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Consumers-resources trait-matching to better quantify detritivores-litter interaction : an aquatic and terrestrial inter-ecosystem approach

Theo Marchand

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THÈSE

En vue de l'obtention du
DOCTORAT DE L'UNIVERSITÉ DE TOULOUSE
Délivré par l'Université Toulouse 3 - Paul Sabatier

Présentée et soutenue par
Théo MARCHAND

Le 25 octobre 2023

**La concordance des traits des consommateurs et des ressources
pour mieux quantifier l'interaction détritivores - litières : une
approche inter-écosystème aquatique et terrestre**

Ecole doctorale : **SDU2E - Sciences de l'Univers, de l'Environnement et de
l'Espace**

Spécialité : **Ecologie fonctionnelle**

Unité de recherche :

Laboratoire écologie fonctionnelle et environnement

Thèse dirigée par
Benjamin PEY

Jury

M. Christopher SWAN, Rapporteur

M. Thibaud DECAËNS, Rapporteur

Mme Catherine FERNANDEZ, Rapporteur

M. Benjamin PEY, Directeur de thèse

M. Franck GILBERT, Président

Elles [Déborah Bird Rose et Val Plumwood] nous rappellent que la mort ne doit pas être considérée comme une simple fin, mais comme un élément totalement central de la vie continue des communautés multi-espèces, dans lesquelles nous sommes toutes et tous, en fin de compte, la nourriture des uns pour les autres (Plumwood, 2021).

[Au sujet des vautours] Mais au lieu de prendre la vie pour produire leur nourriture, ils ne consomment que ce qui est déjà mort, ramenant la chair morte dans des processus de nourriture et de croissance.

Thom Van Dooren, En plein vol : vivre et mourir au seuil de l'extinction. Éditions Wildproject, 2021. Pages 93-94

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Marchand, Théo (2023)

Consumer - resource trait-matching to better quantify detritivore-litter interaction: an aquatic and terrestrial inter-ecosystem approach

Doctor of Philosophy (Ph.D.) thesis, Université de Toulouse.

FOREWORD

This thesis comprises an extensive introduction presenting the context of the thesis, and four chapters. Each chapter is based on a research paper written with several coauthors. At this point, none of the paper is published. Yet, several of them are currently being considered in peer-reviewing journals (Functional Ecology, OIKOS...). Coauthors cannot be accountable for any mistake in this manuscript. Each chapter is preceded by a short paragraph (Prologue) in English and in French, placing the chapter in the context of the thesis and linking it to the other chapters. Each chapter is followed by a short paragraph (Epilogue) in English and in French, placing the results in the context of the thesis. **In the PDF version of this manuscript, links in the Table of Contents are clickable. All references to figures and tables (in blue) are also clickable. The link will guide you directly to the corresponding figure or table.** Figures and tables in the introduction are numbered 1, 2, 3, and so on. Figures and tables in Chapter I and II, and so on, are numbered I.1, I.2, and II.1, II.2, and so on, respectively. Figures and tables in appendices (Supplementary Material) referring to Chapter I and II, and so on, are numbered S.I.1, S.I.2, and S.II.1, S.II.2 and so on, respectively.

ABSTRACT (EN)

Detritivores play fundamental roles in aquatic and terrestrial ecosystems. They are a key component of “brown” trophic networks which are based on dead organic matter. They regulate litter decomposition by fragmenting, ingesting, and digesting detritus. They influence matter and energy flux at the ecosystem level. Detritivores are considered to feed preferentially on high-quality litter, characterized by high macroelement content and little refractory compounds. Yet, the great diversity of detritivores interacts with a great diversity of litter items. The interaction, as well as the resulting influence of detritivores on decomposition, is highly variable and remains difficult to predict as it depends on a complex trophic network which can be represented as the sum of multiple bipartite interactions. Rules of bipartite interactions can be understood by studying functional traits driving the interaction. Traits of both interacting agents may act in interaction, resulting in trait-matching.

In this thesis we aim to better understand the fundamental rules of the interaction between macrodetritivores and leaf litter through (1) identifying detritivores and litter traits associated with constraints driving consumption, (2) testing if trait-matching better explain the interaction, and (3) testing if these rules shape detritivores at the community level. Under a null hypothesis, we expect detritivores to be generalists and to interact with the full range of litter. Under the opposite hypothesis, we expect detritivores to be hyperspecialists and to have narrow feeding niches ruled by strong trait-matching.

