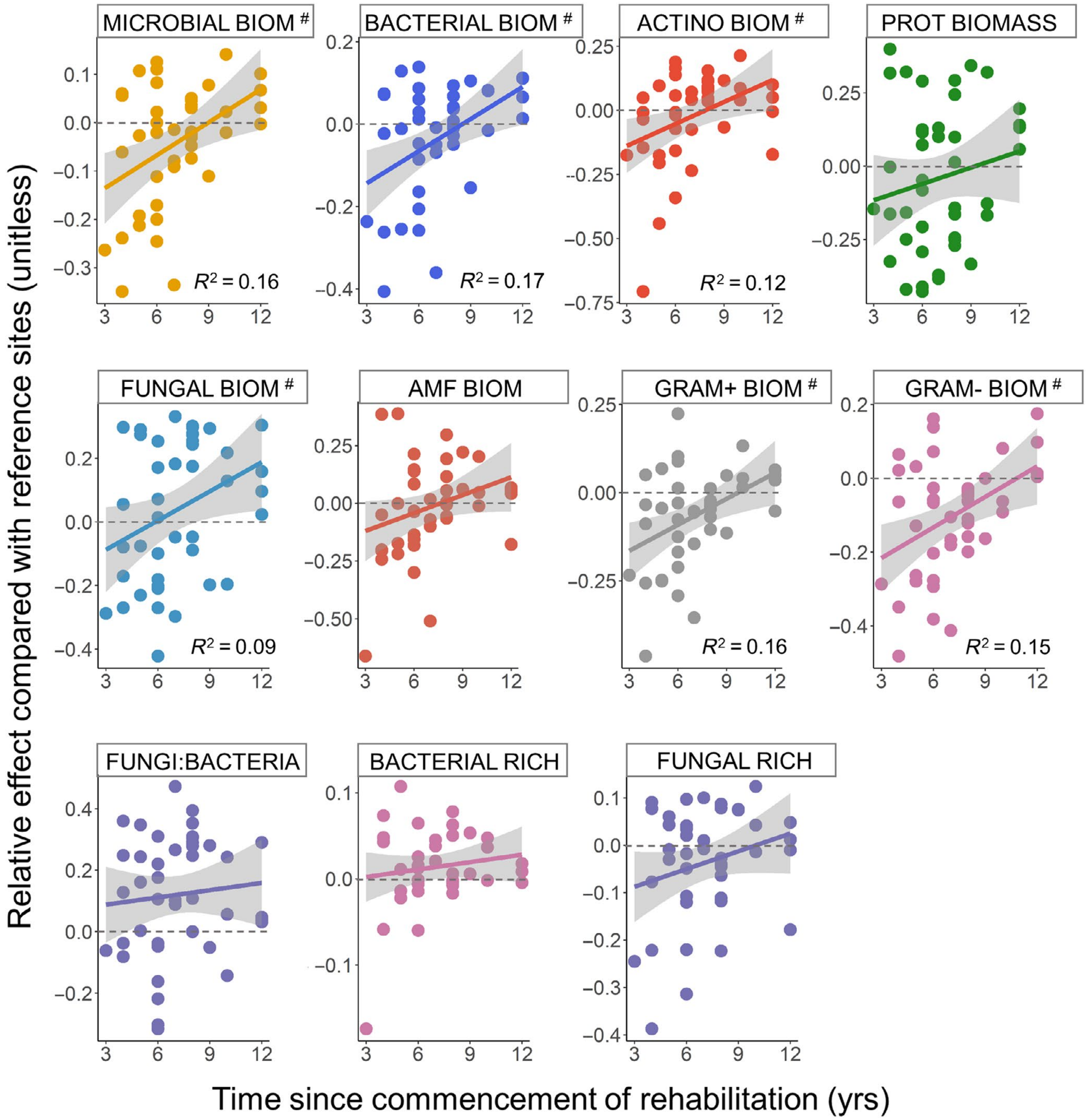

FIGURE 5 Changes in the relative effect of rehabilitated compared with the reference sites (RII) in relation to time since commencement of rehabilitation for different microbial biomass and diversity components. BIOM = biomass, # indicates significant linear relationship at $p < 0.05$. Points refer to 42 sites ranging in 3–12 years since commencement of rehabilitation

