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PERSPECTIVES

Benefits of conductive additive for direct interspecies electron transfer in anaerobic digestion

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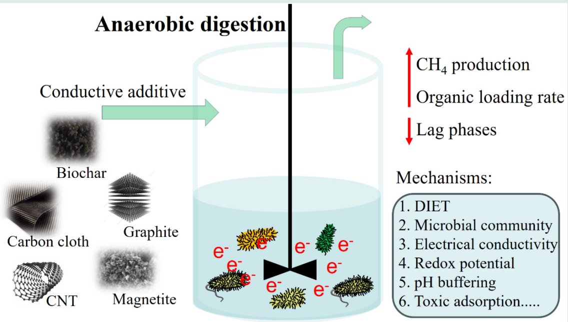
HIGHLIGHTS

- DIET enables direct electron transfer between syntrophic microbes.
- Evidence for conductive additive-facilitated DIET is mostly indirect.
- Direct validation is crucial to validate DIET's role in AD.
- Distinguishing DIET from other mechanisms is key for AD optimization.



ABSTRACT: Conductive additive such as biochar have been extensively employed to enhance anaerobic digestion (AD) performance for over a decade. Among the proposed mechanisms, conductive additive-facilitated direct interspecies electron transfer (DIET) is frequently cited as a key contributor to these performance improvements. Because this process is believed to bypass traditional diffusible intermediates (e.g., H_2 or formate), it can enable more efficient energy transfer between syntrophic partners and accelerate substrate degradation, potentially leading to higher methane yields and improved overall stability of the anaerobic digestion process. However, benefits regarding conductive additive-facilitated DIET often rely on indirect indicators rather than direct experimental evidence. Here, we advocate for a critical reassessment on the benefits of conductive additive for DIET in AD. Specifically, we emphasize the importance of establishing standardized experimental protocols and obtaining direct evidence to confirm the occurrence and significance of DIET in conductive additive-amended AD system. Furthermore, it is essential to distinguish DIET from other enhancement mechanisms such as pH buffering and toxin adsorption that may independently contribute to improved AD performance, with the goal of advancing its practical implementation.

KEYWORDS: Conductive additive, Direct interspecies electron transfer, Anaerobic digestion, Mechanism, Evaluation

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Special Issue—Visions

1 Introduction

Anaerobic digestion (AD) is a microbial process that breaks down organic waste, yielding energy (e.g., methane) and nutrient-rich digestate. Direct interspecies electron transfer (DIET) was first reported in 2010 by David R. Lovley, who observed electrically conductive aggregates (conductive type IV pili and c-type cytochromes) facilitated electron transfer between two *Geobacter s*pecies in a co-culture system (Summers et al., 2010). Compared to conventional mediated interspecies electron transfer (MIET), which depends on the diffusion of soluble electron carriers such as hydrogen or formate, DIET allows for direct and rapid electron exchange between syntrophic partners (Fig. 1) (Martins et al., 2018). This process significantly enhances AD performance by improving system efficiency, stability, and methane production (Wang et al., 2023; Chen et al., 2024). In addition, abiotic conductive materials, such as biochar, Fe_2O_3, magnetite, activated carbon, carbon cloth, and others, have been reported to facilitate DIET by bridging the electron transfer between acidogenic bacteria and methanogens (Nguyen et al., 2021; Akram et al., 2024). Among them, biochar as a charcoal-like material produced via the pyrolysis of organic waste under low-oxygen conditions has been widely applied and extensively studied for AD systems due to its low costs and environmental sustainability (He et al., 2022; Zhang et al., 2023; Zhou et al., 2025). Therefore, in this perspective, biochar is used as a representative example to illustrate the general benefits of conductive additives in facilitating DIET within AD processes. Biochar was first observed to stimulate DIET in 2014 in co-cultures of *Geobacter metallireducens* with *Geobacter sulfurreducens* or *Methanosarcina barkeri* (Chen et al., 2014). It is reported to promote syntrophic electron transfer via both physically conductive mechanisms and chemically mediated redox interactions (Wang et al., 2022; Wu et al., 2023). Consistent with other conductive additives, biochar-facilitated DIET is fre-quently proposed as a primary mechanism driving performance improvements in AD (Wang et al., 2023). However, evidence for conductive additive-facilitated DIET in AD is often based on indirect observations, such as 1) shifts in microbial community composition, 2) enrichment of putative DIET-associated taxa (e.g., *Geobacter*, *Methanothrix*), and 3) elevated methane production (Van Steendam et al., 2019). Besides, the absence of comprehensive mechanistic investigations and well-controlled experimental designs may lead to overestimation of conductive additive-facilitated DIET's role in AD, while underrepresenting alternative mechanisms and influencing factors.

