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Restoration Starts in the Soil

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Abstract:

Global ecosystem degradation has caused catastrophic biodiversity losses, which will continue as extinction debts are realised. Restoration seeks to reverse these losses, yet restoration plantings – the predominant approach to restoring ecosystems – consistently fall short of recovery targets. Here, we quantified recovery across bacteria, fungi, plants, and animals in large-scale restoration plantings and examined how soils mediate their recovery. We demonstrate a cascading recovery pathway where persistent soil agricultural legacies are linked to poor taxonomic and functional recovery of bacterial, fungal and vegetation communities, which have flow-on impacts and limit the recovery of animal communities. Our findings shift contemporary restoration thinking – ecosystem recovery is rooted in soils and ignoring soil biodiversity and condition risks constraining the recovery of whole ecosystems.

Summary:

Ecosystem degradation threatens biodiversity and ecosystem functioning globally [1-3], prompting international commitments including the Kunming–Montreal Global Biodiversity Framework's target to restore 30% of degraded ecosystems by 2030 [4]. Yet restoration remains insufficient in both extent and ecological outcomes, with only 10.4% of the globally pledged area currently under restoration [5] and restoration frequently falls short of biodiversity recovery targets [6,7]. Although soil biodiversity and processes underpin ecosystem functioning [8-10], restoration predominantly focuses on vegetation, leaving the influence of persistent soil degradation on whole-ecosystem recovery poorly understood [11]. Here, we quantified recovery across soil bacterial, fungal, plant and animal communities in large-scale restoration plantings. We show a cascading recovery pathway that links persistent agricultural soil legacies with microbial, vegetation and animal communities. Bacterial community recovery emerged as a central predictor, strongly associated with fungal, vegetation and soil metazoan recovery, while vegetation composition and structure predicted bird community recovery. Our findings show that persistent soil legacies constrain biodiversity recovery across trophic levels [12], challenging global assumptions about restoration needs [11]. Meeting global restoration ambitions requires recognising soil condition and belowground biodiversity as fundamental components of whole ecosystem recovery [13].

Main Text:

Ecosystem degradation is causing catastrophic losses to biodiversity, ecological interactions, and ecosystem services worldwide [1-3]. With 20–40% of global land degraded [14], protecting intact ecosystems remains paramount [15]. However, conservation alone is insufficient to halt these declines [16,17] – ecosystem restoration is essential [18]. This imperative underpins international frameworks including the United Nations Decade on Ecosystem Restoration (2021–2030) and the Kunming–Montreal Global Biodiversity Framework, which call for effective restoration of at least 30% of degraded ecosystems by 2030 [4,19]. However, a 2026 report by the International Union for Conservation of Nature (IUCN) showed that the global area under restoration is only 10.4% of the area pledged [5]. These shortfalls risk perpetuating degradation, estimated to cost US$6.3 trillion annually in lost ecosystem services [20], while raising the importance of meeting restoration targets where projects are underway. Importantly, ecosystem restoration requires recovery belowground as well as aboveground [10,11,21]. Soils harbour 59–>99.9% of Earth's species [8,9], whose activities and interactions underpin the biogeochemical processes essential to life on Earth [8-10,22] – yet belowground biodiversity remains highly underrepresented in conservation research, practice, investment and public attention [23].

Inferring restoration success from individual biological communities can overlook the interactions that underpin ecosystem recovery [24,25]. This reflects the enduring *field of dreams* paradigm in restoration ecology – the assumption that rebuilding aboveground habitat will facilitate broader recovery – 'if you build it, they will come' [6]. Yet above- and belowground communities recover at different rates [10,26,27] and include both facilitators and followers [28]. Measuring ecosystem recovery using only vegetation-based metrics may therefore provide

inadequate estimates of restoration success. This disconnect between the above- and belowground community recovery risks inflating expectations of the speed and completeness of whole ecosystem recovery [6,29].

Persistent soil legacies from previous land uses (e.g., elevated soil nutrients and altered microbial communities from past fertiliser application) can explain why restored ecosystems fail to converge towards desirable states [13] and drive the emergence of novel ecosystems with alternative stable states [30,31]. Numerous examples exhibit altered nutrient cycling, invasive species dominance, disrupted plant–soil feedbacks and depleted native plant seed banks that are maintained in degraded yet stable states that resist restoration despite substantial effort [29,31]. These legacies can decouple visible recovery from recovery of hidden ecosystem functioning – vegetation structure and biomass may return while soil condition and biodiversity can remain fundamentally distinct from reference conditions [7,12]. The restoration sector must therefore consider not only whether vegetation and fauna are recovering, but also interrogate the soil communities which sustain their recovery.

Mediterranean biomes occupy ~2% of Earth's land surface, yet harbour ~16% of the world's plant diversity [32]. Their limited extent and high vulnerability to global change make them both a conservation priority and a valuable model for understanding ecosystem responses to change [32]. Here we quantify whole-ecosystem recovery approximately a decade after restoration planting across 975 ha in Mediterranean woodlands in southern Australia [33]. Using 16 nearby uncleared woodlands as reference sites, we assessed the recovery of plants, birds, soil metazoa, fungi and bacteria, alongside soil conditions (Fig. S1). We tested whether above- and belowground

biodiversity converged towards intact reference conditions and whether persistent agricultural soil legacies constrain this recovery.

Ecosystem recovery cascades from soils to plants and animals

We show strong connected recovery across soils, microbes, plants, and animals. Our structural equation model identifies a cascading recovery pathway from soil conditions to bacterial, vegetation and fungal communities, which had flow-on impacts that limited the recovery of animal communities (Fisher's $C_{72} = 43.65$, $P = 0.991$; Fig. 1A; Tables S1–S2). Soil bacterial community recovery was strongly predicted by exchangeable calcium (pseudo-$R^2 = 0.58$), where bacterial communities were further from those in intact reference sites where exchangeable calcium remained elevated ($\beta std = 0.62$, P = 0.009). Bacterial community recovery (pseudo-$R^2 = 0.66$; $\beta std = 0.70$, P < 0.001) and soil ammonium nitrogen ($\beta std = 0.55$, P = 0.007) predicted soil fungal community recovery. Bacterial community recovery also strongly predicted recovery of both whole and native vegetation composition (pseudo-$R^2 = 0.61$, $\beta std = 1.17$, P < 0.001; and pseudo-$R^2 = 0.55$, $\beta std = 0.98$, P = 0.005, respectively) and soil metazoan communities (pseudo-$R^2 = 0.85$, $\beta std = 0.75$, P = 0.001), placing soil bacterial communities as key mediators of recovery across multiple trophic levels. Aboveground, recovery of vegetation composition (pseudo-$R^2 = 0.59$; $\beta std = 0.56$, P = 0.019) and tree cover ($\beta std = 0.71$, P = 0.010) predicted bird community recovery.

The modelled direct and indirect effects of soil condition properties extended across biological communities (Fig. 1B). Exchangeable calcium had the strongest overall effects, acting both directly and indirectly through bacterial and vegetation responses, while several other soil

properties, especially phosphorus, had predominantly indirect effects across biological groups. Together, these pathways demonstrate an interconnected recovery cascade – soil condition was associated with microbial recovery (or lack thereof), microbial recovery with vegetation and soil metazoa recovery, and vegetation recovery with bird recovery. Such interconnected responses suggest a mechanism through which historical land uses can leave soil legacies that propagate as barriers to recovery across all trophic levels long after land use has changed to ecosystem restoration.

