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REVIEW

The Detri^{2}match conceptual framework: Matching detritivore and detritus traits to unravel consumption rules in a context of decomposition

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Abstract

1. From soil to freshwater ecosystems, decomposition can be conceived as the result of interactions between organic matter and a diversity of organisms. This function is driven in part by detritivores, invertebrates that feed on detritus or graze on its associated microbes and that have a significant but extremely variable contribution to decomposition.
2. In order to better understand and predict detritivore–detritus pairwise interactions, we propose a conceptual framework, called Detri^{2}match, to study the consumption of detritus by detritivores, using a trait-matching approach at the individual detritivore level. Here, we focus on the interaction between saprophagous detritivores that fragment plant detritus.
3. We propose a novel definition of a saprophagous detritivore as an animal that consumes plant detritus when its traits match sufficiently the traits of its resource, passing through five interaction facets of consumption. These include (1) a spatial match rule regarding the encounter, (2) a biomechanical match rule regarding ingestion, (3) a digestive match rule regarding assimilation, (4) an energetic match rule regarding the fulfilment of metabolic needs and (5) a nutritional match rule regarding the fulfilment of chemical element needs in adapted proportions.
4. The main goal of this framework is to guide future research to establish generic rules of misunderstood detritus–detritivore pairwise interactions by identifying relevant interaction facets and their key associated traits for both detritivores and detritus. This investigation should be conducted over the temporal variability of trait-matching

constraints throughout the whole decomposition process. Coupled with adequate accumulation of trait information, the Detri^{2}match framework could also facilitate predictions by inference of non-tested pairwise detritivore–litter interactions.

5. We also outline conceptual, methodological and analytical challenges of this framework. The main challenge would be to scale up these pairwise rules at the detrital network level and to test their genericity, which would contribute to a better understanding of the functioning of the detrital network and its contribution to decomposition.

KEYWORDS
consumption, detritivore, plant detritus, plant litter, trait-matching, trophic interactions

1 | INTRODUCTION

Decomposition can be defined as the gradual transformation of dead organic matter that is ultimately mineralized with the release of CO_2 and nutrients (Petersen & Luxton, 1982). It is the second most important ecosystem function that maintains life on Earth after primary production (Gessner et al., 2010). Detritus refers to the different types of dead organic matter that differ in terms of physical attributes such as size, biochemical quality and hence the type of interactions with other organisms (Moore et al., 2004). From soil to freshwater ecosystems, decomposition is a critical ecosystem function for which consistent abiotic and biotic drivers have been identified (García-Palacios et al., 2021; Handa et al., 2014; Wagener et al., 1998). Interrelations between physicochemical environmental parameters (on a global or local scale, such as climate or soil and water properties), detritus parameters, and microbial and animal actors drive decomposition (García-Palacios et al., 2021; Tonin et al., 2021).

Most animal processing of detritus is performed by a diverse and abundant number of invertebrates, called detritivores. They can be defined as any invertebrate animal that contributes to decomposition by feeding on detritus or grazing on microbial decomposers (fungi, bacteria) associated with detritus (Brussaard, 1998; Marks, 2019). Detritivores can have direct effects on decomposition (e.g. litter elemental transformation and assimilation, Zimmer, 2002) or indirect effects through regulating microbial activities (e.g. by regulating microbial biomass by grazing microbes on litter, or by fragmenting litter detritus, increasing its surface area and making it more available for bacterial colonization) (Brussaard, 1998; David, 2014; Marks, 2019). On average, detritivores increase decomposition rates by around 50% (García-Palacios et al., 2013; Handa et al., 2014), but this contribution is highly variable, from reducing to doubling decomposition (García-Palacios et al., 2013; Tonin et al., 2021). Despite valuable efforts over recent decades (e.g. De Oliveira et al., 2010; Handa et al., 2014; Hättenschwiler & Gasser, 2005; Heemsbergen et al., 2004), the mechanisms linking detritivore diversity and decomposition are far from being completely understood, which strongly limits predictions (Coulis et al., 2015; David, 2014).

Detritus is an ubiquitous and abundant resource, mainly from plant origin (Cebrian, 1999; Cebrian & Lartigue, 2004). It offers a favourable microhabitat for invertebrates through its complex physical structure compared with the surrounding environment; this structure can improve physical properties (e.g. water storage; Ganault et al., 2022) or limit predation (David, 2014; Swan & Palmer, 2006). However, detritus is a nutritionally poor resource for animals (e.g. compared with green plants; Li et al., 2021). The nutritional quality of the plant litter depends on the species of litter and tends to increase with physicochemical and microbial processes. Physical and microbial agents tend to decrease litter toughness, remove refractory compounds and increase the relative nutrient content throughout decomposition (Danger et al., 2012; David, 2014; Marks, 2019). A main paradigm from the current literature is that detritivores feed preferentially on locally available, soft litter, highly colonized by microbes, with high nutritional quality (Evans-White & Halvorson, 2017; Frainer et al., 2016; France, 2011; Graça & Cressa, 2010). Following this paradigm, most studies investigated the interaction between detritivore and litter through the lens of nutritional and digestive constraints (Frainer et al., 2016; Zimmer, 2002; Zimmer & Topp, 1998). Other mechanisms that could theoretically be involved in litter consumption, such as biomechanical constraints, have been far less investigated (Brousseau et al., 2018a; Clissold, 2007). Furthermore, most studies based on traits on decomposition mainly investigated litter traits and neglected detritivores traits, limiting our understanding of these interactions (García-Palacios et al., 2016). The available resources for detritivores are represented by a wide range of mechanically and chemically heterogeneous litters (e.g. toughness, nutrient content and deterrent compounds). Such heterogeneity in resources could drive competition for the softest and highest nutritional quality litter. This putative competition may lead to partial detritivore diet specialization. Several examples such as the early exploitation of the litter by some detritivore species, or detritivores with different consumption strategies (shredding vs. scraping) seem to support this idea (Cummins et al., 1989; Danger et al., 2012; De Oliveira et al., 2010). However, other studies show that detritivores can have higher assimilation rates when feeding on slow-decomposing litter, perhaps due to interactions with litter-colonizing microorganisms (Siders et al., 2021). Therefore, the question of illuminating to what extent detritivores are specialists remains unanswered, as strong evidence for diet-niche differentiation is still missing. To move this field forward, a general conceptual framework is required to study the interactions between detritivores and litter. It must include underlying theoretical mechanisms other than nutritional and digestive constraints.