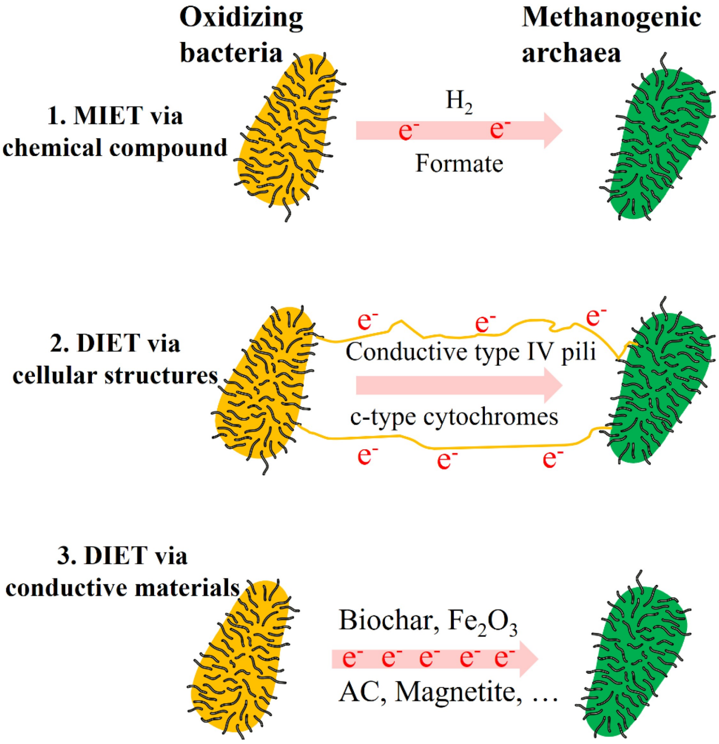

Fig. 1 Possible interspecies electron transfer mechanisms in AD system.

2 Elucidating the microbial mechanisms in conductive additive-facilitated DIET

Numerous studies have examined microbial community dynamics in conductive additive-amended AD, focusing primarily on diversity metrics and taxonomic composition shifts. However, the predominant reliance on conserved 16S rRNA gene amplicon sequencing has restricted these studies to superficial community-level assessments, thereby limiting the detection of functional microbial responses, particularly DIET-related metabolic microbes, linked to conductive additive amendment. Biochar amendment has been shown to selectively enrich known DIET-capable taxa, including *Geobacter*, *Sphaerochaeta*, *Clostridiaceae*, *Methanosarcina*, and *Methanothrix* (Wang et al., 2022; Akram et al., 2024). Nevertheless, some putative DIET-associated microorganisms exhibit metabolic flexibility, allowing them to alternatively utilize MIET pathways. This underscores the complex interplay of electron transfer mechanisms in conductive additive-amended AD systems (Wu et al., 2023). Herein, meta-omics approaches should be implemented to systematically differentiate the molecular signatures of DIET and MIET pathways in conductive additive-amended AD system (Van Steendam et al., 2019). Since conductive additive such as biochar could concurrently enhance MIET via facilitating H_2 diffusion between syntrophic partners and providing a porous scaffold for biofilm development that optimizes microbial proximity and H_2/formate exchange efficiency (Wang et al., 2022).