This cascading pattern was independently supported by our predictive models of individual biological communities (Fig. 2; Table S3). Bacterial recovery was most strongly predicted by soil physicochemical conditions, particularly exchangeable calcium and pH (random forest: out-of-bag $R^2 = 0.57$, leave-one-out cross-validation $R^2 = 0.55$, $r = 0.78$; Fig. 2A; Fig S2; Table S3). Fungal recovery was most strongly predicted by bacterial community composition, followed by soil potassium, sulphur and vegetation composition (out-of-bag $R^2 = 0.33$, leave-one-out cross-validation $R^2 = 0.32$, $r = 0.58$; Fig. 2B; Fig. S2; Table S3). Vegetation recovery was associated most strongly with soil phosphorus and bacterial community composition (out-of-bag $R^2 = 0.18$, leave-one-out cross-validation $R^2 = 0.19$, $r = 0.44$; Fig. 2C; Fig. S4; Table S3). Phosphorus was also the strongest predictor of native vegetation recovery, with greater predictive importance for native than for whole vegetation communities (out-of-bag $R^2 = 0.16$, leave-one-out cross-validation $R^2 = 0.2$, $r = 0.44$; Fig. 2D; Fig. S5; Table S3).

Soil metazoan recovery was best predicted by exchangeable calcium (out-of-bag $R^2 = 0.27$, leave-one-out cross-validation $R^2 = 0.31$, $r = 0.58$; Fig. 2E; Fig. S6; Table S3). Bird recovery was most strongly predicted by vegetation composition and tree cover, followed by soil organic

carbon and soil moisture – environmental covariates representing variation in site productivity and resource availability (out-of-bag $R^2 = 0.41$, leave-one-out cross-validation $R^2 = 0.38$, r = 0.64; Fig. 2F; Fig. S7; Table S3). Within the predictor sets, the dominant predictors of recovery shifted from soil conditions for lower trophic levels to vegetation structure and composition for higher trophic levels, reinforcing the interconnected recovery pathway identified by our structural equation model.

Persistent soil legacies constrain the recovery cascade

Soils beneath restoration plantings retained substantial legacies of previous agricultural land use. Phosphorus showed the greatest difference between restoration and intact reference conditions, with concentrations ~6.8 times those in reference soils (*lnRR* = 1.91, 95% CI = 1.48–2.30). Sulphur, ammonium nitrogen, potassium, several micronutrients and exchangeable cations, and electrical conductivity were also elevated (Fig. S8; Table S4). The prominence of phosphorus was not restricted to our study system. Across temperate Australia, disturbed soils similarly contained ~2.9 times as much phosphorus as natural reference soils (*lnRR* = 1.07, 95% CI = 0.81–1.32), alongside differences in other soil nutrients and properties – including potassium, nitrate nitrogen, and exchangeable calcium, among others (Fig. S8; Table S4). These broader patterns show that phosphorus enrichment in soils that typically underpin restoration extend beyond our study region. In our restoration soils, phosphorus-metabolism genes showed the greatest compositional divergence among the functional gene categories examined (*lnRR* = 0.22, 95% CI = 0.12–0.34; Fig. S9; Table S5). Genes associated with carbon cycling, metabolism of aromatic compounds – including lignin-derived compounds – and stress responses also differed in composition from those in intact reference soils (Fig. S9; Table S5).

Persistent nutrient enrichment is increasingly recognised as a constraint on post-agricultural restoration. In a North American prairie restoration experiment, reducing nitrogen availability through soil carbon addition suppressed weeds and increased native prairie plant biomass [34]. In Australia's naturally phosphorus-poor ecosystems, phosphorus enrichment represents an especially persistent ecological filter [12,35]. Fertiliser-derived phosphorus can remain elevated in soils for decades because of its relatively low mobility, maintaining altered nutrient pools, microbial interactions and plant–soil feedbacks after agricultural inputs cease [12,36]. Elevated phosphorus can further favour competitive non-native plants by relaxing the low-nutrient conditions to which many Australian native species are adapted [29,35,37]. Consistent with these mechanisms, our study shows that phosphorus remains elevated many years after agriculture has ceased and is strongly associated with incomplete vegetation recovery, while phosphorus-metabolism genes show the greatest compositional divergence from intact reference communities. Historical nutrient enrichment can therefore continue to filter community assembly long after the re-establishment of native vegetation, maintaining restoration trajectories that do not converge with intact ecosystems [31].

Soil exchangeable calcium and sulphur were also important predictors of ecosystem recovery. Unlike phosphorus and sulphur, exchangeable calcium did not differ clearly between restoration and intact reference soils, although elevated calcium was identified as a legacy of disturbance across temperate Australia (Fig. S8; Table S4). Despite this, exchangeable calcium was strongly associated with bacterial recovery in the structural equation model (Fig. 1; Table S1) and was among the strongest predictors of both bacterial and metazoan recovery in predictive models (Fig. 2; Fig. S2). Calcium is taken up and retained by both bacteria and soil metazoa, so

biological sequestration may have contributed to divergent communities while reducing detectable differences in exchangeable calcium between restoration and reference soils [38-40]. Sulphur showed a different pattern, being associated with vegetation recovery in the structural equation model and among the strongest predictors of fungal and metazoan recovery (Fig. 1; Fig. 2; Table S1). Together, these associations support the inference that recovery is constrained by historical agricultural land use legacies, rather than phosphorus alone. Elevated phosphorus, sulphur and exchangeable calcium are all consistent with historical fertiliser inputs, including superphosphate application [41,42].

Structural vegetation recovery masks longstanding recovery debts

Despite strong associations among biological communities, their recovery towards intact reference conditions varied markedly (Fig. 3; Fig. S10–S11; Table S6). The most conspicuous recovery occurred in vegetation structure and birds. Native tree cover increased from well below intact reference conditions in 2015 to reference-like levels by 2025, while native shrub cover increased from below to well above reference values (Fig. S12; Table S7). Bird richness similarly increased from below-reference levels in 2015 to values comparable with intact reference sites in 2025 (Fig. 3; Fig S10; Table S6). Bird functional composition also recovered, converging from highly dissimilar communities in 2015 to broadly reference-like conditions by 2025, including convergence in trophic guilds, primary lifestyles, habitats and nesting strategies (Fig. S11–S12; Table S7–S8).

These relatively rapid responses are consistent with the capacity of reconstructed vegetation structure to provide habitat and resources for mobile fauna, such as birds. As trees and shrubs

establish, increased habitat complexity, resource availability and connectivity can facilitate faunal colonisation, consistent with the *field of dreams* hypothesis [43]. The close associations between bird recovery and vegetation composition and tree cover in both our predictive and structural equation models provides further support for this interpretation. Re-establishing vegetation structure was associated with substantial bird recovery within 15 years of restoration plantings.

However, conspicuous structural vegetation recovery masked longstanding compositional differences across the study system. Whole vegetation composition became more similar to intact reference communities between 2015 and 2025, but this convergence was largely due to changes in non-native vegetation (Fig. 2; Fig. S11; Table S6). Native vegetation showed little evidence of compositional recovery, with dissimilarity remaining unchanged between survey periods (2015: $lnRR = 0.12$, 95% CI = 0.10–0.14; 2025: $lnRR = 0.12$, 95% CI = 0.09–0.15; Fig. 2; Fig. S11; Table S6). Native plant species richness also remained below intact reference sites and declined through time (Fig. 2; Fig S10; Table S6). Thus, recovery of trees and shrubs did not equate to recovery of the native plant community, with understory plants remaining notably absent despite being planted during initial restoration efforts. Vegetation structural recovery therefore outpaced compositional recovery. There was also limited bird taxonomic compositional recovery, despite substantial functional convergence (Fig. 3).