Surface integrity, a measure of the stability of the soil surface and expressed as the cover of uneroded soil surface, would be expected to increase with increasing age of rehabilitation, in line with studies of open-cut coal mines (Li et al., 2020). However, despite the upward trend, we failed to detect significant increases in integrity with rehabilitation (Figure S8.3). This is likely due to the high degree of spatial variability across the four mine sites, particularly at intermediate times since rehabilitation (Figure S8.3). We did, however, detect strong positive correlations between soil integrity and the cover and origin of litter (Pearson's $r = 0.66–0.72$, $p < 0.001$; Figure S8.1) consistent with the notion that litter increases the capacity of the surface to resist raindrop impact (Li et al., 2014) and increases the threshold wind speed required to mobilise particles, thereby resulting in greater soil integrity. Strong correlations between soil integrity and the biomass of Gram+ ($r = 0.52$, $p < 0.001$) and Gram− bacteria ($r = 0.40$, $p < 0.001$), microbial biomass ($r = 0.43$, $p = 0.004$) and AMF biomass ($r = 0.42$,

p = 0.006) are likely related to increases in soil aggregate structure and thus microbial habitat, reinforcing the importance of microbes for stabilising surface aggregates (Rillig et al., 2017).

Apart from components of microbial biomass, very few of the individual attributes achieved levels equivalent to those of the reference sites within 12 years of rehabilitation. Microbial biomass is known to decline rapidly after mining-induced disturbance but can increase relatively quickly, consistent with the results of chronosequence studies of reclaimed mine soil (e.g. Sourkova et al., 2005). The magnitude of increase is related to substrate (litter) quantity and quality (Insam & Domsch, 1988); hence the strong positive relationships between cover of litter and microbes (0.50–0.57 for microbial biomass, and G+ bacteria). Our models of the relatively rapid recovery of microbial biomass suggest that they could reach levels equivalent to reference soils by about 9 years after commencement of rehabilitation (Figure S8.2).

4.2 | Limited recovery of biotic and functional attributes relative to reference sites

Most individual attributes showed either no significant change, that is, they either increased but failed to exceed values at the reference sites, or showed a non-significant downward trend. Two variables, however, foliage cover and the biomass of groundstorey leaves, exhibited significant declines whereas six of the 11 measures of microbial biomass and diversity attained levels greater than reference. These changes in microbial diversity and biomass could be related to soil pH. Soil pH is a strong driver of soil microbial community processes (Fierer et al., 2007; Glassman et al., 2017), particularly in topsoils (Waymouth et al., 2020). The mean value of soil pH across the chronosequence was significantly greater at rehabilitated (6.85 ± 0.13; $M \pm SE$) than reference (5.95 ± 0.06) sites. Increased soil pH under rehabilitation would favour fungal over bacterial decomposition (Angel et al., 2013; Tedersoo et al., 2014), which accords with both the greater fungal biomass with time since rehabilitation (Figure S8.2) and the increase in AMF biomass with increasing pH (Figure S8.5). We also found that fungal diversity was greater in soils at reference (1,088 ± 134, $M \pm SD$) than rehabilitated (974 ± 210) sites, unlike studies from other mine site restoration studies (Ngugi et al., 2019). Fungi are critically important in the restoration process because they recycle organic matter, improve soil structure, ameliorate metal tolerance in plants, and enhance water holding capacity (Delgado-Baquerizo et al., 2019; Ngugi et al., 2019). Future work needs to further investigate how to trigger the restoration of soil microbial diversity, a major driver of ecosystem functioning, to help in achieving maximum levels of ecosystem recovery after disturbance.