An understanding of the structure and functioning of trophic networks is needed to better understand the link between biodiversity and ecosystem functions (Bartomeus et al., 2016; Gravel et al., 2016; Schleuning et al., 2015). Past research has indicated the need to describe networks using functional metrics, such as functional traits. This approach enables one to connect functional community structure to network structure. It also gives insights into the dynamic link between community assemblage and its effect on ecosystem functioning (Gravel et al., 2016; Schleuning et al., 2023). In this perspective, Bartomeus et al. (2016) proposed a common framework that can be applied to any type of network interaction (see figure 1 in Bartomeus et al., 2016). Decomposition can be seen as the result of multiple interactions between highly diverse resources (e.g. litter detritus or carrion), consumers (e.g., fungi, bacteria and animals) and their regulators (e.g. predators and pathogens). These interactions constitute the hereafter called detrital network. Furthermore, this network is under the control of a spatio-temporal abiotic gradient (Gessner et al., 2010; Krumins et al., 2013; Wagener et al., 1998).

In the context of the framework proposed by Bartomeus et al. (2016), we suggest that the structure and functioning of the detrital trophic network first depend on species co-occurrence and abundances. Co-occurrence is a prerequisite for any interaction and directly impacts trophic network structure, while abundance may be involved in per component interactions (Canard et al., 2012). The co-occurrence and abundance of components of the detrital network may partially depend on certain non-detrital trophic assembly filters (Figure 1, filters A). These filters may act at several levels: (1) biogeographic filters acting at large spatial scales, (2) landscape filters (landscape diversity and fragmentation), (3) abiotic and nontrophic local filters (e.g. pH, temperature) and (4) biotic constraints with individuals that are not directly implied in the local detrital network (e.g. herbivores impact plant composition and indirectly litter composition) (Figure 1, filters A). Concerning detritivores, a body of concepts already exists in the literature to address non-detrital trophic assembly rules (Belyea & Lancaster, 1999; Boyero et al., 2012; Decaëns et al., 2008). In addition, the co-occurrence and abundance of components of the detrital network components can also depend on the functioning of the trophic network itself (Bartomeus et al., 2016). For example, top-down control, such as predator trophic cascades (e.g. Mancinelli & Mulder, 2015), or bottom-up control (Brousseau et al., 2019, 2021; Marjakangas et al., 2022), can modify the size and composition of trophic levels (Figure 1, mechanisms C).

Following the framework of Bartomeus et al. (2016), we also suggest that the structure and functioning of the detrital network may directly depend on the preference (driving the probability of the interaction) and efficiency (driving the functioning of the interaction) of pairwise interactions. For detritivores, trophic interactions are mainly based on detritivore–detritus interactions (interactions B_1, including associated microorganisms in detritus and their interactions B_2, Figure 1) and predator–detritivore interactions (Figure 1, interactions B_3). Such pairwise interactions could be described using a trait-matching approach (Bartomeus et al., 2016; Gravel et al., 2016; Schleuning et al., 2015). Trait-matching relies on the assumption that a consumer–resource interaction can be predicted by consumer traits (X), resource traits (Y) and their match (interaction between X and Y). For example, as shown for grasshoppers, animals with strong mandibles can eat tough leaves (Ibanez et al., 2013). Similarly, the mandible strength of detritivorous macrofauna, such as millipedes and isopods, or soil predators (Brousseau et al., 2018b, 2019) covaries with the toughness of detrital or prey resources. Here, there would be a match between the traits 'mandible strength' and 'toughness' of the resource (leaf, detritus, or prey). Predator–detritivore interactions (Figure 1, interactions B_3) have been largely studied (Mancinelli & Mulder, 2015), sometimes through trait-matching (Brousseau et al., 2018b), showing the strength of this approach to establish generic interaction rules. However, despite valuable studies exploring detritivore and detrital traits (Ang et al., 2023; Brousseau et al., 2019; Coq et al., 2018; Raymond-Léonard et al., 2019, 2023), no trait-matching framework exists for detritivore–detritus interactions yet (Figure 1, interactions B_1).

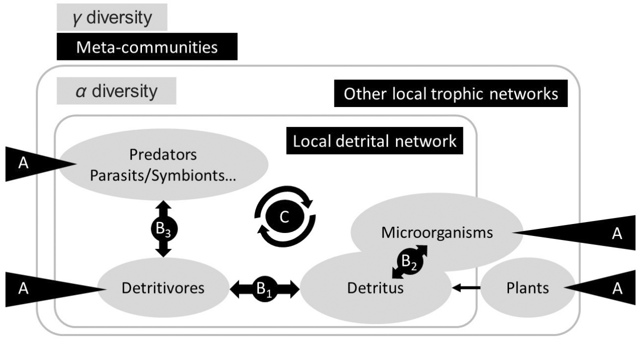

FIGURE 1 Detritivore–detritus interactions in the context of interactions within and outside the detrital network. A: Environmental filtering (biotic and abiotic). $B_{1,3}$: Bipartite consumer–resource interactions. B_2: Direct modifications of the detritus by microorganisms. C: Feedbacks (e.g. trophic cascades, facilitation and competition) within the network.

