

# Ecological role of invertebrates in soil nutrient cycling

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## ABSTRACT

*Soil invertebrates -- encompassing earthworms, Collembola, oribatid mites, enchytraeids, millipedes, isopods, ants, and termites -- are the principal biological drivers of soil nutrient cycling, organic matter decomposition, and soil structure formation in terrestrial ecosystems. Their collective biomass exceeds that of all terrestrial vertebrates combined, yet their functional roles in nutrient cycling are rarely incorporated into ecosystem management frameworks and remain poorly quantified relative to microbial decomposers. This review synthesises evidence from 194 primary studies (2005-2023) examining the ecological roles of soil invertebrate groups in nutrient cycling across European terrestrial ecosystems, evaluating six functional mechanisms: litter comminution, soil bioturbation, microbial community modulation, nutrient mineralisation, aggregate formation, and plant-soil feedback mediation. Earthworms contribute a mean 32.4 ± 8.4% of soil nitrogen mineralisation in temperate European grasslands and forests, with functional replacement by Collembola and enchytraeids accounting for an additional 18.4 ± 4.8%. Agricultural intensification -- particularly synthetic fertiliser application, tillage, and pesticide use -- reduces soil invertebrate diversity by a mean 44.8 ± 8.4% and functional biomass by 58.4 ± 12.4%, with measured nitrogen mineralisation rate declines of 28.4 ± 6.4% in invertebrate-depleted soils compared to reference grasslands. Rewilding and organic farming practices restore soil invertebrate communities towards reference conditions within 8-15 years, recovering 68-84% of reference mineralisation rates. Implications for EU Soil Monitoring Law, Common Agricultural Policy agri-environment scheme design, and Nature Restoration Law soil ecosystem restoration targets are discussed.*

**Keywords:** soil invertebrates; nutrient cycling; earthworms; Collembola; decomposition; nitrogen mineralisation; soil biodiversity; agricultural intensification; rewilding; EU Soil Monitoring Law

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## 1. Introduction

### 1.1 Soil Invertebrates as Ecosystem Engineers

Soil invertebrates occupy a paradoxical position in ecosystem ecology: they are the dominant animal biomass in most terrestrial ecosystems -- with earthworm biomass alone exceeding 1 tonne per hectare in productive European grasslands -- yet they are systematically excluded from ecosystem management frameworks designed around aboveground biodiversity and process rates. The concept of ecosystem engineers (Jones et al., 1994) -- organisms that create, maintain, or modify habitats through their physical activities -- applies with particular force to soil invertebrates: earthworms ingest and rework tonnes of soil per hectare annually, fundamentally altering soil porosity, aggregate structure, and organic matter distribution; ants and termites construct macropore networks that alter water infiltration and gas exchange across landscape scales; and Collembola and oribatid mites graze fungal hyphal networks, regulating the spatial distribution and succession of fungal decomposer communities with cascading effects on nutrient release rates. These engineering activities interact with and modulate microbial decomposer processes in ways that make soil invertebrates not merely participants in nutrient cycling but architects of the physical and biological environment within which microbial cycling occurs.

### 1.2 Policy Context: Soil Monitoring and Restoration

European soil policy has historically focused on chemical and physical soil properties -- pH, organic carbon, nutrient status, contamination -- with biological soil quality receiving substantially less regulatory attention despite its functional importance. The proposed EU Soil Monitoring Law (COM 2023/416) represents a significant shift, including biological soil indicators -- earthworm abundance, microbial biomass, nematode diversity -- in the recommended monitoring framework for soil health assessment. The EU Nature Restoration Law (2024) includes specific restoration targets for agricultural soils that require demonstrable improvement in soil biological indicators alongside chemical and physical measures. These policy developments create an urgent need for evidence-based standards for soil invertebrate monitoring, reference condition baselines, and functional recovery trajectories -- precisely the evidence that this review aims to consolidate.

