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Cadaver imprint on soil chemistry and microbes - Knowns, unknowns, and perspectives

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Cadaver-decomposition unleashes an ephemeral pulse of matter input that modifies microbial communities, as well as nutrient pools and fluxes. This leaves behind a measurable imprint on affected soils. However, the persistence of this imprint remains poorly understood. We define cadaver imprint persistence as the entire period between time of cadaver deposition and time when cadaver effects on microbial community structure and chemical indicators are no longer detectable. We present a brief overview of published results on the cadaver-induced changes in the bio-elements carbon, nitrogen and phosphorus, which regulate the structure and functions of the soil microbiome. Based on this, we identified conceptual and methodological gaps and biases and suggest potential research avenues to address them. This will help to better understand the relationships between cadaver-derived matter and microbial taxa and functions, as well as the role of cadaver-decomposition within and across ecosystems. The proposed future research on cadaver-derived imprint on soils has the potential to serve as a hub for connecting soil chemistry, microbial ecology, forensic sciences, and ecosystems science.

KEYWORDS

cadaver decomposition, bio-elements, soil properties, C, N, P, microbial communities

1 Introduction

After death, the remains of all organisms undergo decomposition. Decomposition of dead material is central to the functioning of all ecosystems and crucial to the redistribution of nutrients and energy (1). It unleashes an ephemeral pulse of matter input that modifies microbial communities as well as nutrient pools and fluxes, leaving behind a measurable imprint on the affected soil (2). The imprint is influenced by a complex set of factors, with interactions between soil microbes and the fluxes of matter and nutrients released by dead material decomposition playing a central, yet poorly understood role (3).

Research on decomposing dead material is predominately focused on plant litter. By contrast, the decay of cadavers has received far less attention. This might be mainly due to animal-derived biomass representing only 1% of the total organic material exposed to decomposition in terrestrial ecosystems (4). Research on cadaver decomposition mainly addresses two issues: (i) successional patterns of different cadaver-related organisms in various taxa, such as bacteria or protists, especially in order to determine the post-mortem interval (5, 6) and (ii) spatial patterns of energy and nutrient flow within and among ecosystems (7–9). Studies targeting spatial patterns have highlighted the key role of cadaver decomposition for shaping environmental heterogeneity (10), but provided no information about the mechanisms involved. Studies of temporal changes in soil chemistry (9, 11, 12) and/or microbial communities in response to cadaver decomposition revealed different decomposition stages (13–17), each characterized by specific microbial taxa (18, 19). Typically, these studies were restricted to determining the imprint of cadaver decomposition on soil chemical and microbial features but payed little attention to the functional linkages between microbes and matter and nutrient fluxes. As a consequence, little is known about the cycling (including translocation, transformation, and immobilisation) of matter that enters the soil during cadaver deposition. Similarly, the contribution of specific microbial taxa and functional groups to processes induced by the input of cadaver-derived matter (e.g., breaking down and transforming dead organic material) remains poorly understood (3, 20). In addition, different cadaver types and weights have been studied – ranging from mice (20) to elephants (15), which influences the extent and persistence of the cadaver imprint on soil and makes comparisons among studies difficult. Studies have also considered different time scales – from two weeks (21) to several years (22). Studies based on the same cadaver type and weight and lasting for several years are rare. The resulting knowledge gaps limit our capability of predicting the impact of cadaver decomposition on soil ecosystems, and thus, hamper the deduction of precise timescales of the individual decomposition stages (23–25) as well as of the extent and persistence of cadaver imprint on soil.

We aim at identifying the key issues impairing the study of cadaver imprint on soil ecosystems for better insight into the functional linkages between microbes and soil matter cycling. We address the potential persistence of changes in carbon (C), nitrogen (N), phosphorus (P), bio-elements that regulate structure and functioning of the soil microbiome (cell compounds, biomass production, activity, energy transfer; Figure 1). We define the persistence of cadaver imprint on soil as the entire period between time of cadaver deposition on soil and time when cadaver effects on microbial community structure and chemical indicators are no longer detectable. Cadaver imprint persistence of 3 (22) to 10 years (11) were already observed, which clearly exceeds the typical duration of most experiments (<1 (26) to 2 years (27)).

We start with a brief summary of the current state of knowledge on temporal changes in soil induced by cadaver decomposition, followed by a list of identified major research issues and their possible relevance for the understanding cadaver-impacted soils. Finally, we propose potential research avenues to overcome these issues.

2 Imprint of cadaver-derived C, N, and P in soil

Cadavers are point sources of bio-elements, exposing the soil underneath to high inputs. These inputs can cause locally elevated concentrations of elements, but their persistence is poorly known and likely varies by element (28, 29). The amount of elemental release and input into soil is a function of cadaver weight (30) and decomposition stage (12). The persistence of elemental changes varies with soil properties affecting their transport and retention (31, 32).