The detection of DIET-associated functional genes (e.g., *pilA*, *omcS*), their transcripts, and corresponding proteins through integrated meta-omics approaches provides a comprehensive strategy for determining whether DIET pathways are actively engaged in conductive additive-amended AD systems. Quantifying both the abundance and expression levels of these molecular markers enables the differentiation of DIET from alternative interspecies electron transfer mechanisms, such as hydrogen- or formate-mediated pathways (Van Steendam et al., 2019; Ostos et al., 2024). To maximize interpretive power, meta-omics datasets should be coupled with temporal sampling across key operational stages (e.g., start-up, peak methane production, steady-state) and with comparative treatments (e.g., with vs. without conductive additives, or conductive vs. non-conductive controls). Statistical and network analyses can then determine whether DIET-related genes and proteins are significantly enriched or co-expressed within syntrophic consortia, specifically under conductive additive-amended conditions (Krohn et al., 2022; Zhu et al., 2024). This mechanistic validation framework can yield direct molecular evidence from the microbial network, providing a definitive demonstration of conductive additive-mediated enhancement of DIET in AD systems.

Additionally, the integrated application of fluorescence *in situ* hybridization with nanoscale secondary ion mass spectrometry, and stable isotope probing can further discrimination between DIET and diffusion-based MIET mechanisms by simultaneously resolving the correlation between interspecies distance, interspecies mixing, and cellular activity at single-cell resolution (Van Steendam et al., 2019). Besides, scanning electron microscopy coupled with energy-dispersive X-ray spectroscopy can show whether biochar particles are integrated within microbial aggregates, suggesting their potential role as conductive mediators in DIET. Additionally, future studies should prioritize investigating metabolic pathways in defined co-culture systems rather than in mixed microbial communities. Given that conductive additives can functionally substitute for components such as PilA and c-type cytochromes to facilitate DIET, exploring DIET-based co-culture formation using conductive additives presents a promising avenue. This is particularly relevant for microorganisms typically incapable of DIET, such as *Geobacter uraniireducens* and *Shewanella oneidensis*. Demonstrating that these organisms can engage in DIET under the amendment of conductive additives would provide compelling evidence for conductive additive's potential in enhancing DIET in AD (Akram et al., 2024). In addition, future studies could also employ targeted genetic approaches to dissect the mechanisms of conductive additive-facilitated DIET. In defined co-culture or bioelectrochemical systems, loss-of-function or knockdown mutants lacking key DIET-associated genes (e.g., *pilA*, *omcS*) can be compared with wild-type strains under conditions with and without conductive additives (Van Steendam et al., 2019). Observing sustained or enhanced methane production in DIET-deficient mutants would provide strong evidence that the conductive additive enables an alternative extracellular electron transfer pathway, functioning as an electron conduit. Such experiments would offer mechanistic clarity and inform the rational design of conductive materials for industrial-scale anaerobic digestion.

3 Exploring the electron uptake and electron donation mechanisms in conductive additive-facilitated DIET

In addition to serving as electron conduits through its graphitic structure, conductive additives also exhibit electron exchange capacity via redox-active organic functional groups (e.g., quinones and hydroquinones) (Zhang et al., 2023). Thus, conductive additives like biochar could function as a biological redox buffer, maintaining microenvironmental redox potential via its capacitor-like electron exchange capacity, analogous to pH buffer in AD (Wang et al., 2023). However, the actual contribution of biochar's electrochemical properties to DIET in AD remains questionable. Many redox-active sites in biochar are located within its internal microporous structure (< 2 nm), creating potential accessibility limitations for microorganisms and possibly leading to overestimated assessments of biochar's role in DIET facilitation (He et al., 2024). Furthermore, conventional electrochemical characterizations of biochar (e.g., cyclic voltammetry and galvanostatic charge-discharge) in AD studies are typically conducted *ex situ* using alkaline electrolytes (e.g., KOH or NaOH solutions), which could not accurately reflect its electrochemical behaviors under actual AD conditions (Zhang et al., 2023). Since the electrochemical properties of biochar in heterogeneous AD systems often deviate substantially from their pristine state, owing to biofilm colonization, adsorption of extracellular polymeric substances, and interactions with dissolved organic and inorganic contaminants, it is essential to assess its *in situ* electron transfer capability under actual operating conditions.