Belowground communities likewise remained incompletely recovered. Bacterial communities remained compositionally distinct from intact reference communities despite comparable richness (Fig. 3; Fig. S10–S11; Table S5–S6). Fungal communities also remained compositionally distinct in restoration sites, despite fungal richness exceeding that of intact

reference sites (Fig. 3; Fig. S10–S11; Table S5–S6). Similarly, soil metazoan communities were compositionally distinct from intact reference sites despite comparable richness (Fig. 3; Fig. S10–S11; Table S5–S6). Across these belowground groups, differences in community composition therefore remained, even where conventional richness and diversity indices suggested substantial recovery (Fig. 3; Fig. S10–S11; Table S5–S6). Fungal recovery depended on the traits examined – broad functional roles and primary lifestyles showed no clear differences from intact reference communities, although fungal growth forms and decay-substrate specialisation remained distinct (Fig. S9; Table S5).

The sites under restoration therefore showed substantial structural recovery, albeit with unresolved taxonomic and functional recovery debts. The lack of native vegetation convergence over a decade, alongside altered belowground communities and microbial functional gene profiles, indicates continuing constraints on whole-ecosystem recovery. These findings demonstrate that visible restoration progress can substantially overstate actual ecosystem recovery.

Restoration must address soil constraints

Our findings challenge the assumption that reconstructing vegetation will reassemble the ecological relationships that sustain whole ecosystems. Instead, restoration should recognise the interdependencies of soil condition, microbes, plants and animals, in which organisms both depend upon and modify their biotic and abiotic environments. Achieving whole ecosystem recovery requires identifying barriers to recovery and determining how to overcome them. Our structural equation (Fig. 1; Tables S1–S2) and predictive models (Fig. 2; Table S3) identify

candidate constraints and pathways – persistent soil nutrient enrichment is an important constraint, and cascading associations among bacterial, fungal, vegetation and animal communities is a potential pathway through which its effects propagate.

Associations between vegetation and soil biota are supported by experimental evidence identifying plausible underlying mechanisms. Plant responses to soil biota can differ among nutrient-acquisition strategies, with consequences for plant coexistence and diversity [44], while manipulation of soil microbiota in restoration field trials can alter native plant establishment, succession and community composition, with effects persisting for at least seven years [45,46]. Soil legacies may therefore persist not simply as altered nutrient concentrations, but also through the biological communities and interactions that those conditions support, with persistent nutrient enrichment and altered microbial communities acting together to filter plant community assembly. Resolving these mechanisms experimentally would identify actions that could redirect restoration trajectories, potentially including the use of topsoil removal to reduce excess nutrient pools [47,48] and soil translocation or microbial inoculation to restore missing soil biodiversity and ecological interactions [18,49]. Because abiotic and biological soil legacies may be mutually reinforcing, restoring soil conditions and soil biological communities together with aboveground biological communities may ultimately be required to overcome persistent barriers to whole-ecosystem recovery.

Meeting global restoration targets requires improving ecosystem recovery at scale, where effective interventions that achieve whole-ecosystem recovery outcomes remain to be established. Our work adds to mounting evidence that shows why soil recovery must be more explicitly integrated into restoration standards, policies, funding, practices and assessments. Soils

286 are increasingly recognised within restoration frameworks, but their assessment remains
287 weighted towards physicochemical condition and remediation rather than recovery of soil
288 biodiversity and its contribution to ecosystem functioning. Pairing soil physicochemical
289 measures with indicators of soil biodiversity and functional recovery would help identify
290 restoration constraints that will otherwise remain mostly hidden beneath recovering vegetation
291 communities.
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Materials and Methods

Experimental design

We collected data in the Ramsar-listed Coorong, Lower Lakes and Murray Mouth (CLLMM) region of southern Australia. We evaluated ecological recovery following the CLLMM Vegetation Program, a landscape-scale restoration initiative done between 2012 and 2016 that established native vegetation across approximately 5 km surrounding lakes Alexandrina and Albert and the Coorong. For the vegetation assessments, we surveyed the 76 woodland sites originally established by Milne [50], comprising 60 restoration sites distributed across public and private land and 16 intact reference sites representing the target vegetation communities. Bird surveys were undertaken in a subset of the restoration sites where 33 sites were assessed. Both vegetation and bird communities were assessed in spring (August to October) 2015 and 2025.

Soil sampling

We collected soil from 47 sites in spring 2025, including 16 intact reference and 31 restoration sites across the CLLMM region (Fig. S1). Soil sampling followed the protocol in Cando-Dumancela et al. [51]. Briefly, we established a 25 m × 25 m quadrat at each site, and collected soil from nine locations (4 corners, 4 edge midpoints and the centre). We combined subsamples into a single composite sample to characterise site-level soil conditions.

We divided each composite sample into three subsamples. We used a 200-g subsample for soil physicochemical analyses, a 100 mL subsample for gravimetric soil moisture determination, and a 15 mL subsample for DNA extraction and amplicon sequencing of bacterial, fungal and soil metazoan communities (see below).

457 **Soil physicochemistry**

458 CSBP Laboratories (Bibra Lake, Western Australia) did the soil physicochemical analyses.
459 Measurements included pH (1:5 H_2O), organic carbon [52], inorganic nitrogen (ammonium and
460 nitrate) [53], sulphur [54], phosphorus and potassium [55], micronutrients (boron, zinc, copper,
461 manganese and iron) [53], and exchangeable cations (sodium, potassium, magnesium, calcium and
462 aluminium) [53].

463

464 To compare patterns in the CLLMM region with Australia-wide trends, we examined soil
465 physicochemical data from the Australian Microbiome dataset (downloaded 5 August 2026) [56].
466 We restricted the dataset to samples collected from the upper 10 cm of soil in temperate climate
467 regions and excluded extreme soil conditions by retaining samples with clay content = 7.5–45%,
468 salinity ≤ 2, and pH = 4.5–9. CSBP Laboratories (Bibra Lake, Western Australia) also did the
469 soil physicochemical analyses for the Australian Microbiome dataset following their protocols,
470 using the same analytical methods applied to samples from the CLLMM region. We classified
471 sites as natural or disturbed according to their recorded land-use category, excluding ambiguous
472 or non-comparable land-use classes from analysis (Table S9).

473

474 **Belowground sampling**

475 To characterise belowground biodiversity, we extracted DNA using the DNeasy PowerLyzer
476 PowerSoil Kit (Qiagen, Hilden, Germany). We generated amplicon libraries for soil metazoa
477 (COI; mlCOIintF–dgHCO2198), bacteria (16S rRNA; 341F–806R) and fungi (ITS; ITS1F–
478 ITS2R), and sequenced them using 300 bp paired-end chemistry on an Illumina NextSeq 2000
479 platform.

480

We processed soil metazoan sequences using VSEARCH [57] following quality filtering and primer trimming with fastp [58]. We clustered zero-radius operational taxonomic units into 97% operational taxonomic units (97OTUs), to which we assigned taxonomy using BLAST against the NCBI nucleotide database. We excluded samples with < 5,000 reads prior to downstream analyses. Because mitochondrial cytochrome oxidase subunit 1 read counts are not reliable estimates of organism abundance, we based our soil metazoan community analyses on presence–absence-transformed data.

We processed bacterial and fungal amplicons using the DADA2 pipeline [59-61]. We used zero-radius operational taxonomic units to assign taxonomy using the SILVA database (v138.2) for bacteria [62]. and the UNITE database (v10.0) for fungi [63]. We rarified sequence libraries to 56,344 bacterial reads and 52,870 fungal reads per sample. We inferred fungal functional guilds using FungalTraits [64].

We characterised microbial functional profiles using shotgun metagenomic sequencing. The Australian Genome Research Facility (Melbourne, Australia) prepared DNA libraries using Illumina DNA Preparation chemistry and sequenced them on an Illumina NovaSeq X platform (150 bp paired-end reads). We quality-filtered reads using fastp [58], assigned functional annotations using SuperFocus against the SEED subsystem database[65,66], and normalised gene abundances to counts per million prokaryotic reads using SingleM [67].

Functional analyses focused on five SEED subsystem level 1 categories (nitrogen, phosphorus and sulphur metabolism, stress response, and metabolism of aromatic compounds), together with

eight level 3 categories representing microbial utilisation of plant- and soil-derived carbon substrata (hereafter, carbon cycling genes) [68,69].