The biochemical composition of cadavers resembles that of major degraders. The stoichiometries of major bio-elements is similar (33). This promotes rapid utilisation of cadavers for biomass growth of degraders, such as bacteria and other microbial taxa, with the extent being modified by environmental conditions controlling the balance of biomass built-up and mineralisation.

The potential imprint of cadaver-derived C depends on soil conditions supporting the long-term stabilisation of microbial metabolites and necromass (34). In contrast to plants, cadavers contain much of the C in compounds prone to simple enzymatic breakdown, such as lipids, sugar derivatives, and protein (13). Consequently, cadaver fluids are rapidly consumed by microorganisms upon entering the topsoil, with only small portions leached into deeper soil layers (35). Efficient C use by microorganisms results in production of metabolites and built up of microbial biomass (36). In soils containing reactive minerals (three-layer clay minerals,

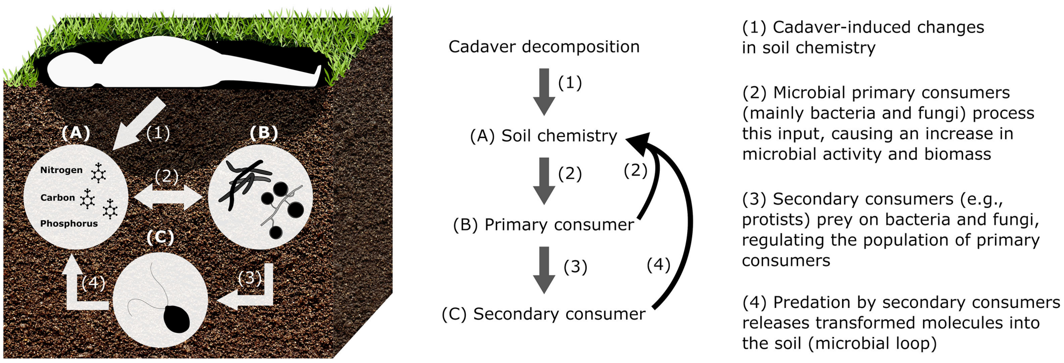

FIGURE 1
Simplified scheme of cadaver imprint on soil, including coupled chemical-microbial processes. **(A)** Cadaver-induced nutrient and matter changes soil chemistry. **(B)** Microbial primary consumers (mainly bacteria and fungi) process the cadaver-derived input and subsequent increase in microbial activity and biomass. **(C)** Secondary consumers (e.g., protists) prey on bacteria and fungi, and thus, regulate the population of primary consumers and the release of transformed molecules into the soil. Please note, temporal and spatial facets are not considered, since largely unknown. Furthermore, the rest of the food chain including plants, meso- and macro-fauna is not shown since we focus on soil chemistry and microbes.

hydrous oxides of aluminum and iron), part of the microbial metabolites and necromass becomes mineral-bound, and thus, stabilized against degradation (37). This could increase C storage underneath cadavers (38), however, the period of time until it vanishes is unknown. In soils where the mineral phase is not supporting stabilisation of organic compounds or, as in many topsoils, is already saturated, microbial metabolites and necromass will cycle rapidly. Rapid metabolization of cadaver-derived C and subsequent release into the atmosphere as CO_2 and/or CH_4 explains the often insignificant increase in total C content in soil directly underneath decomposing cadavers (39, 40). High input of easily available C beneath cadavers can even cause decreases in soil C due to what is commonly referred to as priming (41, 42). Additionally, microbial oxidation of available C may result in O_2 consumption underneath cadavers exceeding its replenishment *via* diffusion (43). The resulting anoxic conditions may drive the fate of cadaver-derived N (44) and support C losses *via* anaerobic respiration.

Cadavers, due to their narrow C/N ratios (<6) (45), represent an immense N concentration as compared to the underlying soil, which is often N limited (46). Most N in cadavers is within proteins but also amino sugars (13), which are all prone to simple enzymatic breakdown. Cadaver fluids delivers proteins into the soil; their subsequent decomposition cause increasing concentrations of free amino acids, peptides, and mineral N species (38). Solutions underneath cadavers feature often very narrow C/N ratios due to the production of amines (47). These might become leached from the soil or rapidly degraded, to unknown extents. Under toxic conditions, N mineralisation results in nitrate, which is mobile and easily leachable from soil in case production exceeds uptake by plants and microorganisms. In alkaline soils, ammonium released during decomposition may deprotonate and the resulting gaseous ammonia can be emitted into the atmosphere (48). Under anoxic conditions, which may establish under cadavers upon excessive O_2 consumption (see above), nitrate is transformed into gaseous forms (N_2, N_2O) and released into the atmosphere. Anoxic conditions, however, terminate nitrification, and so N mineralisation is limited to the release of ammonium. Nevertheless, much of cadaver-derived N becomes incorporated into the microbial biomass and is linked to its stabilization and cycling, as described for C. Overall, it seems unlikely that cadaver-derived N accumulates more strongly in soils than cadaver-derived C. And as for C, it remains unresolved how long the imprint of the tremendous N input from cadavers into underlying soils will last.