To directly and quantitatively assess biochar's functional role as an electron conduit within the operational AD environment, advanced electroanalytical and imaging techniques should be applied. *In situ* scanning electrochemical microscopy can spatially resolve local electron transfer rates across the biochar surface in the digester, enabling the mapping of microbial extracellular electron transfer "hot spots" and tracking temporal changes as the surface becomes conditioned (Ren et al., 2018; Barroo et al., 2020). Microelectrode array sensors inserted directly into the sludge matrix can measure local redox gradients, electron flux densities, and micro-scale potentials adjacent to biochar particles, offering quantitative linkage between biochar conductivity and syntrophic partner activity (Lovley and Holmes, 2020). Spectroelectrochemical methods (e.g., *in situ* Raman, electrochemical Fourier transform infrared spectroscopy) can be used to monitor redox-state changes of biochar's surface functional groups or bound cytochromes under applied potentials, revealing real-time electron storage and release dynamics (Van Steendam et al., 2019; Liu et al., 2021). Combining these approaches allows differentiation between biochar acting as a true DIET conduit versus merely providing surface area for microbial aggregation and hydrogen/formate-mediated MIET.

Additionally, the regulatory role of biochar in facilitating DIET between syntrophic microorganisms remains poorly understood, thus, more studies are required. Given the complexity of syntrophic processes, the electron exchange capacity of biochar in AD can be evaluated by collecting mixed sludges from a long-term biochar amended AD reactor, and then further culturing them using a dual-chamber microbial electrochemical cell. This approach enables functional spatial segregation of the syntrophic oxidation of organic substrates (e.g., propionate and butyrate) from the subsequent CO_2-reduction phase of methanogenesis. Importantly, by selectively inhibiting either the electron-donating or electron-accepting capacity using specific chemical reagents, the predominant electrochemical role of biochar in facilitating DIET might be identified (Wang et al., 2020). Besides, as mentioned above, control experiments employing nonconductive additives (e.g., chemically modified biochar with intentionally reduced conductivity or inert polymer particles with similar size and porosity) are indispensable for disentangling the specific effects of conductivity from other confounding factors in conductive additive-facilitated DIET within AD systems (Martins et al., 2018). Such controls allow researchers to assess whether observed enhancements in methane yield, syntrophic partner enrichment, or extracellular electron transfer related gene expression are genuinely attributable to direct electrical conduction, rather than to secondary benefits such as increased surface area for biofilm development, improved mixing, adsorption of inhibitory compounds, or micro-niche stabilization.

4 Genuinely evaluating the benefits of conductive additive-facilitated DIET in AD

In addition to conductive additive-facilitated DIET, numerous other mechanisms contribute to enhanced AD performance after conductive additive amendment. These include pH buffering, mitigation of inhibition, toxin adsorption, microbial immobilization, biofilm formation, and enhanced MIET (Fig. 2) (Wang et al., 2022; Akram et al., 2024). Given the potential interactions among these mechanisms, attributing AD improvement predominantly to conductive additive-facilitated DIET is both scientifically unreliable and methodologically unsound. Comprehensive assessment is necessary to disentangle the direct effects of conductive additive's intrinsic physicochemical properties on AD performance from its indirect influences mediated via microbial community shifts or the improvement in DIET and MIET processes. Comprehensive investigations are required to delineate the individual contributions of each promotion mechanism to overall process optimization.