Aboveground sampling

Nature Glenelg Trust surveyed vegetation communities using Braun–Blanquet methods [70]. BirdLife Australia surveyed bird communities using 20-minute surveys within 2-ha plots. We assigned bird functional traits from published databases [71,72], including trophic niche, primary habitat, primary lifestyle and nesting strategy. Functional guilds therefore reflect species' general ecological roles rather than observed behaviour at individual sites.

Statistical analysis

Variable importance

We used random forest models to identify environmental variables most strongly associated with divergence from intact reference-like conditions. For each ecosystem component, the response variable was the difference from intact reference conditions, calculated using the dissimilarity metrics described above (Table S10). We removed collinear ($|r| > 0.65$) predictor variables prior to modelling.

We fitted random forest models (500 trees; *mtry* = 6) separately for each ecosystem component. We assessed model performance and variable importance using leave-one-out cross-validation, in which we withheld each observation in turn for model testing while using the remaining observations for training. We quantified predictor importance from the cross-validated models. We used Spearman's rank correlations and random forest partial dependence plots to examine

univariate associations and modelled predictor–response relationships, respectively, with community divergence.

We selected predictor sets based on hypothesised ecological relationships. Bird models included vegetation characteristics together with selected soil properties (soil moisture, electrical conductivity and organic carbon) as indicators of habitat condition and productivity. Plant models included soil physicochemical variables together with soil bacterial and fungal communities. Models for bacterial, fungal and soil metazoan communities included soil physicochemical variables and vegetation community composition. Predictor sets reflected hypothesised ecological linkages among ecosystem components. Consequently, we included cross-community predictors where ecologically justified, such as vegetation variables predicting fungal communities and fungal variables predicting vegetation communities.

Response ratios

We quantified differences between restoration and intact reference sites using natural log-transformed response ratios following Zhou, et al. [27] and Watson, et al. [73]. We calculated response ratios for univariate variables (e.g., richness, Shannon diversity, plant cover and soil physicochemical properties) and multivariate measures describing community composition and heterogeneity. We estimated sampling uncertainty using non-parametric bootstrapping (9,999 iterations), whereby we resampled sites with replacement and recalculated response ratios for each iteration. We used median bootstrap estimates and 95% percentile confidence intervals to quantify uncertainty and compare recovery trajectories among ecosystem components.

Univariate response ratios

We calculated differences in alpha diversity, plant cover and soil physicochemical variables between restoration and intact reference sites as:

$$\mathrm{RR}_{univariate} = \log_e \frac{\overline{Y}_t}{\overline{Y}_c}$$

where $\underline{Y_t}$ and Y_c are the mean values for restoration (treatment) and intact reference (control) sites, respectively. Intact reference sites represented the restoration target throughout all analyses.

Compositional response ratios

We quantified community composition using community dissimilarity matrices. We calculated Bray–Curtis distances for plants, bacteria and fungi, Jaccard distances for birds and soil metazoa, and Euclidean distances for soil physicochemical variables. Following Zhou et al. [27], we considered response ratios derived from these different dissimilarity metrics directly comparable because estimates of ecological recovery are robust to the choice of beta-diversity metric (see Table S10). We calculated recovery of community composition towards intact reference conditions as:

$$RR_{composition} = \log_e \frac{\overline{D}_b}{\overline{D_c + D_t}}$$

where D_b is the mean distance between restoration and intact reference sites, and $D_c + D_t$ are the combined mean within-intact reference and within-restoration distances, respectively.

Community heterogeneity (beta diversity) is:

$$\mathrm{RR}_{beta} = \log_e \frac{\overline{D}_t}{\overline{D}_c}$$

572 We applied the same framework to soil physicochemical variables, allowing divergence in soil
573 condition and environmental heterogeneity to be quantified relative to intact reference sites.
574
575 We used these response ratios to quantify three complementary aspects of ecosystem recovery:
576 recovery baselines (initial divergence between restoration and intact reference sites in 2015),
577 recovery progress (movement towards intact reference-like conditions between 2015 and 2025),
578 and recovery gaps (remaining divergence between restoration and intact reference communities
579 in 2025).
580
581 *Piecewise structural equation modelling.*
582 We used piecewise structural equation modelling to evaluate hypothesised direct and indirect
583 pathways linking community recovery across abiotic soil properties, microbial communities,
584 vegetation and higher trophic groups [74]. We constrained our structural equation modelling to
585 replicate restoration sites that were successfully sampled for all data types (e.g., soil properties,
586 bacteria, fungi, soil metazoa, vegetation, and birds) relative to intact reference sites (n = 20). To
587 avoid overfitting, we first reduced soil physicochemical variables to a candidate set based on
588 hypotheses generated from our random forest models, after which we removed highly correlated
589 variables ($|r| > 0.7$). We then constructed a maximal structural equation model including the
590 retained soil variables and all hypothesised pathways predicting the dissimilarity of restoration
591 sites to intact reference sites for birds, soil metazoa, native vegetation, tree cover, bacteria and
592 fungi (Fig. S13A; Table S11). We fitted each component model as a generalised linear model
593 with a gamma error distribution and log link function. We modelled bacterial dissimilarity using
594 retained soil physicochemical variables, while fungal dissimilarity additionally included bacterial
595 dissimilarity. We also modelled vegetation, native vegetation, tree-cover and soil metazoan

596 dissimilarity using retained soil variables, bacterial and fungal dissimilarity. We modelled bird
597 dissimilarity using vegetation and tree-cover dissimilarity and soil organic carbon. We specified
598 correlated errors among soil physicochemical variables to account for their shared covariance,
599 and between vegetation and native vegetation to account for residual non-independence between
600 these responses.
601
602 We then developed a simplified piecewise structural equation model using a reduced predictor
603 set identified through a maximum-likelihood multi-model inference approach [75]. For each
604 component model, we retained predictors if they occurred in any models within $\Delta AIC_c < 2$ of the
605 top-ranked model (Table S12). We used these retained predictors to construct a minimum
606 adequate structural equation model (Fig. S13B; Table S13). We fitted all component models as
607 gamma-error generalised linear models. We then compared the structural equation models using
608 global model AIC, which provided strong support for the minimum adequate structural equation
609 model (AIC = -260.7, AIC_c = -220.8, k = 38, n = 20) over the initial maximal structural equation
610 model (AIC = −239.3, AIC_c = -106.1, k = 62, n = 20).
611
612 To compare effect sizes among variables measured on different scales, we fitted standardised
613 effects using model-based queries, following the general approach of Grace et al. [76]. For each
614 path, the focal predictor was varied across a one-standard-deviation interval centred on its
615 observed mean (mean ± 0.5 SD), while all other predictors were held at their observed means.
616 Predictions were generated from the fitted component model on the response scale, and the
617 resulting change in the predicted response was divided by the observed standard deviation of the
618 response variable.
619

620 Standardised effect size was quantified as:

621 $$E_{std} = \frac{\hat{Y}\,(\bar{X} + 0.5\,SD_X) - \hat{Y}\,(\bar{X} - 0.5\,SD_X))}{SD_Y}$$

622 where $\hat{Y}\,(\bar{X} + 0.5\,SD_X)$ and $\hat{Y}\,(\bar{X} - 0.5\,SD_X)$ are the model-predicted response values when
623 the predictor is set to 0.5 standard deviations above and below its observed mean, respectively,
624 with all other predictors held at their observed means. SD_X and SD_Y are the observed standard
625 deviations of the focal predictor and response variable, respectively.
626
627 Finally, we summarised the direct and indirect relationships of soils and bacteria on fungi,
628 vegetation, soil metazoa and bird community dissimilarity to intact reference sites. Direct effects
629 were represented by the standardised path coefficients from the fitted minimum adequate
630 structural equation model, while indirect effects were calculated by multiplying standardised
631 coefficients along each mediated pathway. Where multiple indirect pathways linked the same
632 predictor and response, their products were summed. These effects were used to characterise the
633 relative magnitude and direction of relationships represented by our model.
634

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Writing – original draft: RJH, SJ, ADB, CL, SDP, JMR, MFB

Writing – review & editing: all authors contributed to review and editing of the manuscript

Diversity, equity, ethics, and inclusion:

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678

679 **Competing interests:**

680 Authors declare that they have no competing interests

681

682 **Data, code, and materials availability:**

683 All code and data will be made publicly available at DOI: 10.25451/flinders.34004379 (DOI
684 will be made active upon acceptance of publication). Sequence data are hosted at NCBI's
685 sequence read archive (PRJNA1524945).