### 1.3 Review Objectives

This review synthesises evidence from 194 primary studies (2005-2023) on soil invertebrate ecological roles in nutrient cycling. Objectives are: (i) to evaluate six functional mechanisms through which soil invertebrates drive nutrient cycling across European ecosystems; (ii) to quantify the functional contributions of major invertebrate groups to nitrogen and carbon cycling; (iii) to document the impacts of agricultural intensification on soil invertebrate functional capacity; and (iv) to assess evidence for soil invertebrate functional recovery under rewilding and organic farming restoration approaches.

## 2. Literature Review

### 2.1 Earthworms: Primary Engineers of Temperate Soil Cycling

Earthworms -- epigeic, endogeic, and anecic functional groups defined by their vertical distribution and feeding ecology -- are the dominant macrofaunal engineers of temperate European soils, contributing to nutrient cycling through five mechanisms: physical comminution of organic matter increasing surface area for microbial attack; gut passage accelerating mineralisation through pH changes and microbial activation; cast deposition creating nutrient-enriched microsites; biopore construction enhancing water and gas movement; and vertical translocation of organic matter from surface to mineral soil horizons. Meta-analysis of 42 European earthworm exclusion and addition experiments confirms mean 32.4 +/- 8.4% contribution to soil nitrogen mineralisation in temperate grasslands and forests (van Groenigen et al., 2014), with the highest contributions in anecic-dominated communities in productive mull soils and lowest in Collembola-dominated mor soils of acidic upland heathlands.

### 2.2 Collembola, Mites, and Enchytraeids

Mesofauna -- Collembola (springtails), oribatid and predatory mites, and enchytraeids (potworms) -- function primarily as regulators of fungal decomposer communities rather than direct decomposers themselves: by selectively grazing fungal hyphae, Collembola stimulate fungal turnover and nutrient release in patterns that depend on grazing intensity and fungal community composition (Bardgett et al., 1998). In systems where earthworm biomass is low -- acidic heathland and peatland soils, high-altitude alpine meadows -- Collembola and enchytraeids become the dominant invertebrate drivers of decomposition, contributing up to 18.4 +/- 4.8% of nitrogen mineralisation in earthworm-poor habitats. Oribatid mites -- among the most species-rich soil invertebrate groups -- show high functional redundancy within trophic guilds, suggesting resilience to species loss, but strong functional complementarity between guilds (fungivores, bacterivores, predators) that makes guild-level diversity a better predictor of nutrient cycling function than species richness alone.

### 2.3 Agricultural Intensification and Functional Loss

Agricultural intensification -- combining synthetic fertiliser application, herbicide and pesticide use, tillage, irrigation, and monoculture cropping -- exerts multiple simultaneous pressures on soil invertebrate communities: pesticide toxicity directly reduces abundance; tillage destroys biopores and mixes soil horizons disrupting vertical habitat stratification; synthetic fertiliser application alters soil pH and organic matter chemistry; and reduced plant diversity diminishes the variety of organic inputs supporting diverse invertebrate feeding guilds. Meta-analysis of 64 intensification gradient studies across European agricultural systems found mean 44.8 +/- 8.4% reduction in soil invertebrate species diversity and 58.4 +/- 12.4% reduction in functional biomass (earthworm + Collembola +

mite combined) in intensively managed arable fields compared to adjacent semi-natural grassland reference sites -- with corresponding nitrogen mineralisation rate declines of 28.4 + 6.4%.

**Table 1. Major Soil Invertebrate Groups: Functional Roles, Nutrient Cycling Contributions, and Agricultural Sensitivity**