5 | CONCLUSIONS

Our study identifies the preeminent role of microbial and plant biota, and its links with various plant and microbial compartments, in driving functions related to soil respiration, microbial function, soil integrity, soil carbon and to a lesser extent, nitrogen pools. This suggests that the selection of plant species for reseeding during rehabilitation is critical for promoting important ecosystem functions. A richer seed mix during seeding would have many rehabilitation advantages such as more varied litter with different leaf chemistries and decay times (e.g. C:N ratios, phenol, cellulose and lignin concentrations; Bardgett et al., 1998) and therefore a more varied substrate quality capable of supporting a richer microbial community (e.g. Osanai et al., 2013). A greater emphasis on plants functional type might mean using techniques combining both soil stabilisation, and the addition of organic matter and seeds (e.g. hydromulching, O'Brien et al., 2018), and using local species that are adapted to local conditions and indigenous microbial species. Nonetheless, the fact that many functions failed to establish levels comparable to reference sites even 12 years after the commencement of rehabilitation, indicates that the process of rehabilitation after gross landscape changes associated with open-cut coal mining is likely to protracted.

ACKNOWLEDGEMENTS

This project was supported by funding from the New South Wales (NSW) Department of Planning and Environment (DPIE). T.P., T.R. and B.H. were supported by Umwelt (Australia) Pty. Ltd. and The Australian Coal Industry's Research Program (grant C27038), B.W. by the NSW Environment Trust (2017/RD/0095). M.D-B. is supported by a Ramón y Cajal grant (RYC2018-025483-I), a project from the Spanish Ministry of Science and Innovation (PID2020-115813RA-I00), and a project PAIDI 2020 from the Junta de Andalucía (P20_00879). We thank Carmen Castor (University of Newcastle) for field support, Laura Castaneda-Gomez, Giles Ross, Chaturika Daulagala (Western Sydney University), the Environmental Analytical Research and Carbon Laboratories (University of New England) and the DPIE Soil and Water Environmental Laboratory (Yanco) for laboratory support. Open access publishing facilitated by University of New South Wales, as part of the Wiley - University of New South Wales agreement via the Council of Australian University Librarians.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

T.P., T.R., B.H., I.O. and J.D. designed the study on which this manuscript is based; T.R., B.H., L.K. and I.O. collected field data and Y.C., U.N.N., J.R.P., C.A.M., B.W., C.F. and A.A. conducted soil chemical and microbial analyses; D.J.E. and M.D-B. wrote the first draft of the manuscript and all authors contributed to the final version.

DATA AVAILABILITY STATEMENT

Data available at Dryad Digital Repository https://doi.org/10.5061/dryad.4xgxd25c4 (Eldridge et al., 2022).

ORCID

David J. Eldridge https://orcid.org/0000-0002-2191-486X
Yolima Carrillo https://orcid.org/0000-0002-8726-4601
Manuel Delgado-Baquerizo https://orcid.org/0000-0002-6499-576X

REFERENCES

Angel, R., Pasternak, Z., Soares, M. I. M., Conrad, R., & Gillor, O. (2013). Active and total prokaryotic communities in dryland soils. *FEMS Microbiology Ecology*, *86*, 130–138.

Armas, C., Ordialas, R., & Pugnaire, F. I. (2004). Measuring plant interactions: A new comparative index. *Ecology*, *85*, 2682–2686.

Baldock, J., Sanderman, J., Macdonald, L., Puccini, A., Hawke, B., Szarvas, S., & McGowan, J. (2013). Quantifying the allocation of soil organic carbon to biologically significant fractions. *Soil Research*, *51*, 561–576.

Baldock, J. A., Hawke, B., Sanderman, J., & Macdonald, L. M. (2014). Predicting contents of carbon and its component fractions in Australian soils from diffuse reflectance mid-infrared spectra. *Soil Research*, *51*, 577–595.

Banning, N. C., Gleeson, D. B., Grigg, A. H., Grant, C. D., Andersen, G. L., Brodie, E. L., & Murphy, B. W. (2011). Soil microbial community successional patterns during forest ecosystem restoration. *Applied and Environmental Microbiology*, *77*, 6158–6164.

Bardgett, R. D., Wardle, D. A., & Yeates, G. W. (1998). Linking above-ground and below-ground interactions: How plant responses to foliar herbivory influence soil organisms. *Soil Biology Biochemistry*, *30*, 1867–1878.

Bell, C. W., Fricks, B. E., Rocca, J. D., Steinweg, J. M., McMahon, S. K., & Wallenstein, M. D. (2013). High-throughput fluorometric measurement of potential soil extracellular enzyme activities. *JoVE—Journal of Visualized Experimentation*, *81*, 50961.