Cadaver residues are also high in P, which – aside of bones – is mainly contained in phospholipids and nucleotides. These compounds are labile, and cleavage of phosphate ester bonds results in rapid release of ortho-phosphate (49). In contrast to C and N, P is rather immobile in most soils (50). Organic and especially mineral P species tend to sorb strongly to soil minerals, and therefore, are not prone to leaching as, e.g., nitrate. Also, P cycling in soils does not involve formation of gaseous species. However, P has been less frequently considered in studies on cadaver decomposition than C and N. Therefore, little is known about the potential intermediate storage of P in microorganisms (49, 51). On short-term, a strong increase in microbial P can be expected in the soil underneath cadavers. On long term, the overall low mobility of P is probably the decisive factor. Thus, of all bio-elements, P is likely to leave the strongest and longest lasting imprint on soils underneath cadavers (31).

3 Imprint of cadaver decomposition on soil microbial communities

The changes in soil C, N, and P following cadaver decomposition described above induce a strong response by soil microbial communities. The high input of bio-elements significantly changes their biomass, activity, diversity, and composition (18, 52, 53), with taxa-specific temporal trends varying with environmental conditions (18).

3.1 Microbial biomass and activity

Since free-living soil microorganisms are strongly C-limited (54), the C input derived from cadaver decomposition stimulates microbial activity and may promote biomass production. However, activity and biomass of some taxa, such as testate amoeba, are negatively impacted by the high input of bio-elements (22, 55). The effect of N and P on microbial biomass and activity is far less known. Soil microbial activity can start increasing within 24 hours (56–58) and peak within the first ten days after death (18, 59). Microbial biomass production peaks during the active decay phase and slows down thereafter (18). The exact timing and magnitude of the peaks depend on environmental conditions, such as temperature, with microbial biomass production being potentially more affected than activity (58). After their initial peaks, microbial biomass and activity can remain elevated for a long period of time. For instance, microbial biomass C remained elevated for 430 days after burial of pig cadavers (60) and bacteria colony forming units were found to be increased in soil underneath the carcasses for even 42 months after burial (61). Since burial can slow down decomposition (62, 63), the results of the latter two studies may not be representative for aboveground cadavers.

It is noteworthy that the different methods used to determine microbial biomass (e.g., substrate-induced respiration (60), lipid-P extraction (12), chloroform-fumigation extraction (64), colony-forming units (61), and microbial activity/carbon mineralisation (58)) all capture different fractions of the soil microbial biomass or activity, which may contribute to diverging conclusions by individual studies.

3.2 Diversity and community composition

Advances in high-throughput multi-taxa identification using environmental DNA (65, 66) allowed for better characterization and understanding of changes in microbial community diversity and composition induced by cadaver decomposition.

The initial input pulse of nutrients constitutes a major disturbance of the soil microbial food web. This disturbance causes decreased microbial diversity by favouring few well-adapted taxa. In a deciduous forest, decomposing pig cadavers caused a drastic decrease in the abundance and richness of testate amoebae (22, 55). In turn, the relative abundance of *Proteobacteria* and *Firmicutes* increased while that of *Acidobacteria* decreased during the phase of active decomposition of human remains (18). Generally, studies point at a clear succession in microbial communities during cadaver decay, with the majority of microbial taxa occurring only during specific decomposition stages (53, 67). Nevertheless, the specific role of the different microbial taxa and functional groups in breaking down and transforming cadaver material remains poorly known.

Effects of cadaver impact on soil microbial community composition are long-lasting and vary as a function of the environmental settings (68). Differences in soil microbial community composition between cadaver-impacted and control plots were detectable for up to 1051 days (22). Interestingly, cadaver imprint on the microbial community composition appears to last longer than its imprint on functions. For instance, the study of Singh et al. (69) observed 732 days after the onset of cadaver decomposition only differences in soil bacterial community composition but not in soil functions. It has also been shown there is microbial fauna specifically associated with cadaver decomposition, including an important proportion of taxa not yet described (22). Only about 40% of these organisms are present in bulk soil while the remaining ones come from various sources, including blow flies and other scavengers, or derive from the cadaver itself (70).