In this paper, we present the Detri^{2}match conceptual trait-matching framework to better understand and study the detritus–detritivore pairwise interactions, via a trait-matching approach at the individual detritivore level (Figure 2). Its main goal is to guide future research to establish generic rules of misunderstood detritus–detritivore pairwise interactions by identifying relevant interaction facets and their associated traits for both detritivores and detritus (see Wootton et al., 2023 for a generic modular framework of pairwise interactions of co-occurring species). By accumulating enough information on these interaction facets and associated key

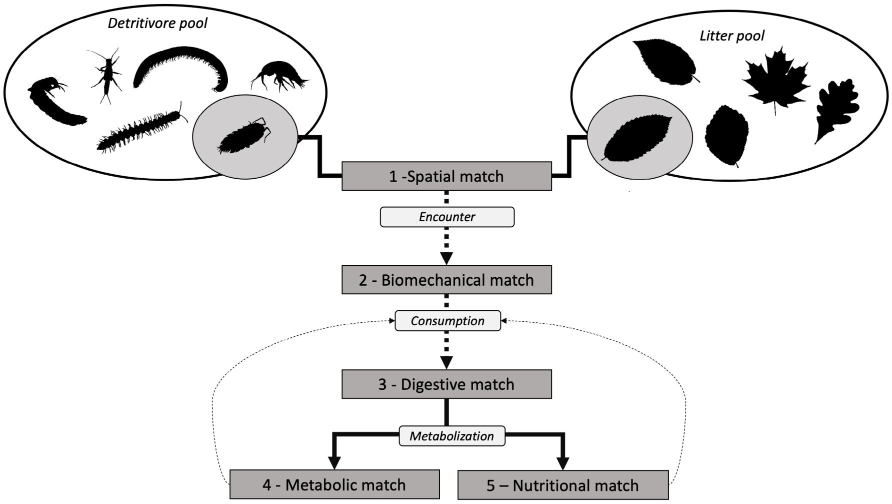

FIGURE 2 Conceptual Detri^{2}match (detritus–detritivore pairwise interactions studied via a trait-matching approach at the individual detritivore level) framework of pairwise interactions between a given detritivore and a detritus item. Dark-shaded boxes represent trait-matching facets. Pale boxes with italic letters represent mechanisms of the trophic interaction. A thick dotted arrow indicates that an interaction facet could govern both the feasibility and efficiency of the interaction. A solid arrow indicates that the interaction facet mainly governs the efficiency of the interaction. Thin dotted arrows indicate feedbacks of interaction facets on detritus consumption.

traits, we should also be able to infer non-tested pairwise detritivore–litter interactions. Our proposed Detri^{2}match framework is based on existing knowledge on detritivores and detritus. We focus on particulate detritus originating from organic plant matter (e.g. leaf litter, dead wood and dead roots) as plants are the main generator of detritus (Moore et al., 2004). We also focus on the critical consumption phase of saprophagous detritivores that mechanically fragment detritus through cutting, scratching or grinding. This fragmentation is based on specific apparatus, such as mandibles for arthropods, a gizzard for earthworms or a radula for gastropods. Fragmented particles are subsequently transformed once ingested (incorporated into tissue, respired, excreted and egested) depending on the metabolic strategy of the detritivore (David, 2014; Marks, 2019). Because we focus on detritivores that fragment litter and consume litter with associated microorganisms, we consider microbial decomposers as an integral part of detritus. They contribute to define its identity (detritus is defined by its plant matrix and the associated microorganisms) and temporal dynamic (microorganisms actively modify the traits of detritus). Abiotic drivers, such as leaching, also influence detritus. Therefore, we intentionally included these microbial and abiotic effects through the characterization of litter traits across the five facets.

We assert that the preference and efficiency of the detritus–detritivore interaction is governed by five complementary but distinct interaction facets. These facets cover all individual biological processes that could directly or indirectly influence the consumption of a detritus item by a detritivore individual: (1) a spatial match between a detritivore and detritus, by indirect (random match) and/or direct (detritus detection by detritivores) mechanisms, (2) a biomechanical match between the mouthparts of the detritivore and the biomechanical properties of the detritus, (3) a match between the digestion abilities of a detritivore and the chemical deterrents of the detritus, (4) a match between detritivore metabolism and the energy content of the detritus, and finally, (5) a nutritional match between the macroelement composition of the detritivore and the detritus (Figure 2). As the first two trait-matching facets occur before litter ingestion, we advocate that they govern both the feasibility and efficiency of detritus consumption (see examples in the following section). The last three facets mainly influence the efficiency of the interaction, since they occur after litter ingestion. Our Detri^{2}match framework is built at the individual level, as intraspecific detritivore consumption variability has been shown to be substantial compared with interspecific variability (Fontana et al., 2019; Rota et al., 2022). We thus aim at characterizing detritus–detritivore pairwise interactions at a given time, at the individual detritivore and detritus item level.

2 | FORMAL DESCRIPTION OF THE FIVE TRAIT-MATCHING FACETS AT THE INDIVIDUAL DETRITIVORE AND DETRITUS ITEM LEVEL

In the literature, trophic interactions of saprophagous detritivores are often studied at the species level rather than at the individual level. We considered that trophic interactions at the species level can be seen as the range of trophic interactions of individuals (Fontana et al., 2019; Rota et al., 2018). We therefore used published detritivore–detritus examples of trophic interactions at a species level to indirectly support and illustrate our individual-centred conceptual Detri^{2}match framework. When no specific example was available, we used illustrations from other close biological models.

2.1 | Spatial match: Litter attractivity and encounter

Detritivores are highly dependent on chemoreception using sensory organs involved in both olfaction and taste for food detection and selection, respectively (Crespo, 2011; Erktan et al., 2020). Detritivores may detect volatile chemical cues with their olfactory receptors (e.g. sensilla located on the antennae), while solid or liquid cues are recognized by their gustatory receptors (e.g. sensilla with gustatory function located on the mouthparts). Studies on earthworms (Zirbes et al., 2011), dung beetles (Dormont et al., 2010), Oribatida (Brückner et al., 2018) or Collembola (Hedlund et al., 1995) demonstrated the key importance of volatile cues for detecting food resources. In soils, where most species are blind, detritivores mainly use olfactory cues to localize food and these cues are presumably only detected over a few centimetres compared with surface detritivores due to pore size and soil hydration state (Auclerc et al., 2010; Erktan et al., 2020). In the aquatic environment, the distinction between olfaction and taste to detect and select food is even more vague (Crespo, 2011; Zacharuk, 1980), but the propagation of chemical signals in water is well preserved at great distances from the source compared with the terrestrial environment (Murlis et al., 1990).