Notably, while enhanced methane production has often been cited as evidence for biochar-facilitated DIET in AD, this interpretation requires careful examination. Methane yield demonstrates strong dependence on three key biochar properties: 1) electrical conductivity, 2) surface area, and 3) pH buffering capacity—all of which are fundamentally governed by production parameters including pyrolysis temperature and feedstock selection (He et al., 2024; Tan and Yu, 2024). Pyrolysis temperature critically governs biochar's structural and chemical charac-teristics and largely influences its graphitization degree, surface functional groups, and pore architecture, thereby affecting its conductivity, electron transfer capacity, and microbial affinity (Wang et al., 2023). In terms of feedstocks, manure-derived biochar shows limited DIET facilitation potential, while wheat straw biochar, despite its DIET-enabling properties, proves impractical for full-scale applications due to its low bulk density and associated AD operational challenges. Besides, biochar produced from waste-derived feedstocks may contain toxic contaminants (e.g., heavy metals, polycyclic aromatic hydrocarbons) that could inhibit DIET-active microorganisms (Tan and Yu, 2024). Similarly, the physicochemical properties of other conductive additives, such as activated carbon and iron-based materials, are strongly influenced by their feedstocks and production parameters, making it challenging to isolate and evaluate the true benefits derived from DIET.

As a data-driven approach that operates independently of the assumptions and simplifications inherent in mathematical models, machine learning (ML) offers a powerful means to unravel the complex relationships between biochar properties and AD performance, thereby enabling accurate assessment of DIET contributions and the rational design of optimized biochar materials (Andrade Cruz et al., 2022; Khan et al., 2025). However, most of these studies focus solely on predicting methane yield or linking macroscopic operational parameters to AD performance, with limited attention to underlying mechanisms such as DIET and associated microbial indicators (Long et al., 2021; Andrade Cruz et al., 2022). Multidimensional datasets such as microbial community composition, the abundance or expression of DIET-related genes (e.g., *pilA*, *omcS*), and the physicochemical properties of

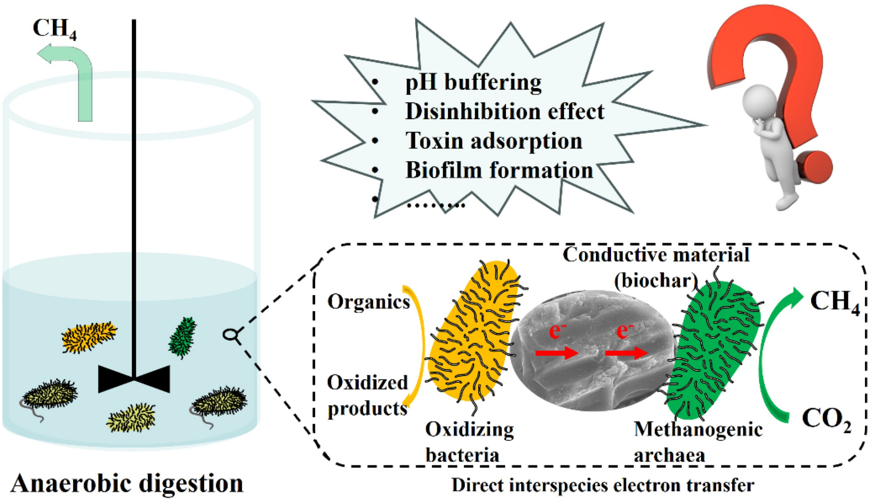

Fig. 2 Potential mechanisms underlying the enhanced performance of conductive additive-amended AD, and the direct interspecies electron transfer pathways adopted by methanogenic archaea and organics-oxidizing bacteria via conductive material (biochar).