4 Research gaps and perspectives

When compiling the literature, we identified gaps and biases in research on the fate of cadavers and related matter cycling in soil (Table 1). We grouped them according to three broad overarching issues, arranged hierarchically.

We propose that the first priority should be to address conceptual shortcomings, since a strong conceptual framework directly contributes to tackling methodological issues and scale and context dependencies. For instance, holistic approaches based on profound theoretical frameworks, e.g., ecological stoichiometry theory (33), metacommunity theory (71), meta-ecosystem theory (72) can help identifying mechanistic relationships and causal linkages among microbial taxa and functional groups and matter fluxes, as well as their role for the rest of the food chain

TABLE 1 Identified gaps and biases in studies on the imprint of cadaver-derived biomass on soil ecosystems.

Overarching issues	Gaps and biases	Research avenues and -> perspectives
(1) **Conceptual shortcomings**	Incomplete theoretical framework	Development of a theoretical framework to explain the formation and persistence of cadaver imprint on soil -> Conceptualization and contextualization: links between observed patterns and identified processes -> Modelling: improved predictions and hypotheses to guide future experiments
	Non-holistic approach	Focus on matter cycling and coupled chemical and biotic processes in soil -> Identification: causal relationships and mechanistic linkages between microbe and matter fluxes and their role in soil ecosystem dynamics
(2) **Experimental shortcomings**	Insufficient documentation of descriptors of environmental and experimental settings	Definition of best practice in reporting experimental procedures and environmental settings (e.g., location, soil, climate, cadaver type and weight) -> Improvement: reproducibility and transparency of studies -> Facilitation: meta-analyses, and identification of indicators of system change
	Insufficient focus on soil imprint in sampling design (as opposed to current cadaver decomposition stage-centred sampling scheme)	*In-situ* continuous measurements of key variables indicating soil system changes (e.g. redox potential) -> Characterization: temporal changes in cadaver-impacted soil ecosystems (i.e. cadaver imprint on soil), including potential tipping points -> Identification: key sampling moments
	Underrepresentation of studies on buried cadaver	Comparative studies on the imprint of cadavers buried at different depths -> Determination: rates of belowground decomposition processes and their variability
	Insufficient long-term investigations beyond one year	Longer-term studies that last until no differences to control can be detected -> Understanding: long-term persistence of cadaver imprint on soil
	Taxonomic biases in studies on microbial communities	Systematics and metagenomics of cadaver-associated microbial taxa -> Identification: functional role of less-studied taxa such as archaea and protists -> Understanding: feeding of energy and matter derived from cadavers into the microbial loop
(3) **Context- and scale-dependencies**	Drivers of the spatial extent and persistence of cadaver imprint	*In-situ* spatially- and temporally-resolved measurements of the changes and spatial distribution of elements and microbial taxa across multiple environmental contexts -> Identification of site-specific and regional drivers of: (1) the distribution of elements and microbial taxa, (2) element cycling and temporal changes in microbial community -> Assessment: context- and scale-dependency of the spatial extent and persistence of cadaver imprint on soils

The specific gaps and biases have been classified into three overarching issues. Potential research avenues are suggested to address each gap and bias. Although we focus on soil chemistry and microbes, the identified gaps also apply to soil meso- and macro-fauna.

(plants and soil meso- and macrofauna). Improved knowledge of these linkages is key to develop innovative long-term experimental approaches that allow for continuously tracking the progressing changes in cadaver-impacted soils and to identify microbial taxa with key functional roles. Promising indicators of continuous changes in soil include gas fluxes and redox potential. Comparative studies on cadavers buried at different depths, although technically challenging, are needed to determine the rates of belowground decomposition processes and their variability. Belowground decomposition has a relatively marginal importance for ecosystem processes but is highly relevant for forensic applications. Improved documentation of descriptors of environmental and experimental settings are required to facilitate meta-analyses and comparisons among studies dealing with different environmental conditions and spatial scales. This would allow for generalizing the scale and context dependency of the temporal persistence and spatial extent of cadaver imprint in different soil ecosystems. This knowledge would, in turn, feed back to the validation and/or improvement of the theoretical framework.

In conclusion, solving the identified issues will support better understanding the linkages between cadaver-derived matter and microbial taxa and functions, as well as the ecological role of cadaver decomposition within and across ecosystems. In turn, an improved mechanistic understanding of the cadaver imprint on soil ecosystems would contribute to better transferability of models and consequently scaling the role of cadaver decomposition in global organic matter cycle. Practically, it would also pave way to new forensic applications, including improved detection of buried cadavers, identification of new bioindicators, and prediction and mapping of potential cadaver imprint persistence according to regions. Overall, the proposed future research on cadaver-derived imprint on soils has the potential to serve as a hub for connecting soil chemistry, microbial ecology, forensic sciences, and ecosystems science.

Author contributions

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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