Regarding the compounds that attract detritivores at distance, volatile organic compounds (VOCs) and CO_2 seem particularly involved. For example, Moursi (1961) reported that Collembola sense and direct their movement toward CO_2 sources associated with microbial activity, while Staaden et al. (2011) demonstrated that Collembola differentiate fungi using olfactory cues. However, only few studies identified VOCs involved in such attractiveness, limiting our understanding of the mechanisms underlying food detection. For example, Zirbes et al. (2011) identified two compounds (ethyl pentanoate and ethyl hexanoate) involved in the distance attraction of the earthworm *Eisenia fetida* to the fungi *Geotrichum candidum*. Additionally, and even if their volatility is low, other compounds including amino acids, fatty acids, sugars or alcohols have been reported to attract soil detritivores at a distance (Brückner et al., 2018; Salmon & Ponge, 2001). For example, Brückner et al. (2018) showed that *Cheloribates* sp. (fungivorous Oribatid mite) was highly attracted to the alcohol 1-octen-3-ol produced by fungi.

Interestingly, despite detritivores possessing olfactory receptors, several studies performed in both aquatic and terrestrial systems identified that food search is characterized by random individual movements followed by a food choice only based on gustatory cues (Motyka et al., 1985; Tuck & Hassall, 2004). This food selection has been reported to depend on the nutritional status of the litter (Swan & Palmer, 2006) as well as on microbial colonization improving the nutritional quality of this litter (Graça & Cressa, 2010; Motyka et al., 1985). To disentangle the mechanisms through which microorganisms increase detritivore consumption, Zimmer et al. (2003) tested whether leaf-colonizing microorganisms would increase *Porcellio* (Isopoda) consumption by (1) increasing the nutritive value of leaf litter, (2) increasing the digestibility of leaf litter and (3) increasing the attractiveness of leaf litter. Their findings supported the third hypothesis, without excluding the two first ones.

To date, no studies have used a trait-matching approach between detritivorous traits involved in olfaction or taste and detrital traits. Traits of detritivores involved in olfaction for food detection at distance, or in taste for food selection by contact, include the morphology of the antennae or the mouthparts, their sensilla (e.g. shape, size, presence/absence of pores and socket type; Garza et al., 2021), the brain structures associated with processing chemical information (e.g. antennal lobes, mushroom bodies), and the behavioural responses associated with the detection of chemical cues (e.g. shift from nondirectional (random or search strategy) to directional (target-oriented) movements; Auclerc et al., 2010). Detrital traits involved in olfaction are VOCs or CO_2, mostly produced by microorganisms, while those involved in taste are nutrient content or chemicals associated with microbes.

2.2 | Match between mouthpart abilities and litter mechanical properties

Once a given detritivore decides to ingest a detritus item, the next facet concerns the ability of the individual to ingest the detritus. This ability may be controlled by mechanical constraints. Mechanical interactions between detritivores and their detrital resources can imply different actions (cutting, grinding and scratching) and organs (mandibles, chelicera and radula). Although each action and mouthpart type involve different biomechanical processing, the overall principle remains the same, namely the ability for a detritivore to manipulate the resource and be strong enough to overcome resource physical resistance. Leaves, and other plant structures such as stem and roots, possess different traits such as thickness and toughness that can impede physical consumption by detritivores. Leaf toughness is mainly related to the amount and organization of fibres such as lignin and cellulose in cell walls (Clissold, 2007).

Leaf thickness is a well-recognized matching trait for herbivore caterpillars (e.g. Bernays, 1998). Danger et al. (2012) also pointed out that litter thickness acts differently depending on detritivore body size. Small Leuctridae were not affected by leaf litter thickness as they scraped the surface, whereas larger shredders had to cut through the entire limb. However, leaf litter thickness was shown to correlate with the mandibular gap of millipedes and isopods (Brousseau et al., 2019) and with the apical tooth development of Collembola with chewing mouthparts (Raymond-Léonard et al., 2019) in forest ecosystems. Similarly, previous studies demonstrate a negative relationship between leaf litter thickness and detritivore consumption rate (Canhoto & Graça, 1995; Ponge, 1991), but it was unclear whether this was due to a direct limitation imposed on the mandibular gap.

Leaf toughness represents the physical resistance of the leaf to puncturing, tearing and rasping/scratching (Padilla, 1989; Sanson et al., 2001). Tougher leaves can possess a defence against herbivory (Malishev & Sanson, 2015) that can also impede the consumption of detritivores. In the case of arthropods, mandibles specialized for scraping food can harbour several apical teeth instead of the single apical tooth of animals specialized in cutting their food (Godfrey et al., 1989), but the overall biomechanics and trait-matching are comparable. The main constraint is the strength applied at the tip of the mandible, which varies with its shape and the size of related muscles (Clissold, 2007; Raymond-Léonard et al., 2019). Strength can be measured directly with a force transducer (Weihmann et al., 2015) or with allometric models (Brousseau et al., 2019). Some species possess mandibles with zinc and silica (Laiolo et al., 2021), which allow eating tougher leaves, but the proper allometry to include such aspects is still missing in the literature. Although less studied, the presence of trichomes or spicules in leaves could also limit the consumption of litter by detritivores. Experimental evidence is scarce, but recently, Nakamura et al. (2022) demonstrated that high densities of silicious trichomes reduced meso- and macrofauna impacts on decomposition.