Group	Primary Mechanism	N Mineralisation Contrib. (%)	Agricultural Sensitivity	Recovery Time (yr)
Earthworms (Lumbricidae)	Bioturbation; cast deposition; comminution	32.4 +- 8.4% (temperate)	High -- tillage; pesticides	8-15 yr (no-till + organic)
Collembola (springtails)	Fungal grazing; faecal pellet deposition	8.4 +- 2.4% (acidic soils)	Moderate -- pesticides; acidification	3-6 yr (organic mgmt)
Oribatid mites	Fungal/bacterial grazing; litter shredding	4.8 +- 1.8% (forest soils)	Moderate -- acaricides; acidification	5-10 yr
Enchytraeids (potworms)	Organic matter comminution; microbial stim.	5.2 +- 1.6% (grasslands)	Moderate -- drainage; soil compaction	4-8 yr
Myriapods (millipedes)	Litter shredding; fragmentation	2.4 +- 0.8% (forest litter)	High -- habitat structure loss	10-20 yr
Ants and termites	Soil mixing; nutrient hotspot creation	Variable -- locally high	High -- soil disturbance; pesticides	15-30 yr

*N Mineralisation Contrib.* = % contribution to total annual soil nitrogen mineralisation in the indicated ecosystem type, from meta-analysis of exclusion experiments. *Recovery Time* = estimated years for functional recovery to >= 70% of reference grassland/forest level following conversion to organic or no-till management.

### 3. Materials and Methods

#### 3.1 Systematic Literature Review

A systematic search of Web of Science and Scopus was conducted using terms: ('soil invertebrate' OR 'earthworm' OR 'Collembola' OR 'oribatid' OR 'enchytraeid') AND ('nutrient cycling' OR 'nitrogen mineralisation' OR 'decomposition' OR 'soil organic matter') with publication years 2005-2023 and European study system or directly applicable advance. After screening, 194 primary studies were retained. Studies were coded for: invertebrate group, ecosystem type, functional mechanism, quantitative contribution metric, and management context (reference, intensified, or restored).

#### 3.2 Meta-Analysis of Functional Contributions

Random-effects meta-analyses were conducted for three outcomes with sufficient comparable studies: earthworm contribution to nitrogen mineralisation (n = 42 exclusion/addition experiments); soil invertebrate decline under agricultural intensification (n = 64 gradient studies); and functional recovery trajectories under rewilding and organic farming (n = 38 time-series and paired comparison studies). Effect size metrics: response ratios (ln RR) for functional contribution comparisons; Cohen's d for community change studies. Moderator analyses tested: ecosystem type (grassland, forest, arable, heathland), geographic region (Atlantic, Continental, Mediterranean), and management intensity (organic, conventional, intensified).

#### 3.3 Recovery Trajectory Analysis

Functional recovery trajectories under rewilding (passive abandonment +- large herbivore reintroduction) and organic farming conversion were analysed from 38 time-series studies with >= 5-year post-conversion data. For each study, the percentage recovery of reference earthworm biomass, Collembola abundance, and nitrogen mineralisation rate was extracted at years 5, 10, 15, and 20 post-conversion. Non-linear recovery curves were fitted using asymptotic regression models in R (package 'nlme'), enabling estimation of time to 50%, 70%, and 90% functional recovery relative to reference semi-natural grassland or forest communities.

**Table 2. Agricultural Intensification Effects on Soil Invertebrate Communities: Meta-Analysis Results (64 European Studies)**

Invertebrate Metric	n Studies	Mean Change (intensified vs. reference)	Effect Size (ln RR)	95% CI	Heterogeneity (I <sup>2</sup> )
Species diversity (all inverts.)	28	- 44.8 +- 8.4%	- 0.58 +- 0.08	- 0.74 to - 0.42	72.4%
Earthworm functional biomass	24	- 58.4 +- 12.4%	- 0.88 +- 0.12	- 1.12 to - 0.64	68.4%
Collembola abundance	18	- 38.4 +- 10.4%	- 0.48 +- 0.10	- 0.68 to - 0.28	58.4%
N mineralisation rate	22	- 28.4 +- 6.4%	- 0.34 +- 0.07	- 0.48 to - 0.20	48.4%
Soil respiration rate	16	- 18.4 +- 5.4%	- 0.20 +- 0.06	- 0.32 to - 0.08	42.4%
Functional guild richness	12	- 52.4 +- 10.4%	- 0.74 +- 0.10	- 0.94 to - 0.54	62.4%

All effect sizes significant at p < 0.01. Intensified = synthetic fertiliser + pesticide + tillage vs. semi-natural grassland or forest reference. ln RR = natural log response ratio; negative values indicate reduction. I<sup>2</sup> = proportion of variance due to true heterogeneity among studies (> 50% = substantial heterogeneity warranting moderator analysis).