To have a comprehensive understanding of the constraints and the associated traits, we built a conceptual framework about detritivore-litter interactions at the individual level (Chapter I). We identified 5 main constraints that can influence detritivore–litter interaction, namely spatial, biomechanical, digestive, metabolic, and elemental constraints. To identify the relative importance of constraints and test if trait-matching allows us to better explain these constraints, we performed laboratory consumption tests by feeding a range of detritivore species from aquatic and terrestrial ecosystems with a range of leaf litter (Chapter II). We identified mechanical constraints as being predominant over elemental constraints. Litter toughness was an especially important trait in preventing consumption. Elemental constraints were mostly due to constraints in phosphorus element. To test if the identified mechanical constraints rule the interaction throughout the decomposition process, we performed laboratory consumption tests by feeding a range of detritivore species from aquatic and

terrestrial ecosystems with 2 leaf litter species under a gradient of natural decomposition (Chapter III). We showed that litter toughness has a non-linear influence on the consumption rate, with a detritivore-specific threshold effect. To test if the constraints identified in Chapter II result in an elemental match between detritivore communities and leaf litter, we characterized soil detritivore communities in 12 pairs of sites differing by their available litter (Chapter IV). Detritivore communities' chemistry weakly matched local litter chemistry. This effect was better explained by changes in detritivore abundances than by changes in detritivore chemistry.

To conclude, our results show consistent rules in aquatic and terrestrial ecosystems: litter toughness stands as a major trait influencing litter consumption by macrodetritivores, even though mechanical constraints are traditionally neglected compared to elemental constraints. Plus, trait-matching only has a weak influence. Detritivores are mainly limited by litter properties but also have species-specific capacities to overcome these limitations. Detritivores then appear as generalist consumers with a trend toward specialization.

Keywords: Trait-matching, Functional ecology, Decomposition, Functional trait, Trophic interactions, Forests

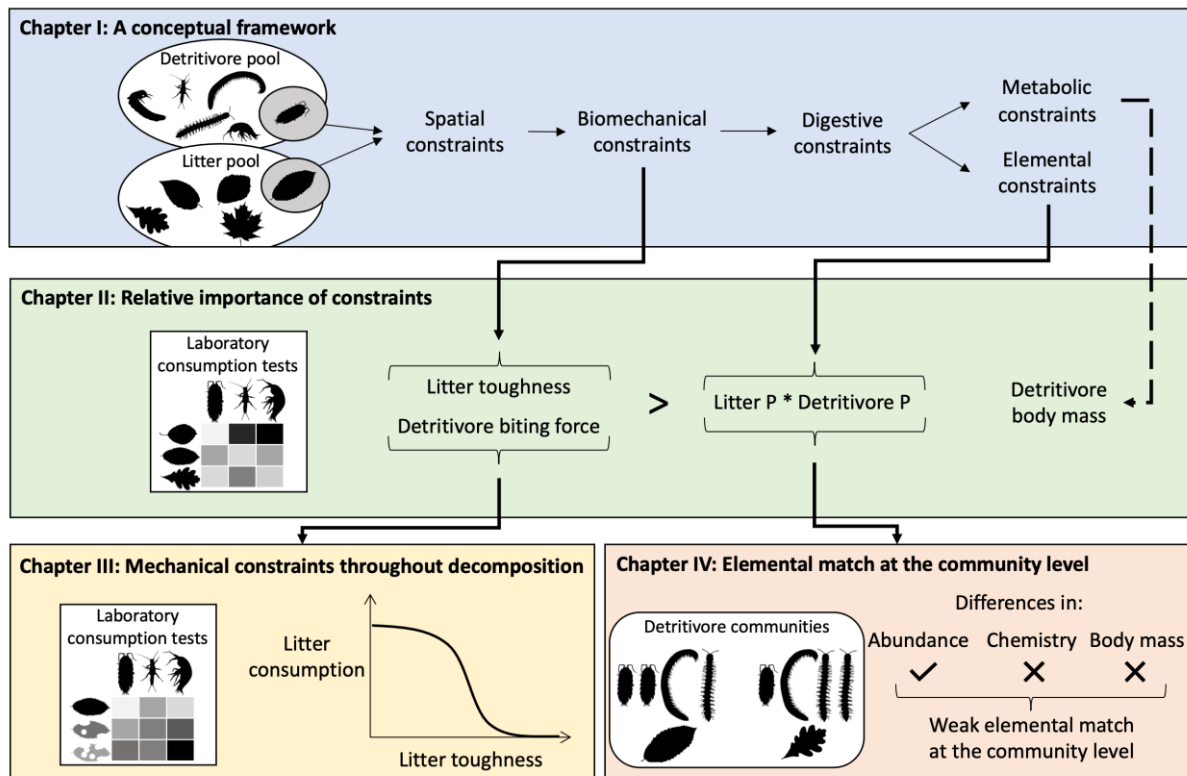


Figure 1: Graphical abstract. Links and articulations between chapters are represented by thick arrows. In Chapter II, mechanical constraints predominated over elemental ones. Elemental constraints mostly depend on phosphorus (P) constraints, with a matching effect (represented by an asterisk *). Metabolism constraints were taken into account with detritivore body mass only and were not linked to any litter trait, hence the dotted arrow. In Chapter III litter toughness decreased with conditioning (illustrated by discolored leaves with holes) and influenced litter consumption with a detritivore species-specific threshold effect. In Chapter IV, elemental constraints influenced detritivore abundance, but not body chemistry. This resulted in a weak elemental match at the community level with litter chemistry.