The radula of Gasteropoda consists of a thin cuticular sheet with embedded rows of teeth that is actioned by muscles from the buccal area. The biomechanics and functions of radula were less well studied than arthropod mandibles (but see Padilla, 1989), but have attracted some attention lately (Krings et al., 2021). Krings et al. (2021) found a correlation between body mass and radula force when considering five species. The presence of detritivorous snails in communities can also facilitate decomposition for other arthropods, as the radula enables them to process tougher detritus, such as freshly fallen leaf litter, otherwise less accessible to arthropods with chewing mandibles such as millipedes that prefer partially decomposed detritus (De Oliveira et al., 2010). Annelids, such as earthworms and enchytraeids, represent a particular case, as they do not possess rigid mouthparts. Therefore, the main biomechanical constraint is the match between the size of the particles and the size of the mouth. However, earthworms possess a gizzard, which is a functional analogue of the mouthparts of arthropods, as it crushes ingested material.

The match of traits between mouthpart force and leaf toughness was tested in terrestrial environments with herbivorous grasshoppers (Ibanez, 2012; Le Provost et al., 2017) and in aquatic environments with limpets feeding on algae (Padilla, 1989). Although this trait-matching was not experimentally tested with detritivores, the covariation in mandibular force and leaf litter toughness was observed in forest ecosystems (Brousseau et al., 2019).

2.3 | Match between digestion abilities and detritus digestibility

Once ingested, the food is partially digested. The quantity of nutrients that is assimilated depends on both the digestion processes and the digestibility of the detritus. Matches between consumed items and digestion abilities are of utmost importance for individual fitness, as animals basically rely either on endogenous enzymes or on their microbiota in digestion. Detritus such as woody vegetation may be composed of 75% or more refractory (i.e. resistant to digestion) cell wall material not eligible for rapid digestion with endogenous enzymes. Due to plant nutrient remobilization and leaching of soluble compounds, nitrogen and phosphorus concentrations decrease significantly from green leaves to leaf litter (Li et al., 2021). Likewise, the soluble sugar content is more than five times lower in leaf litter compared with green leaves, while the proportion of lignin increases by 25% in multiple tree species (Li et al., 2021). Thus, leaf litter generally has very low N and P concentrations and a large proportion of recalcitrant structural carbon compounds, such as lignin (Martinson et al., 2008; Moore et al., 2004). Being rich in refractory compounds and poor in macronutrients, leaf litter has very high assimilation constraints. Detritivores therefore evolved multiple strategies to match their physiological requirements regarding the rather refractory materials they rely on for their diets and their food and energy requirements may strongly differ at different development stages (Charron et al., 2014). Basically, there is a continuum of species called 'feeders' that assimilate non-refractory materials and pass the refractory ones mainly undigested, and 'digesters' that extract considerable energy from refractory materials (Abe & Higashi, 1991). Differences in enzymatic activities between species of detritivores may reflect these different strategies. For example, the millipede *Polydesmus angustus* showed higher activity of the gut extract toward polysaccharides than the woodlouse *Oniscus asellus* (Beck & Friebe, 1981). Similarly, different carbohydrase activities were observed between two sciarid fly larvae (*Plastosciara falcifera* and *Bradysia confinis*; Deleporte & Charrier, 1996). Bärlocher and Porter (1986) found that while all three detritivore (*Gammarus tigrinus*, *Tipula caloptera* and *Hydropsyche betteni*) were able to digest starch and laminarin, *T. caloptera* was the only one capable of hydrolysing proteins from microbially unconditioned maple leaves. This is due to the fact that *T. caloptera* has a much more alkaline intestinal pH than other detritivores. The multiple genomes of the gut microbiota (i.e. microbiome) are also very relevant (Sanders, 2002). The presence of microbial exoenzymes released in the gut during digestion is a common strategy used by detritivores to acquire their energy (Zimmer, 2002). For example, the efficiency of the utilization of plant structural polysaccharides was significantly increased after the ingestion of fungal (*Penicillium* sp.) cellulase by the woodlouse *Trachelipus rathkei* (Kukor & Martin, 1986). Autocoprophagous behaviours can also increase assimilation efficiency (Zimmer, 2002), and a single species or a group of species can turn from feeders to digesters due to their gut microbiota. Only traits that are complex and take time to measure, such as enzyme activities, would differentiate both guilds, even if traits related to faeces would also discriminate individuals of a single species belonging to one or the other guild. Furthermore, it is known that leaf litter subjected to leaching, which removes several refractory compounds such as phenolics and tannins, as well as microbial conditioning, are preferred by detritivores compared with 'unconditioned' or 'unleached' leaves (see David, 2014 and citations therein). Zimmer (2002) showed that litter consumption by isopods depends both on litter traits (especially the C:N ratio and phenolic concentrations) and isopod species, with terrestrial isopods being better adapted than semiterrestrial ones to phenolic concentrations found in their daily resources.

2.4 | Match between metabolism and litter energy content

Once assimilated, detrital molecules are used by the consumer organism to gain energy through catabolism. The energy content of the assimilated food should then meet the metabolic requirements. Plant detritus is energetically poor, with very low nutrient content (Li et al., 2021). In addition to the low-energy content of the detritus, the low digestibility of plant litter places detritivores at the bottom of the assimilation efficiency pyramid. A systematic analysis of the energetic traits of aquatic and terrestrial arthropods yielded a mean energy assimilation efficiency of 16% for detritivores, approximately three times lower than the estimated value estimated for herbivores (Lang et al., 2017). Unfortunately, assimilation is rarely expressed with energy units (joules and calories) (Nilsson, 1974). Most often, it is estimated with mass budgets. In addition to this low assimilation efficiency, the feeding rate can vary greatly between detritivores; for example, aquatic detritivores are reported to consume between 10% and >100% of their body mass per day (Santonja et al., 2018). The existence of different strategies among detritivores to cope with this challenging energetic situation can explain the variability in feeding rates.