conductive materials should be incorporated into ML models. Advanced deep learning algorithms such as long short-term memory networks and convolutional neural networks can be employed to model the performance of conductive additive-amended AD systems due to their strong capability to capture complex interdependencies among parameters (Khan et al., 2025). Besides, interpretable ML methods such as SHapley Additive exPlanations can help distinguish DIET-specific enhancements from other parallel mechanisms like adsorption or buffering, ultimately supporting a more mechanistically informed and targeted use of conductive additives (Gupta et al., 2023). Furthermore, current AD models (e.g., ADM1) remain constrained by their exclusive reliance on conventional MIET mechanism (Emebu et al., 2022). Model refinement through DIET and conductive additive incorporation would greatly improve predictive accuracy while advancing fundamental understanding of these enhancement mechanisms in AD performance (Akram et al., 2024). Additionally, ML can be integrated with mechanistic models to develop hybrid frameworks that combine data-driven insights with established process understanding. This approach could provide possibility to distinguish DIET from other enhancement mechanisms and guide the rational application of conductive additives in practical AD systems.

5 Toward industrialization of conductive additive-facilitated DIET in AD

While numerous studies have investigated conductive additive-facilitated DIET in AD, the majority have been limited to laboratory-scale systems (< 5 L), with few examining its implementation in full-scale digesters (Martins et al., 2018; Wang et al., 2023). Systematic pilot-scale studies are needed to elucidate these mechanisms under realistic engineering conditions. Besides, the long-term operational stability and efficacy of conductive additive-mediated DIET in continuous AD system remains unknown, necessitating comprehensive evaluation of its sustained performance under real-world, year-long operating conditions. While some conductive additives (e.g., biochar from waste biomass) are relatively low-cost, others (e.g., carbon nanotubes, graphene) remain prohibitively expensive. Their recovery and reuse from digested sludge are technically and economically challenging, raising concerns about accumulation, toxicity, and lifecycle impacts (Chen et al., 2022; Kalantzis et al., 2023). Moreover, if the digestate for agriculture application, the incorporation of carbon-based conductive additives, particularly those with nanoscale features, may introduce ecotoxicological risks, or changes in nutrient bioavailability in soils (Katti et al., 2025). Therefore, clear guidelines on environmental impact assessments, sludge handling procedures, and disposal routes for spent conductive additives will be necessary to address both public and regulatory concerns. Besides, as there are many types of conductive additives that have been amended in AD systems, it is essential to establish best-practice guidelines for selecting, characterizing, dosing, and monitoring conductive additives across different AD platforms to support reproducibility and scalability (Chen et al., 2022).

Additionally, the long-term performance, aging, and regeneration potential of conductive additives like biochar or activated carbon are poorly understood at scale. Particularly, biochar aging presents a significant challenge in prolonged AD operation. The dynamic, heterogeneous nature of digestate can induce substantial deterioration of biochar's properties, particularly its electrochemical characteristics, potentially diverging markedly from its pristine state (Akram et al., 2024; Tan and Yu, 2024). Such transformations may lead to misinterpretations of biochar's functional role if based solely on initial material properties. These uncertainties highlight the necessity of developing *in situ* analytical techniques to accurately characterize biochar-facilitated DIET mechanisms and their enhancement of syntrophic processes in operational AD systems. Besides, upon biochar amendment to AD, distinct partitioning occurs between suspended and biofilm-attached fractions, each exhibiting unique physicochemical and functional properties. Similar challenges arise with other carbon-based conductive additives, such as activated carbon and carbon cloth. Therefore, rigorous quantitative assessments are essential to differentiate their relative contributions and integrate these measurements to elucidate their collective role in AD performance under realistic engineering conditions.

In all, the amendment of conductive additives like biochar in AD represents a synergistic integration of thermochemical and biological conversion pathways, offering a promising approach for advanced waste biomass valorization. Future research should employ a multi-modal analytical framework to comprehensively validate both the mechanistic basis and practical benefits of conductive additive-facilitated DIET in AD, enabling optimized implementation.

Conflict of Interests Professor Han-Qing Yu is an Advisory Board Member of *Frontiers of Environmental Science & Engineering*. 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.

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