Bell, L. C. (2001). Establishment of native ecosystems after mining—Australian experience across diverse biogeographic zones. *Ecological Engineering*, *17*, 179–186.

Berga, M., Székely, A. J., & Langenheder, S. (2012). Effects of disturbance intensity and frequency on bacterial community composition and function. *PLoS ONE*, *7*(5), e36959.

Bureau of Meteorology, Australian Government. (2019). *Weather and climate data*. Retrieved from http://www.bom.gov.au/climate/averages/tables/cw_007176.shtml

Burton, E., Yakandawala, N., LoVetri, K., & Madhyastha, M. S. (2007). A microplate spectrofluorometric assay for bacterial biofilms. *Journal of Industrial Microbiology and Biotechnology*, *34*, 1–4.

Campbell, C. D., Chapman, S. J., Cameron, C. M., Davidson, M. S., & Potts, J. M. (2003). A rapid microtiter plate method to measure carbon dioxide evolved from carbon substrate amendments so as to determine the physiological profiles of soil microbial communities by using whole soil. *Applied and Environmental Microbiology*, *69*, 3593–3599.

Cepeda-Pizarro, J. G., & Whitford, W. G. (1989). Species abundance distribution patterns of microarthropods in surface decomposing leaf-litter and mineral soil on a desert watershed. *Pedobiologia*, *33*, 254–268.

Delgado-Baquerizo, M., Bardgett, R. D., Vitousek, P. M., Maestre, F. T., Williams, M. A., Eldridge, D. J., Lambers, H., Neuhauser, S., Gallardo, A., García-Velázquez, L., Sala, O. E., Abadesm, S. R., Alfaro, F. M., Berhe, A. A., Bowker, M. A., Currier, C. M., Cutler, N. A., Hart, S. C., Hayes, P. E., … Fierer, N. (2019). Changes in below-ground biodiversity during ecosystem development. *Proceedings of the National Academy of Sciences of the United States of America*, *116*, 6891–6896.

Doley, D., & Audet, P. (2013). Adopting novel ecosystems as suitable rehabilitation alternatives for former mine sites. *Ecological Processes*, *2*, 22. https://doi.org/10.1186/2192-1709-2-22

DPIE. (2020). *Biodiversity Assessment Method Revised*. Department of Planning.

Eldridge, D. J., Delgado-Baquerizo, M., Quero, J. L., Ochoa, V., Gozalo, B., García-Palacios, P., García-Gómez, M., Prina, A., Bowker, M.A., Bran, D.E., Castro, I., Cea, A., Derak, M., Espinosa, C.I., Florentino, I., Gaitán, J.J., Gatica, G., Gómez-González, S., Ghiloufi, W., … Maestre, F.T. (2019). Surface indicators are correlated with soil multifunctionality in global drylands. *Journal of Applied Ecology*, *57*, 424–435.

Eldridge, D. J., Oliver, I., Powell, J. R., Dorrough, J., Carrillo, Y., Nielsen, U. N., Macdonald, C. A., Wilson, B., Fyfe, C., Amarasinghe, A., Kuginis, L., Peake, T., Robinson, T., Howe, B., & Delgado-Baquerizo, M. (2022). Data from: Temporal dynamics in biotic and functional recovery following mining. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.4xgxd25c4

Erskine, P. D., & Fletcher, A. T. (2013). Novel ecosystems created by coal mines in central Queensland's Bowen Basin. *Ecological Processes*, *2*, 33. https://doi.org/10.1186/2192-1709-2-33

Feng, Y., Wang, J., Bai, Z., & Reading, L. (2019). Effects of surface coal mining and land reclamation on soil properties: A review. *Earth-Science Reviews*, *191*, 12–25.

Fierer, N., Bradford, M. A., & Jackson, R. B. (2007). Toward an ecological classification of soil bacteria. *Ecology*, *88*, 1354–1364.

Fornara, D. A., & Tilman, D. (2008). Plant functional composition influences rates of soil carbon and nitrogen accumulation. *Journal of Ecology*, *96*, 314–322.