Lang et al. (2017) demonstrated no significant difference between the trophic groups in mass-corrected metabolic rate, suggesting that detritivores generally cope with the low digestibility of their resource by increasing the ingestion rate rather than lowering their energy demand. The existence of a compensatory feeding strategy (i.e. when some detritivore species exhibit greater ingestion rates on nutrient-poor compared with nutrient-rich litter) would support this idea (Cruz-Rivera & Hay, 2000; Danger et al., 2013; Mas-Marti et al., 2015; Ott et al., 2012), even though compensatory feeding is not systematically observed in detritivores (Evans-White & Halvorson, 2017; Fenoy et al., 2021; Hättenschwiler & Bretscher, 2001). Interestingly, Ehnes et al. (2011) found that among detritivores, some had lower respiration rates than the predictions of the linear model. This would indicate that some detritivore taxa have a lower metabolism as a different strategy to cope with their poor food resource. The existence of different energetic strategies is also illustrated by Fenoy et al. (2021) who identified detritivores with different abilities to maintain energetic reserves when exposed to detritus of different qualities, depending on the species of detritivores. Different energetic strategies could result from different metabolic needs. For example, differences in metabolism related to reproduction or sex-specific behaviour (e.g. mate guarding) can lead to differences in energy requirements and in detritus selection (Rota et al., 2018). Depending on the developmental stage, the importance of the caloric content of the detritus can also change. Juveniles can have specific requirements due to energetic growth needs and rely on specific resources (Crenier et al., 2017). Unfortunately, the quality of detritus is rarely expressed with direct or indirect calorimetric measures (Mathews & Kowalczewski, 1969) and doing so would be an interesting future step, even though the low digestibility of litter molecules would have to be taken into account. Other relevant measurements to better understand this interaction include the systematic measurement of carbohydrates, lipids, and proteins of detritus and the energetic reserves (lipids and glycogen) of detritivores to compute precise energy budgets (Fenoy et al., 2021).

Rota et al. (2018) also point out differences in the foraging strategy between large and small detritivores. In their study, small individuals of an aquatic detritivore species (*Gammarus fossarum*) were found to spend more time feeding on leaf litter than large ones. Therefore, it is plausible that the low-energy assimilation efficiency in detritivores imposes a limit on body mass through foraging trade-offs. This idea is consistent with the fact that detritivores reach smaller sizes than herbivores; typically, animals classified as megafauna include herbivores and predators, but never typical detritivores. Thus, body size can be viewed as a matching trait that makes detritivores adapt to the low-energy content of plant litter.

2.5 | Nutritional match between detritivores and detritus

Parallel to energy needs, detritivores must meet their elemental requirements by getting the necessary chemical elements in the adapted proportions. All consumers are made up of the same essential chemical elements that occur in variable amounts in their bodies. Ecological stoichiometry corresponds to an approach of ecology specifically taking into account the balance between consumer elemental requirements and element availability in their resources (Sterner & Elser, 2017). Any elemental imbalance that arises between consumer requirements and their diet will ultimately impact their performance traits (Pey et al., 2014; Violle et al., 2007). Stoichiometric approaches have mainly considered carbon (C), nitrogen (N) and phosphorus (P) as some of the most biologically important elements on Earth, but can be extended to other essential elements such as calcium, sodium or magnesium, for example (e.g. Ott et al., 2014).

Stoichiometric constraints are especially important since most of the detritus available in ecosystems, at least that produced by plants, is extremely depleted in nutrients. To overcome these constraints, detritivores, as well as herbivores, generally exhibit low body nutrient requirements/high body C:N:P ratios, when compared to carnivorous taxa (Cross et al., 2005; Martinson et al., 2008). However, due to the low concentrations of N and P in the detritus, detritivores also need to adopt different strategies to cope with the potential limitation of nutrients. One way to reduce elemental imbalances is to consume more resources to obtain enough of the most limiting elements: the before-mentioned compensatory feeding mechanism (Jochum et al., 2017). Detritivores can also select the most nutrient-rich patches of the detritus, as the detritus is generally quite heterogeneous in terms of elemental contents (Grimmett et al., 2012).

Microorganisms are especially important here as they increase the relative elemental content of litter, sometimes through the incorporation of nutrients from the water column (Pérez et al., 2013). Detritivores may also complement their detrital resources with a sufficient amount of other nutrient-rich resources (e.g. algae for Gammarids; Crenier et al., 2017). Lastly, excretion modulation can help regulate body elemental composition in regard to food content (Balseiro & Albariño, 2006).

One of the current limitations of stoichiometric approaches is that, in numerous studies, elemental imbalances have simply been approximated as the difference between the elemental composition of the consumer and that of the resource (e.g. Cross et al., 2005). However, using the C:N:P contents of detritivores as a proxy of their elemental requirements leads to neglect of the metabolic and biochemical costs necessary for processing and assimilating their diet. To estimate the real elemental requirements of a consumer, one can evaluate its threshold elemental ratios (i.e. the ratios at which the nutrient limitation of consumer growth switches from one element to another; Frost et al., 2006). Second, it is necessary to investigate whether and how much these elemental and metabolic requirements depend on environmental conditions (e.g. Ruiz et al., 2020). Finally, it is necessary to improve our knowledge of what detritivores effectively ingest and assimilate from their resources in terms of chemical elements, since they partly depend upon the other matching detritivore–detritus facets. As current ecological stoichiometry focuses on elemental stoichiometry, we used this to consider the nutritional match of the interaction. However, consumers must also meet the requirements for essential fatty acids, specific proteins and essential amino acids (Anderson et al., 2017).