686

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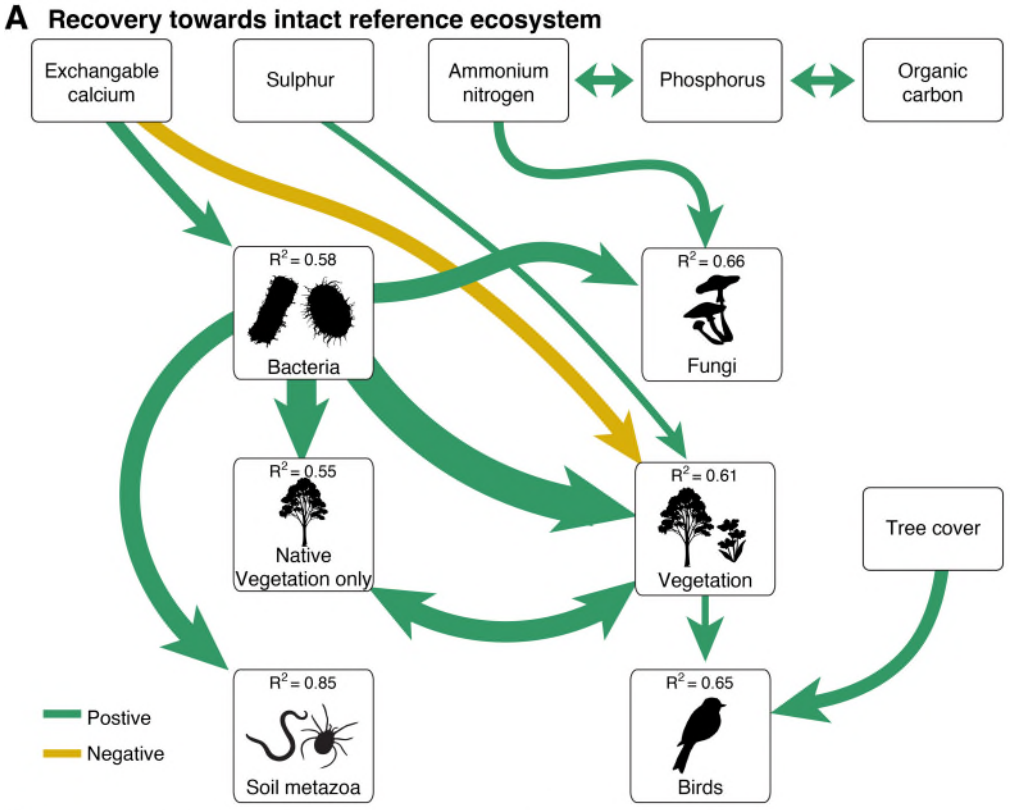
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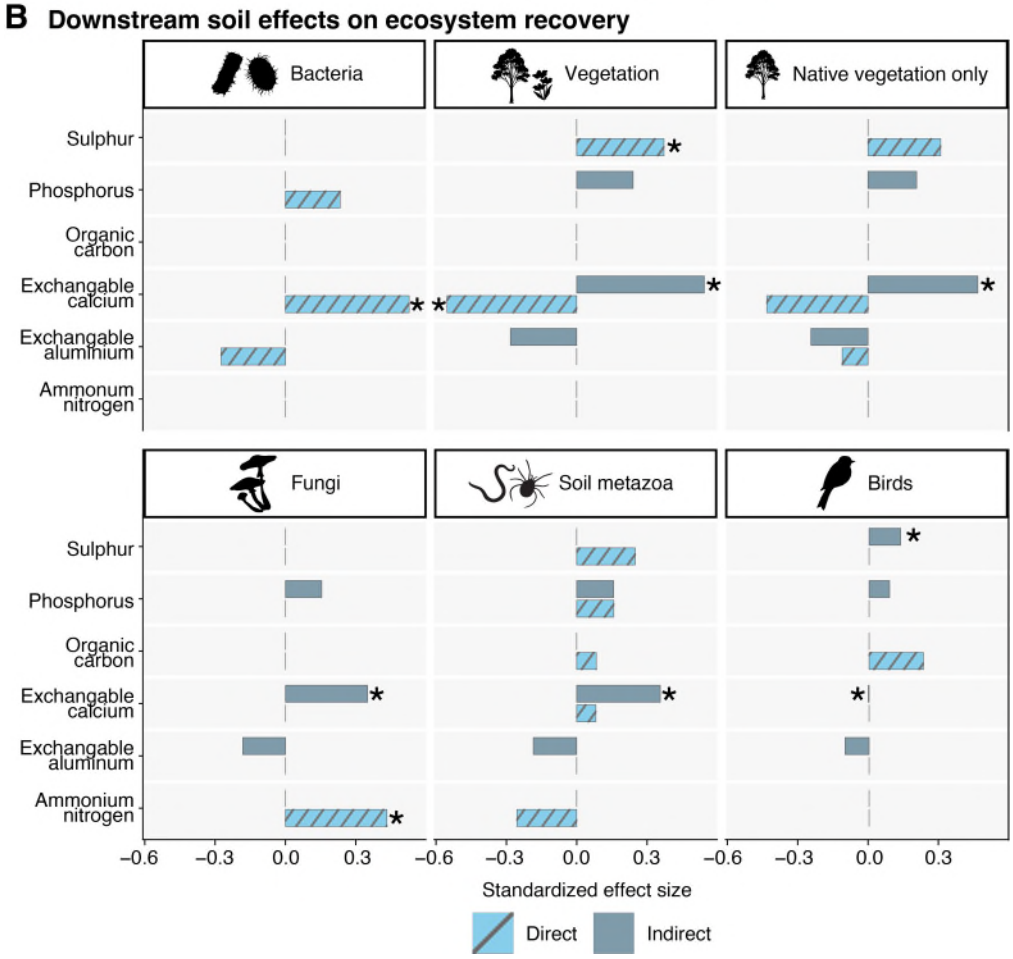
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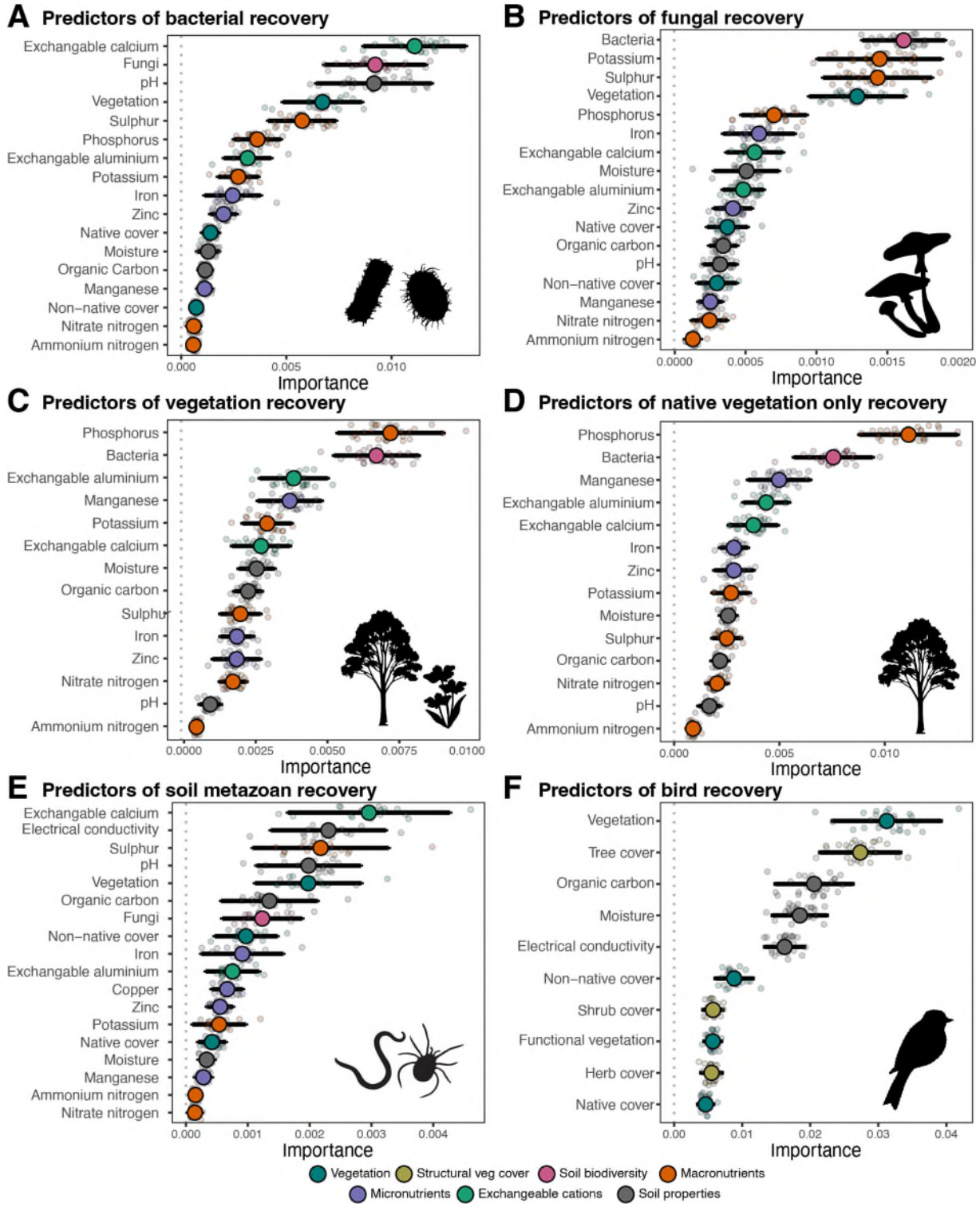
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A Recovery towards intact reference ecosystem
Exchangable calcium
Sulphur
Ammonium nitrogen
Phosphorus
Organic carbon
R² = 0.58
Bacteria
R² = 0.66
Fungi
R² = 0.55
Native Vegetation only
R² = 0.61
Vegetation
Tree cover
R² = 0.85
Soil metazoa
R² = 0.65
Birds
Postive
Negative