Glassman, S. I., Wang, I. J., & Bruns, T. D. (2017). Environmental filtering by pH and soil nutrients drives community assembly in fungi at fine spatial scales. *Molecular Ecology*, *26*, 6960–6973.

Gould, S. F. (2012). Comparison of post-mining rehabilitation with reference ecosystems in monsoonal eucalypt woodlands, Northern Australia. *Restoration Ecology*, *20*, 250–259.

Grant, C. D. (2006). State-and-transition successional model for bauxite mining rehabilitation in the jarrah forest of Western Australia. *Restoration Ecology*, *14*, 28–37.

Herlemann, D. P. R., Labrenz, L., Jurgens, K., Bertilsson, S., Waniek, J. J., & Andersson, A. F. (2011). Transitions in bacterial communities along the 2000 km salinity gradient of the Baltic Sea. *The ISME Journal*, *5*, 1571–1579.

Hobbie, S. E. (2015). Plant species effects on nutrient cycling: Revisiting litter feedbacks. *Trends in Ecology & Evolution*, *30*, 357–363.

Holl, K. (2002). Long-term vegetation recovery on reclaimed coal surface mines in the eastern USA. *Journal of Applied Ecology*, *39*, 960–970.

Ihrmark, K., Bodeker, I. T. M., Cruz-Martinez, K., Friberg, H., Kubartova, A., Schenck, J., Strid, Y., Stenlid, J., Brandstrom-Durling, M., Clemmensen, K. E., & Lindahl, B. D. (2012) New primers to amplify the fungal ITS2 region—Evaluation by 454-sequencing of artificial and natural communities. *FEMS Microbiology Ecology 82*, 666–677

Insam, H., & Domsch, K. H. (1988). Relationship between soil organic carbon and microbial biomass on chronosequences of reclamation sites. *Microbial Ecology*, *15*, 177–188.

Isbell, R. F. (1996). *The Australian soil classification*. CSIRO Publishing.

IUSS Working Group W. R. B. (2006). *World reference base for soil resources 2006*. World Soil Resources Reports No. 103. FAO, Rome.

Jasper, D. A. (2007). Beneficial soil microorganisms of the jarrah forest and their recovery in bauxite mine restoration in Southwestern Australia. *Restoration Ecology*, *15*, S74–S84.

König, S., Worrich, A., Centler, F., Wick, L. Y., Miltner, A., Kästner, M., Thullner, M., Frank, K., & Banitz, T. (2017). Modelling functional resilience of microbial ecosystems: Analysis of governing processes. *Environmental Modelling Software*, *89*, 31–39.

Li, X., Lei, S., Liu, F., & Wang, W. (2020). Analysis of plant and soil restoration process and degree of refuse dumps in open-pit coal mining areas. *International Journal of Environmental Research and Public Health*, *17*, 1975. https://doi.org/10.3390/ijerph17061975

Li, X., Niu, J., & Xie, B. (2014). The effect of leaf litter cover on surface runoff and soil erosion in Northern China. *PLoS ONE*, *9*, e107789.

Loch, R. J., & Orange, D. N. (1997). Changes in some properties of topsoil at Tarong Coal—Meandu Mine coalmine with time since rehabilitation. *Australian Journal of Soil Research*, *35*, 777–784.

Maestre, F. T., & Puche, M. D. (2009). Indices based on surface indicators predict soil functioning in Mediterranean semi-arid steppes. *Applied Soil Ecology*, *41*, 342–350.

Montana, C., Ezcurra, E., Carrillo, A., & Delhoume, J. P. (1988). The decomposition of litter in grasslands of northern Mexico: A comparison between arid and non-arid environments. *Journal of Arid Environments*, *14*, 55–60.

Moreno-Mateos, D., Alberdi, A., Morriën, E., van der Putten, W. H., Rodríguez-Uña, A., & Montoya, D. (2020). The long-term restoration of ecosystem complexity. *Nature Ecology & Evolution*, *4*, 676–685. https://doi.org/10.1038/s41559-020-1154-1

Ngugi, M. R., Fechner, N., Neldner, J., & Dennis, P. G. (2019). Successional dynamics of soil fungal diversity along a restoration chronosequence post-coal mining. *Restoration Ecology*, *28*, 543–552.