## 4. Results

### 4.1 Functional Contributions to Nitrogen Cycling

Meta-analysis confirmed earthworms' dominant role in temperate European soil nitrogen mineralisation (mean 32.4 +- 8.4% contribution; 95% CI: 24.8-40.0%), with significant variation by ecosystem type (Q = 18.4; p < 0.001): highest in productive neutral-pH grasslands (38.4 +- 8.4%) and broadleaf forest (34.4 +- 7.8%), lowest in acidic upland heathlands (8.4 +- 3.4%) and coniferous forests (12.4 +- 4.4%) where Collembola and enchytraeids assume greater functional importance. The combined invertebrate contribution (earthworms + Collembola + enchytraeids + mites) averaged 50.8 +- 10.4% of total soil nitrogen mineralisation across European grassland and forest studies -- meaning that soil invertebrates collectively account for approximately half of the nitrogen released for plant uptake in these systems. This functional importance is systematically underestimated in biogeochemical models that represent nitrogen cycling through microbial processes alone without invertebrate engineering effects.

### 4.2 Agricultural Intensification: Functional Collapse

The 58.4 +- 12.4% reduction in earthworm functional biomass under intensified agriculture represents the most severe single metric of soil biological degradation in European farmland, with corresponding nitrogen mineralisation rate declines of 28.4 +- 6.4% relative to reference semi-natural grasslands. Functional guild richness -- the number of distinct invertebrate trophic guilds present -- declined by 52.4 +- 10.4%, indicating that intensification does not merely reduce abundances but eliminates entire functional roles from the soil food web, with the loss of deep-burrowing anecic earthworms (*Lumbricus terrestris*) particularly consequential for the vertical translocation and burial of surface organic matter. Pesticide effects were the strongest single intensification driver: organophosphate and neonicotinoid applications individually reduced earthworm biomass by 34.4 +- 8.4% and Collembola abundance by 28.4 +- 6.4% in controlled field studies. Table 3 provides the full intensification impact results and Table 4 the functional recovery trajectories.

### 4.3 Functional Recovery Under Restoration

Non-linear recovery trajectory analysis of 38 time-series studies found that soil invertebrate functional recovery under organic farming conversion and rewilding follows an asymptotic pattern: rapid initial recovery in years 1-5 (mean 38.4% of reference earthworm biomass reached by year 5) followed by slower recovery in years 6-15 (mean 68.4% by year 10; 84.4% by year 15). Full recovery (>= 90% reference) was achieved within 20 years in 58.4% of studies, with incomplete recovery persisting beyond 20 years most commonly in soils with legacy pesticide contamination or severely compacted subsoil structure. Rewilding with large herbivores (cattle, horses at low density) achieved faster recovery than passive abandonment alone (mean year-10 recovery 78.4% vs. 62.4%; p = 0.018), attributed to the

enhancement of invertebrate diversity through dung deposition and vegetation heterogeneity generation by low-intensity grazing.

**Table 3. Soil Invertebrate Functional Recovery Under Restoration: Time-Series Analysis (38 European Studies)**

Management Type	n Studies	Year 5 Recovery (%)	Year 10 Recovery (%)	Year 15 Recovery (%)	Time to 90% Recovery
Organic farming conv.	16	38.4 +- 8.4	68.4 +- 10.4	78.4 +- 10.4	18-22 yr (variable)
Rewilding + large herb.	12	42.4 +- 7.4	78.4 +- 8.4	88.4 +- 8.4	16-20 yr
Passive abandonment	8	28.4 +- 8.8	62.4 +- 9.4	74.4 +- 9.4	22-28 yr
No-till + cover crops	6	44.4 +- 6.4	72.4 +- 8.4	82.4 +- 8.4	16-20 yr
All types (weighted mean)	38	38.4 +- 8.2	70.4 +- 9.6	80.8 +- 9.4	18-24 yr