B Downstream soil effects on ecosystem recovery
Bacteria
Vegetation
Native vegetation only
Fungi
Soil metazoa
Birds
Sulphur
Phosphorus
Organic carbon
Exchangable calcium
Exchangable aluminium
Ammonum nitrogen
Exchangable aluminum
Ammonium nitrogen
−0.6
−0.3
0.0
0.3
Standardized effect size
Direct
Indirect

764 **Fig. 1. Soil conditions drive interconnected recovery across trophic levels.** (**A**) Minimum
765 adequate structural equation model showing hypothesised pathways linking change in soil
766 properties to the recovery of microbial, vegetation, and animal communities (dissimilarity
767 distances to intact reference conditions). Arrows represent statistically supported directional
768 relationships among variables, with width proportional to standardised coefficients (β_{std}; Tables
769 S1–S2). Double-headed dashed arrows represent correlated errors accounting for residual
770 covariance between variables. Exchangeable aluminium was omitted from the path diagram
771 because it had no statistically supported links within the final structural equation model (Tables
772 S1–S2). (**B**) Direct and indirect effects of soil physicochemical property change on biological
773 community dissimilarity to intact reference communities. Direct effects represent individual
774 pathways from a soil predictor to a biological response, whereas indirect effects represent the
775 summed products of coefficients across all mediated pathways linking each soil predictor to each
776 response. Asterisks indicate effects comprising statistically supported pathways ($P < 0.05$).
777



778

779 **Fig. 2. Predictors that limit recovery across biological communities**. Predictors of taxonomic

780 community divergence from remnant conditions in 2025, estimated using leave-one-out cross-

781 validation random forest models for (**A**) bacterial, (**B**) fungal, (**C**) vegetation, (**D**) native

vegetation only, (**E**) soil metazoan and (**F**) bird communities. Small points show importance scores from individual leave-one-out cross-validation iterations, large points show mean importance estimates, and horizontal bars show ±1 SD; colours denote broad predictor categories.