3 | CHALLENGES TO ASSESSING TRAIT-MATCHING RULES

3.1 | Conceptual challenges

The Detri^{2}match framework can be seen as a conceptual tool to define generic and fundamental rules at the pairwise level (i.e. by isolating pairwise detritivore–detritus interactions from any other interaction). This tool can be applied to any interaction between a detrital item and a detritivore. Defining such fundamental rules depends on identifying the relative importance of each interaction facet, and the relevant associated traits, by going beyond the current interpretation focusing on digestive, energy and nutritional constraints. Furthermore, such rules depend on answering to what extent detritivores are diet specialists or diet generalists. The level of specialization depends on the quantitative contribution of trait-matching (i.e. the contribution of the interaction between detritivore and detrital traits) to explain the interaction. As a concrete example, dissimilar patterns of consumption rates were frequently observed between detritivore species in similar experimental studies using consumption tests of a single leaf litter type by a given detritivore species. Most of these unexpectedly dissimilar consumption rate patterns were interpreted as compensatory feeding, compensating for animal needs in terms of digestive, energy and/or nutritional constraints (Cruz-Rivera & Hay, 2000; Hättenschwiler & Bretscher, 2001; Jochum et al., 2017; Mas-Marti et al., 2015; Ott et al., 2012). Furthermore, such studies did not formally test for interactions between litter and detritivore traits, since detritivore traits are generally not measured. Our Detri^{2}match framework offers the opportunity to unravel these unexpected dissimilar consumption rate patterns by identifying the relevant interaction facets acting on the interaction, and to test for trait-matching (specialization or not) by associating relevant litter and detritivore traits (Table 1). In addition, as the Detri^{2}match framework is built at the individual level, it would also allow us to clarify whether intraspecific trait should be taken into account for each interaction facet. For example, detritivore chemical traits involved in the nutritional match may have a lower intraspecific variability than individual behaviours involved in the spatial match. Finally, as the Detri^{2}match framework could predict novel interactions, it could also be very useful in the context of invasive species introduction.

The Detri^{2}match framework may require specific conceptual adjustments to correctly include all aspects of social insect trophic interactions (ants and termites). Adjustments may also be needed for detritivores that do not fragment detritus (e.g. phagocytosis for protists or Collembola with piercing mouthparts). Finally, this framework considered plant detritus even though other, less abundant detritus, such as carrion and dung, is crucial for some other detritivores. Additionally, to fully understand the contribution of detritivores to detritus consumption, this pairwise framework must be replaced in the context of the detrital network functioning throughout the decomposition process (see Figure 1; figure 1 in Bartomeus et al., 2016). First, pairwise rules could be modulated by trait change over time. Change over time is particularly pronounced for detrital traits under the influence of abiotic parameters (leaching and photodegradation) and microorganisms. Abiotic parameters and microorganisms decrease litter toughness and increase the relative proportion of nutrients over time (Wickings et al., 2012). This temporal dynamic also applies to detritivore traits through developmental stages and seasonal variations of metabolism, related to ambient temperatures (Nilsson, 1974). The Detri^{2}match framework must then be applied throughout the decomposition process to assess fundamental rules over time. This would rely on assessing the relative importance of each interaction facet and its relevant associated traits over time. For example, we can expect biomechanical constraints to be more important during the first stages of decomposition than during the final stages, when microbial conditioning and abiotic parameters have decreased the toughness of detritus (Marchand, Estabes, et al., 2024; Marchand, Pey, et al., 2024). Additionally, fundamental rules of pairwise interactions can be modulated by competition or facilitation mechanisms, resulting from multiple interactions, whether intra- or interspecific (Rota et al., 2018; Zimmer et al., 2005), between different detritivores consuming different resources. Fundamental rules could also be indirectly modulated by interactions with other network detrital

TABLE 1 Non-exhaustive but illustrative description of detritivore–detritus matching traits used in the literature. We only collected literature containing at least both a detritivore trait and a detrital trait, theoretically involved in a same matching facet. We found no studies investigating both a detritivore trait and a litter trait related to the spatial facet of the interaction.

Facet of the interaction	Detritivore trait	Litter trait	References
Spatial match	NA	NA	NA
Biomechanical match	Mandibular gape	Litter thickness	Brousseau et al. (2019)
	Mandibular strength	Litter toughness	Brousseau et al. (2019)
Digestive match	Surfactants in the gut fluids	Phenolics	Zimmer (1997)
	Gut microbiota individuals	Hydrolysable tannin content	Zimmer (1999)
	Gut cellulase activity	Cellulose content	Zimmer and Topp (1998)
Metabolic match	Metabolism, body mass	Litter caloric content	Ott et al. (2012)
	Metabolism, body mass, energetic storage	Litter caloric content	Fenoy et al. (2021)
Nutritional match	Body C:N	C:N	Frainer et al. (2016); García and Pardo (2015); Ohta et al. (2016); Tagliaferro et al. (2021)
	Body C:P	C:P	Frainer et al. (2016); García and Pardo (2015); Ohta et al. (2016); Tagliaferro et al. (2021)
	Body N:P	N:P	Frainer et al. (2016); García and Pardo (2015); Tagliaferro et al. (2021)

components, such as detritivore–predator interactions (Figure 1, interactions B_3) or with components of another connected network (see figure 1 in Schleuning et al., 2023). All these interactions can lead to top-down (trophic cascades; Mancinelli & Mulder, 2015) or bottom-up (driven by the resource, Brousseau et al., 2019, 2021; Marjakangas et al., 2022) feedbacks emerging from the detrital network functioning itself (Figure 1, mechanisms C). Such feedbacks can directly change the interaction rules (such as facilitation process; see, for instance, Zimmer et al., 2005) but also indirectly change the co-occurrence and abundance of network components. Co-occurrence and abundance may also change with environmental filtering (Figure 1, A). Finally, detritivore faeces undergo their own decomposition process and influence matter cycling (David, 2014; Marks, 2019). The Detri^{2}match framework must then be coupled with faeces assessment to fully understand the contribution of detritivores to decomposition. Faeces traits may represent conceptual bridges between detritivore consumption and ecosystem processes (Coq et al., 2022; Joly et al., 2015).