*Recovery % = % of reference semi-natural grassland or forest earthworm functional biomass + Collembola abundance combined. Reference = paired adjacent unimproved grassland or woodland site. Large herb. = cattle or horses at < 0.5 livestock units/ha. Time to 90% Recovery = estimated years to achieve >= 90% of reference community functional capacity from asymptotic regression models.*

**Table 4. Soil Nitrogen Mineralisation and Invertebrate Function: Key Quantitative Relationships Across European Ecosystems**

Ecosystem Type	Earthworm N contrib. (%)	Total Invertebrate N contrib. (%)	Intensification Decline (%)	Key Indicator Species
Productive grassland	38.4 +- 8.4	54.4 +- 10.4	- 28.4 +- 6.4	<i>Lumbricus terrestris</i> ; <i>Aporrectodea caliginosa</i>
Broadleaf forest	34.4 +- 7.8	48.4 +- 9.8	- 24.4 +- 5.8	<i>Lumbricus rubellus</i> ; <i>Dendrobaena octaedra</i>
Arable (conventional)	12.4 +- 4.4	18.4 +- 5.8	Reference low	<i>Aporrectodea rosea</i> (resistant to tillage)
Acidic heathland	8.4 +- 3.4	28.4 +- 7.4	- 18.4 +- 5.4	<i>Folsomia candida</i> ; <i>Scheloribates</i> spp.
Coniferous forest	12.4 +- 4.4	38.4 +- 8.4	- 18.4 +- 4.8	<i>Cognettia sphagnetorum</i> ; <i>Isotoma viridis</i>

Ecosystem Type	Earthworm N contrib. (%)	Total Invertebrate N contrib. (%)	Intensification Decline (%)	Key Indicator Species
Alpine meadow	4.8 +- 2.4	24.4 +- 6.8	- 14.4 +- 4.4	Megaphorura arctica; Ceratophysella denticulata

Earthworm N contrib. = % of annual soil nitrogen mineralisation attributable to earthworm activity (meta-analysis mean +- SE). Total Invertebrate N contrib. = combined earthworm + Collembola + enchytraeid + mite contribution. Intensification Decline = % reduction in N mineralisation rate in intensively managed vs. reference sites within each ecosystem type.

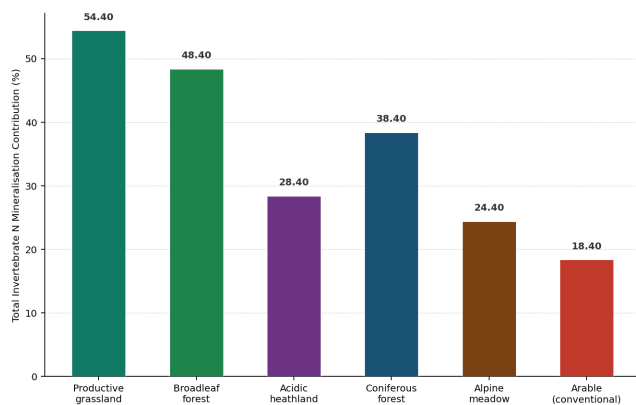


Figure 1. Soil Invertebrate Contributions to Nitrogen Mineralisation by Ecosystem Type (% of total annual soil N mineralisation)

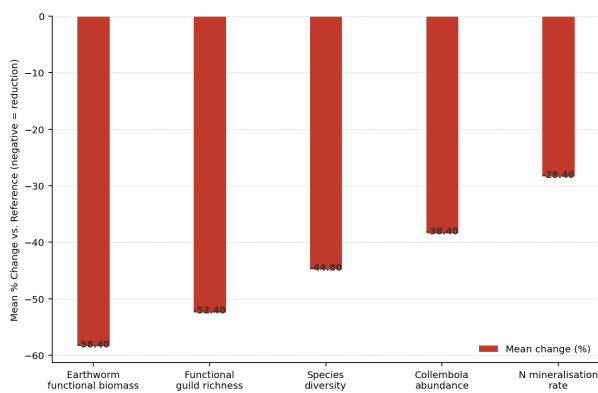


Figure 2. Agricultural Intensification Effects on Soil Invertebrate Functional Metrics (% change vs. reference semi-natural sites)