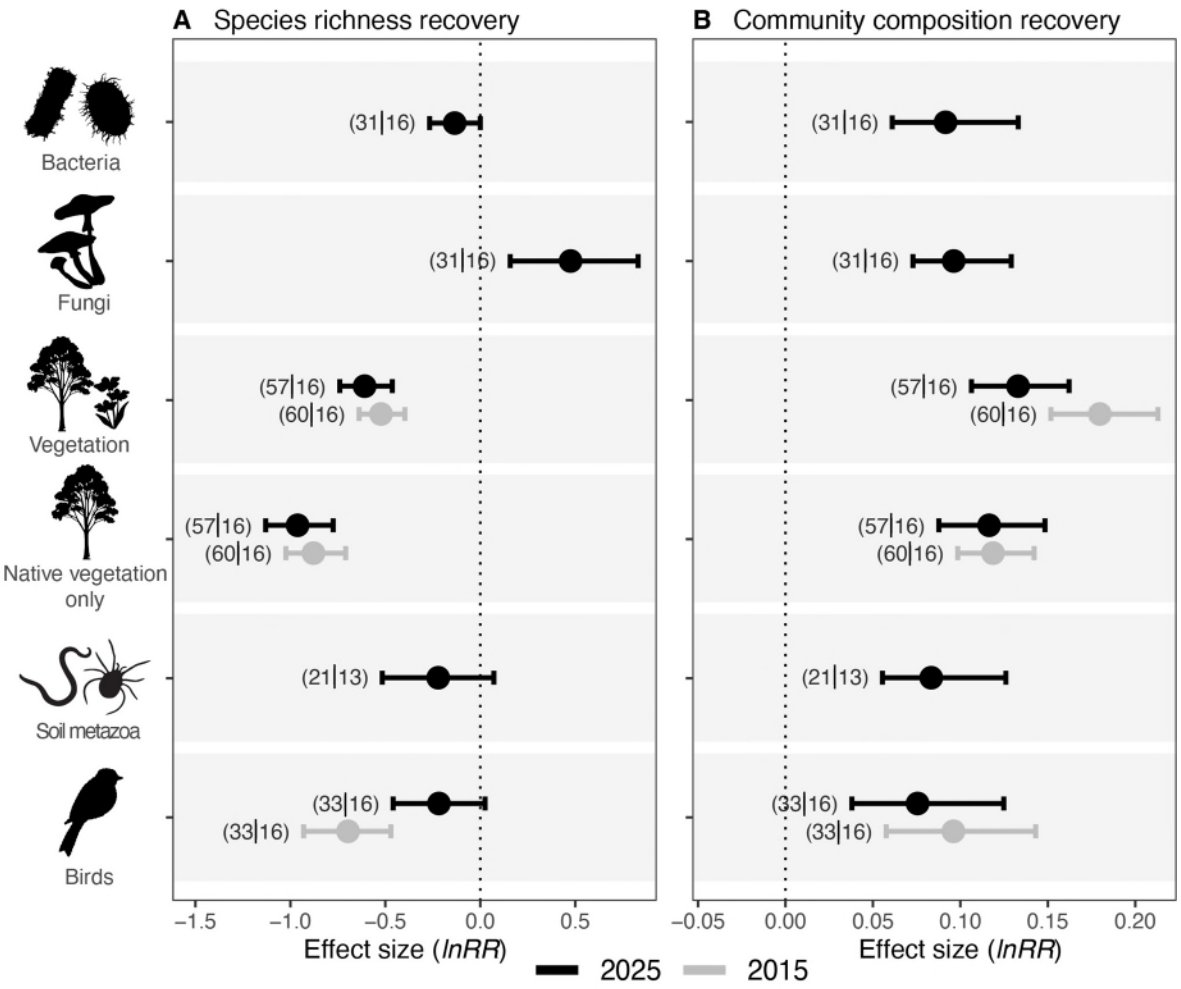


Fig. 3. Divergent species richness and community composition recovery trajectories. Recovery effect sizes (*lnRR*) for multi-trophic (**A**) species richness and (**B**) community composition at initial monitoring in 2015 and follow-up surveys in 2025 (see supplementary methods). Effect sizes quantify differences between restoration plantings and intact reference sites. For species richness, negative and positive effect sizes indicate lower and higher richness relative to intact communities, respectively, whereas increasingly positive effect sizes for community structure indicate greater compositional difference to intact reference communities. Points represent median recovery estimates and error bars represent bootstrapped confidence intervals. Sample sizes used to derive bootstrapped estimates are shown to the left of each estimate as the number of restoration | intact reference sites.

Figures

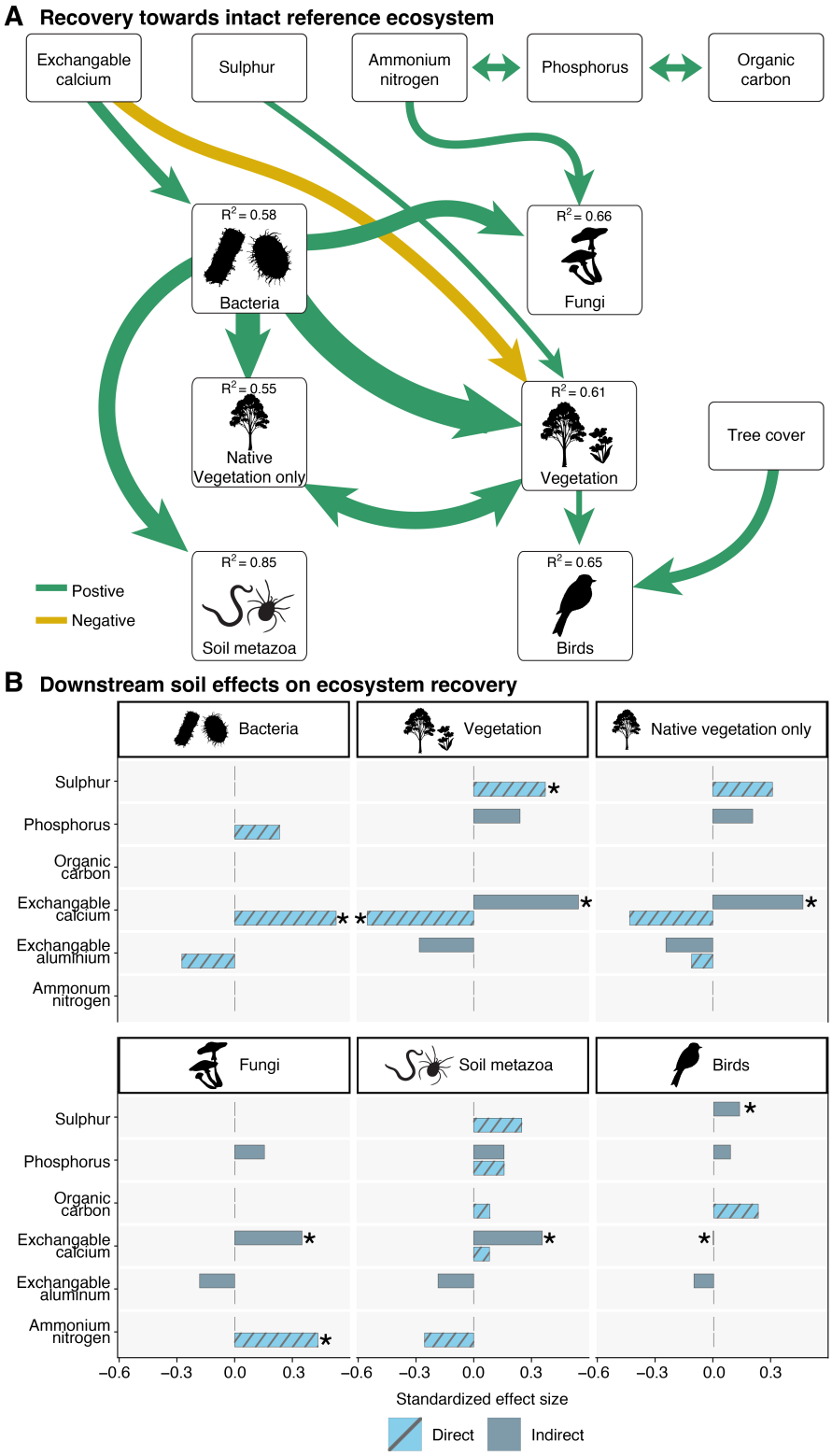


Figure 1

Soil conditions drive interconnected recovery across trophic levels. (**A**) Minimum adequate structural equation model showing hypothesised pathways linking change in soil properties to the recovery of microbial, vegetation, and animal communities (dissimilarity distances to intact reference conditions).

Arrows represent statistically supported directional relationships among variables, with width proportional to standardised coefficients (β_{std}; Tables S1–S2). Double-headed dashed arrows represent correlated errors accounting for residual covariance between variables. Exchangeable aluminium was omitted from the path diagram because it had no statistically supported links within the final structural equation model (Tables S1–S2). (**B**) Direct and indirect effects of soil physicochemical property change on biological community dissimilarity to intact reference communities. Direct effects represent individual pathways from a soil predictor to a biological response, whereas indirect effects represent the summed products of coefficients across all mediated pathways linking each soil predictor to each response. Asterisks indicate effects comprising statistically supported pathways ($P < 0.05$).