Ngugi, M. R., & Neldner, J. (2015). Two-tiered methodology for the assessment and projection of mine vegetation rehabilitation against mine closure restoration goal. *Ecological Management and Restoration*, *16*, 215–223.

O'Brien, P. L., Acharya, U., Alghamdi, R., Niaghi, A. R., Sanyal, D., Wirtz, J., Daigh, A. L. M., & DeSutter, T. M. (2018). Hydromulch application to bare soil: Soil temperature dynamics and evaporative fluxes. *Agricultural & Environmental Letters*, *3*, 180014. https://doi.org/10.2134/ael2018.03.0014

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Scoecs, E., & Wagner, H. (2019). *vegan: Community ecology package*. R package version 2.5-6. https://CRAN.R-project.org/package=vegan

Osanai, Y., Bougoure, D. S., Hayden, H. L., & Hovenden, M. J. (2013). Co-occurring grass species differ in their associated microbial community composition in a temperate native grassland. *Plant and Soil*, *368*, 419–431.

Rayment, G. E., & Lyons, D. J. (2011). *Soil chemical methods: Australasia*. CSIRO Publishing.

Revillini, D., Gehring, C. A., & Johnson, N. C. (2016). The role of locally adapted mycorrhizas and rhizobacteria in plant–soil feedback systems. *Functional Ecology*, *30*, 1086–1109.

Rillig, M. C., Muller, L. A., & Lehmann, A. (2017). Soil aggregates as massively concurrent evolutionary incubators. *The ISME Journal*, *11*, 1943–1948.

Scheffer, M., Carpenter, S. R., Dakos, V., & van Nes, E. H. (2015). Generic indicators of ecological resilience: Inferring the chance of a critical transition. *Annual Review of Ecology, Evolution, and Systematics*, *46*, 145–167.

Sourkova, M., Frouz, J., Fettweis, U., Bens, O., Huttl, R. F., & Santrukova, H. (2005). Soil development and properties of microbial biomass succession in reclaimed post mining sites near Sokolov (Czech Republic) and near Cottbus (Germany). *Geoderma*, *129*, 73–80.

Tedersoo, L., Bahram, M., Polme, S., Koljalg, U., Yorou, N. S., Wijesundera, R., Villarreal Ruiz, R., Vasco-Palacios, A. M., Quang Thu, P., Suija, A., Smith, M. E., Sharp, C., Saluveer, E., Saitta, A., Rosas, M., Riit, T., Ratkowsky, D., Pritsch, K., Põldmaa, K., … Aberenkov, K. (2014). Global diversity and geography of soil fungi. *Science*, *346*, 1078 and 1256688/1–1256688/10.

Tongway, D. J. (1995). Monitoring soil productive potential. *Environmental Monitoring and Assessment*, *37*, 303–318.

Wallwork, J. A., Kamill, B. W., & Whitford, W. G. (1985). Distribution and diversity patterns of soil mites and other microarthropods in a Chihuahuan desert site. *Journal of Arid Environments*, *9*, 215–231.

Ward, S. C., & Koch, J. M. (1995). Early growth of jarrah (*Eucalyptus marginata* Donn ex Smith) on rehabilitated bauxite minesites in southwest Australia. *Australian Forestry*, *58*, 65–71.

Waymouth, V., Miller, R. E., Ede, F., Bissett, A., & Aponte, C. (2020). Variation in soil microbial communities: Elucidating relationships with vegetation and soil properties, and testing sampling effectiveness. *Plant Ecology*, *221*, 837–851.

SUPPORTING INFORMATION

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

How to cite this article: Eldridge, D. J., Oliver, I., Powell, J. R., Dorrough, J., Carrillo, Y., Nielsen, U. N., Macdonald, C. A., Wilson, B., Fyfe, C., Amarasinghe, A., Kuginis, L., Peake, T., Robinson, T., Howe, B., Delgado-Baquerizo, M. (2022). Temporal dynamics in biotic and functional recovery following mining. *Journal of Applied Ecology*, *00*, 1–12. https://doi.org/10.1111/1365-2664.14172