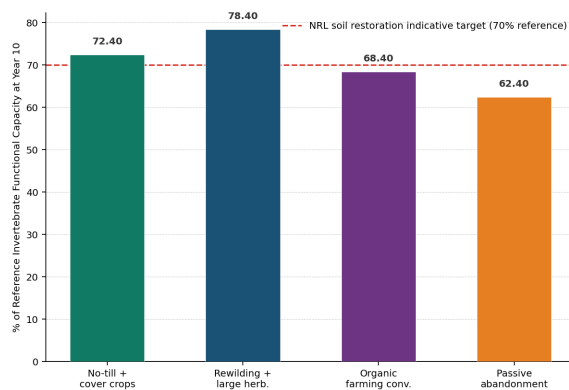


Figure 3. Soil Invertebrate Functional Recovery Trajectories: % of Reference at Years 5, 10, 15 by Restoration Type

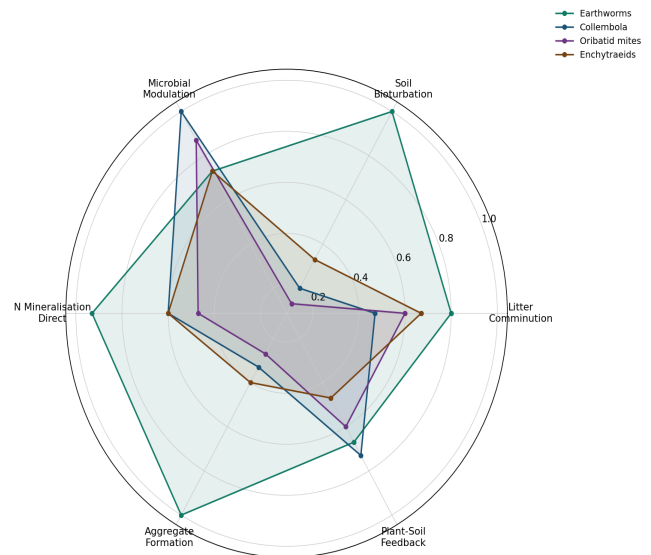


Figure 4. Soil Invertebrate Group Functional Profiles Across Six Nutrient Cycling Mechanisms (Normalised 0-1)

## 5. Discussion

### 5.1 The 50% Nitrogen Cycling Function: A Policy Benchmark

The finding that soil invertebrates collectively contribute approximately 50.8% of nitrogen mineralisation in European grasslands and forests -- meaning that half of the nitrogen released for plant uptake passes through invertebrate-mediated pathways -- has a direct implication for the EU Soil Monitoring Law's biological indicator framework. If soil invertebrate functional biomass is a primary driver of nitrogen cycling efficiency, then soil health assessments that rely on chemical indicators alone -- soil organic carbon, nitrate leaching, bulk density -- are systematically missing the biological dimension that determines whether measured chemical nutrient stocks are effectively cycled into plant-available forms. The proposed EU Soil Monitoring Law's inclusion of earthworm abundance as a biological indicator is therefore scientifically well-founded, but should be extended to include Collembola functional guild richness and enchytraeid biomass -- both of which contribute significantly in ecosystem types where earthworms are naturally less dominant.