3.2 | Methodological challenges

Many studies have previously shown that the structure and functioning of food webs cannot be described and understood on the basis of their nodes' identity and of their initial properties (e.g. traits) solely (Ulanowicz et al., 2014), as emergent properties could appear (Bartomeus et al., 2016). Our Detri^{2}match framework should be considered as a reference baseline that functionally describes detritivore–detritus interactions, using pairwise fundamental interaction rules. These fundamental interaction rules must be tested in complete trophic networks, as many processes operating within the network (e.g. above-mentioned facilitation/competition; bottom-up or top-down regulation) could drastically change them. Thus, a better understanding of the structure and functioning of trophic networks through fundamental bipartite interaction rules requires the complementarity of several experimental approaches, from the pairwise interaction level to the network level. In this section, we suggest a general experimental strategy that will enable the evaluation of the discrepancy between interactions based on these fundamental bipartite rules and realized interactions. This strategy requires a two-pronged approach. A mechanistic, bottom-up approach will attempt to aggregate the knowledge derived from these fundamental rules into incrementally complex networks. A top-down approach will confront modelling of observed or simulated networks, with or without considering fundamental rules of pairwise interaction.

In a bottom-up experimental approach, fundamental rules at the pairwise level could be obtained from laboratory feeding tests of monospecific combinations with a representative range of detritivore and detritus traits (Marchand, Estabes, et al., 2024; Marchand, Pey, et al., 2024). Once fundamental rules are identified, their generality in more and more complex detrital networks can be tested (e.g. mixing several litter types with several detritivore species). From a practical point of view, these experiments could take the form of controlled laboratory consumption tests with increasingly complex controlled networks. Mesocosm approaches at a field scale, where detritivore and detritus interaction traits can be manipulated, should also be considered (see Hättenschwiler & Gasser, 2005 in which litter traits only were manipulated).

Given the complexity of describing all the dynamic interactions of food web components, many modelling approaches have been developed (e.g. Potapov et al., 2023). These approaches enable modelling food web structure and its functioning and to compare it with process measurements in field conditions to assess their predictive power (Potapov et al., 2023). Recently, new modelling approaches have explicitly considered trait data of network components (Barel et al., 2023; Bloor et al., 2021; Boukal, 2014; Potapov, 2022). Some of these approaches even inferred interactions from a matrix of pairwise interaction traits (Bloor et al., 2021; Potapov, 2022). Thus, defining fundamental rules of pairwise interactions could help to identify key interaction traits that could enrich these modelling approaches. Comparing predictions of the structure and functioning of modelled networks with or without these trait data could demonstrate or refute the power of these fundamental rules to predict realized interactions.

The convergence of these bottom-up and top-down experimental approaches would certainly facilitate the identification of rules applying to real detrital trophic networks. In this way, the Detri^{2}match framework offers a solid conceptual basis for studying the detritivore–detritus interaction. This framework would bring generality and predictive power to the detritivore contribution to detritus consumption, and also give insights into the dynamics of the detrital trophic network at the community level and its effects on decomposition at the ecosystem level.

3.3 | Analytical challenges

From an analytical perspective, one way to test trait-matching is by using the RLQ and fourth-corner approaches (Legendre et al., 1997). Spitz et al. (2014) successfully applied both methods to characterize interactions between Atlantic marine mammals and their prey. They used the methods recommended by Dray and Legendre (2008) to test null hypotheses. The importance of using null models was also underlined by Marjakangas et al. (2022), who used simulations creating null models to estimate the importance of morphological matching, density dependence and stochastic interactions in a plant–frugivore network. However, the RLQ approach enables the characterization of actors only at the species, and not at the individual level.

Rohr et al. (2016) provided a different and elegant approach based on the probability of a link in the network to happen. This probability is expressed as the sum of a *matching* term based on traits influencing the matching between two nodes (e.g. mandible size and food toughness), and of a *centrality* term based on inherent traits influencing the number of interactions of each node (i.e. animal metabolism and a litter palatability index). This model is very flexible and allows for the use of complementary approaches. For example, Pearse et al. (2013) suggested using both traits and phylogeny to predict new plant–herbivore interactions, and research on predatory arthropods demonstrated that both can be included simultaneously in a matching-centrality model (Brousseau et al., 2018b). Finally, Pichler et al. (2020) showed that Random Forest, Boosted Regression Trees and Deep Neural Networks performed better than traditional Generalized Linear Models in predicting interactions based on trait information and in identifying the most important trait-matching rules. Yet, this machine learning approach often requires large data sets to train the models.

4 | CONCLUSIONS

Reasons why some animals have evolved toward detritivory are probably related to the ubiquity and abundance of plant detritus in many habitats (Cebrian, 1999). Plant detritus has been reported to improve the physical environment of detritivores, for instance, through moisture retention on the forest floor and attenuation of predation due to complex habitat structure. On the contrary, unconditioned plant detritus is among the lowest quality food resources for animals on the nutritional level, suggesting that trophic adaptations are a core component of the fitness and evolution of detritivores.

Resource competition triggers trophic specialization, which should result in adaptive divergence in foraging traits among coexisting species. However, there is mixed evidence to support trophic niche partitioning among detritivores. Most detritivores tend to select higher quality detrital patches (i.e. highly microbially colonized litter with low toughness, low recalcitrant compounds, high caloric content and high macroelemental concentrations), but competition may be alleviated by temporal niche partitioning, such as manifested through species exploiting resources at different decomposition stages or occurring at different seasons (Cummins et al., 1989). Different species have also been reported to feed on different parts of leaf litter, with some species taking large bites from the edge or interior of coarse materials and others scraping the surface (Danger et al., 2012). The application of trait-matching approaches on other models revealed strong (e.g. predator–prey system), relaxed (e.g. herbivore–plant system) or barrier trait-matching (e.g. plant–pollinator systems) and informed the degree of specialization of the interactions (Bartomeus et al., 2016). Assessing to what extent trait-matching acts on detritivore–detritus interactions, making them generalists or specialists, would be an important step forward. The Detri^{2}match framework could strongly contribute to its formal testing.

AUTHOR CONTRIBUTIONS

BP conveyed the idea. AL, BP and TM constructed the conceptual framework architecture and established the manuscript's main ideas and plan. All authors actively contributed to the writing of the manuscript. TM and BP are the main contributors and harmonized the text. AL is the second main contributor. All authors reviewed the final version.

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CONFLICT OF INTEREST STATEMENT

The authors declare they have no conflict of interest.

DATA AVAILABILITY STATEMENT

This paper used no data.

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