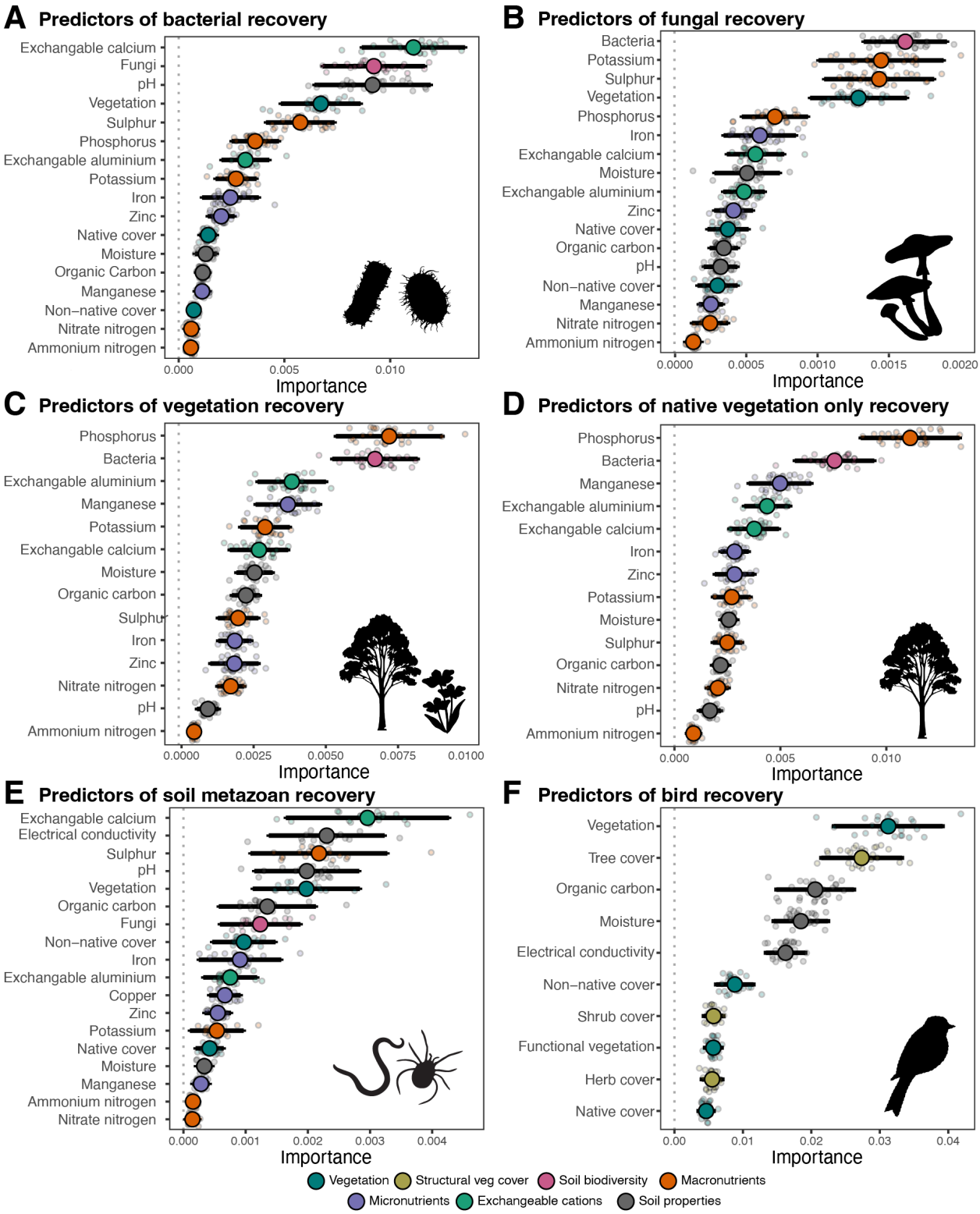


Figure 2

Predictors that limit recovery across biological communities. Predictors of taxonomic community divergence from remnant conditions in 2025, estimated using leave-one-out cross-validation random forest models for (**A**) bacterial, (**B**) fungal, (**C**) vegetation, (**D**) native vegetation only, (**E**) soil metazoan and (**F**) bird communities. Small points show importance scores from individual leave-one-out cross-

validation iterations, large points show mean importance estimates, and horizontal bars show ±1 SD; colours denote broad predictor categories.

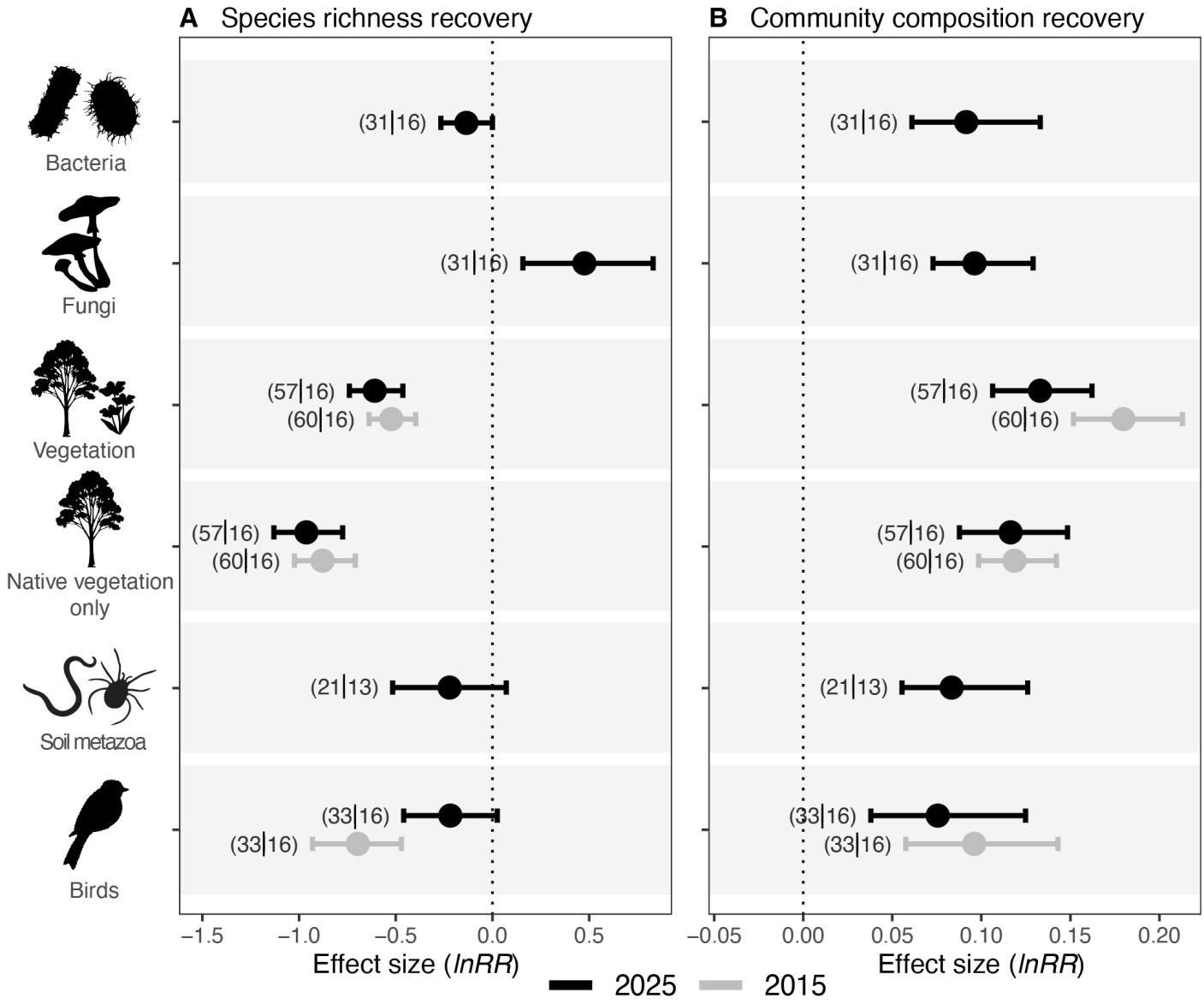


Figure 3

Divergent species richness and community composition recovery trajectories. Recovery effect sizes (*lnRR*) for multi-trophic (**A**) species richness and (**B**) community composition at initial monitoring in 2015 and follow-up surveys in 2025 (see supplementary methods). Effect sizes quantify differences between restoration plantings and intact reference sites. For species richness, negative and positive effect sizes indicate lower and higher richness relative to intact communities, respectively, whereas increasingly positive effect sizes for community structure indicate greater compositional difference to intact reference communities. Points represent median recovery estimates and error bars represent bootstrapped confidence intervals. Sample sizes used to derive bootstrapped estimates are shown to the left of each estimate as the number of restoration | intact reference sites.

Supplementary Files

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- CLLMMsupplementaryResearchSquare.docx