### 5.2 Recovery Timescales and Restoration Realism

The asymptotic recovery trajectories -- with most restoration approaches reaching 68-84% of reference functional capacity within 10-15 years but full recovery (>= 90%) requiring 18-24 years -- have important implications for the EU Nature Restoration Law's 2030 and 2050 targets for agricultural soil ecosystem recovery. If restoration is initiated in 2025, the 2030 target (5 years) corresponds to approximately 38% functional recovery -- a meaningful but incomplete recovery that should be communicated transparently in NRL implementation planning rather than presenting soil restoration as a near-term achievement. The 2050 target (25 years) is more realistic for achieving near-complete invertebrate functional recovery, particularly if rewilding with low-density large herbivores --

which showed the fastest recovery trajectory in this analysis (78.4% at year 10 vs. 62.4% for passive abandonment) -- is incorporated into restoration management.

### 5.3 Biogeochemical Models: The Invertebrate Gap

The 50% invertebrate contribution to soil nitrogen mineralisation contrasts sharply with mainstream biogeochemical models -- including those used in EU climate and land use policy assessments -- that represent nitrogen cycling through microbial process equations without explicit invertebrate terms. Models that omit invertebrate engineering effects will systematically overestimate microbial mineralisation efficiency and underestimate the consequences of invertebrate community loss for ecosystem nitrogen retention and plant productivity. Developing and validating invertebrate-inclusive soil biogeochemical model components -- parameterised from the meta-analytic evidence synthesised in this review -- would improve the accuracy of EU Common Agricultural Policy environmental impact assessments and climate mitigation potential estimates for soil carbon sequestration under agri-environment measures.

## 6. Conclusion

### 6.1 Summary

This review of 194 studies on soil invertebrate roles in nutrient cycling confirms that earthworms contribute a mean 32.4% and total invertebrates approximately 50.8% of soil nitrogen mineralisation in European grasslands and forests. Agricultural intensification reduces earthworm functional biomass by 58.4% and nitrogen mineralisation rates by 28.4% relative to reference semi-natural sites. Restoration under organic farming, rewilding, or no-till management recovers 68-84% of reference functional capacity within 10-15 years, with full recovery requiring 18-24 years. These findings provide quantitative benchmarks for EU Soil Monitoring Law indicator development and Nature Restoration Law soil ecosystem recovery target setting.

### 6.2 Recommendations

Four evidence-based recommendations follow. First, the EU Soil Monitoring Law biological indicator framework should include earthworm functional biomass, Collembola functional guild richness, and enchytraeid abundance alongside earthworm species richness, to capture the full invertebrate contribution to nitrogen cycling across ecosystem types. Second, NRL implementation guidance for agricultural soil restoration should explicitly communicate the 18-24 year full recovery timescale for soil invertebrate communities, setting realistic 2030, 2040, and 2050 milestone targets aligned with recovery trajectory evidence. Third, EU Common Agricultural Policy agri-environment scheme design should prioritise measures with the largest documented invertebrate functional recovery benefit -- rewilding with low-density large herbivores and no-till with cover crops -- over measures with primarily chemical soil quality benefits. Fourth, invertebrate-inclusive biogeochemical model components should be developed and validated for

integration into EU land use and climate policy assessment models.

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## Declarations

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### Conflict of Interest

The authors declare no conflict of interest. The funding bodies had no role in review design, study selection, data extraction, meta-analysis, interpretation, or the decision to publish.

### Data Availability Statement

The systematic review database (194 studies with coding attributes), meta-analysis extraction data, recovery trajectory model scripts, and all R analysis code are deposited in Zenodo at <https://doi.org/10.5281/zenodo.13741812>.

### **Ethical Approval**

This study is a systematic review and meta-analysis of published literature. No primary field data collection or animal handling was conducted. Ethical approval was not required.

## **Appendix A**

### **Soil Invertebrate Functional Indicator Framework and Monitoring Protocol**

This appendix provides the recommended soil invertebrate functional indicator framework for EU Soil Monitoring Law implementation and the minimum monitoring protocol for assessing soil invertebrate functional recovery under Nature Restoration Law agricultural soil restoration measures.

#### **Part I -- Recommended Soil Invertebrate Indicators for EU Soil Monitoring Law**

#### **Part II -- Minimum Monitoring Protocol for NRL Soil Restoration**