RÉSUMÉ (FR)

Les détritivores sont des organismes régulant la décomposition des détritits en les fragmentant, les ingérant et les digérant. Ils influencent les flux de matière et d'énergie au sein des écosystèmes. Les détritivores sont connus pour se nourrir préférentiellement de matière organique de haute qualité, caractérisée par une teneur élevée en macroéléments et une teneur faible en composés réfractaires. Cependant, la grande diversité des détritivores interagit avec une grande diversité de détritits. Cette interaction et ses conséquences sur la décomposition est très variable et difficile à prévoir car elle dépend d'un réseau trophique complexe qui peut être représenté comme la somme d'interactions bipartites. Les règles des interactions bipartites peuvent être identifiées en étudiant les traits fonctionnels qui les sous-tendent. Les traits des deux agents du réseau peuvent agir en interaction, ce qui résulte en une concordance de traits.

Dans cette thèse, nous cherchons à mieux comprendre les règles fondamentales de l'interaction entre les macrodétritivores et la litière en (1) identifiant les traits des détritivores et des litières, associés aux contraintes qui régissent la consommation, (2) en testant si la concordance de traits aide à expliquer l'interaction, et (3) en testant si ces règles influencent les détritivores à l'échelle de la communauté. Sous une hypothèse nulle, nous nous attendons à ce que les détritivores soient généralistes et interagissent avec l'ensemble de la litière. Sous l'hypothèse opposée, nous nous attendons à ce que les détritivores soient hyperspécialistes et aient des niches alimentaires restreintes, régies par une forte concordance de traits.

Pour mieux comprendre les contraintes et les traits associés, nous avons construit un cadre conceptuel des interactions entre détritivores et litière au niveau individuel (chapitre I). Nous avons identifié 5 contraintes principales : les contraintes spatiales, biomécaniques, digestives, métaboliques et élémentaires. Pour identifier l'importance relative des contraintes et tester si la concordance de traits permet de mieux les expliquer, nous avons réalisé des tests de consommation en laboratoire avec plusieurs espèces de détritivores et plusieurs litières (chapitre II). Les contraintes mécaniques, surtout liées à la résistance de la litière, étaient prédominantes par rapport aux contraintes élémentaires, surtout liées au phosphore. Pour tester si les contraintes mécaniques identifiées régissent l'interaction tout au long du processus de décomposition, nous avons réalisé des tests de consommation en laboratoire avec plusieurs espèces de détritivores et deux espèces de litière selon un gradient de

décomposition naturelle (chapitre III). La résistance de la litière avait une influence non linéaire sur le taux de consommation, avec un effet seuil spécifique à chaque espèce de détritivore. Pour tester si les contraintes identifiées dans le chapitre II entraînaient une concordance chimique entre les détritivores et la litière, nous avons caractérisé les communautés de détritivores du sol dans 12 paires de sites différant par leur litière disponible (chapitre IV). La composition chimique des communautés de détritivores concordait légèrement avec la chimie de la litière locale.

En conclusion, nos résultats identifient des règles communes aux écosystèmes aquatiques et terrestres : la résistance de la litière apparaît comme un trait majeur influençant la consommation de litière par les macrodétritivores, alors que les contraintes mécaniques sont traditionnellement négligées par rapport aux contraintes élémentaires. De plus, la concordance de traits n'a qu'une faible importance. Les détritivores sont principalement limités par les propriétés de la litière mais ont également des capacités spécifiques à surmonter ces limitations. Les détritivores apparaissent donc comme des consommateurs généralistes avec une tendance à la spécialisation.

Mots-clés : Concordance de traits, Écologie fonctionnelle, Décomposition, Trait fonctionnel, Interactions trophiques, Forêts

POPULARIZED ABSTRACT (EN)

Most of the plant matter is not consumed by herbivores and enters the process of decomposition. Among actors of decomposition, detritivores are diverse organisms, mostly invertebrates such as crustaceans, insect larvae, or millipedes. They consume leaf litter and regulate its decomposition hence influencing ecosystem processes such as the carbon cycle. Yet, their effect is still poorly predictable because of the diversity of plant litter and detritivores. We then aimed to identify which detritivore and litter characteristics (thereafter called traits) rule their interaction. Our results show that detritivore–litter interaction is mainly constrained by litter toughness. Phosphorus constraints also ruled the interaction, but this effect was limited. Different detritivore species differently react to these constraints but overall, detritivore–litter interactions are first constrained by litter properties, then by detritivore specificities.

RÉSUMÉ VULGARISÉ (FR)

La majorité de la matière végétale n'est pas consommée par les herbivores et se décompose. Parmi les acteurs de la décomposition, les détritivores sont des organismes variés, principalement des invertébrés comme des crustacés, des larves d'insectes ou des millepattes. Ils consomment les feuilles mortes et régulent leur décomposition, influençant ainsi les processus de l'écosystème comme le cycle du carbone. Cependant, leur effet est encore difficilement prévisible en raison de la diversité de la litière végétale et des détritivores. Nous avons donc cherché à identifier quelles caractéristiques des détritivores et de la litière (appelées par la suite *traits*) régissent leur interaction. Nos résultats montrent que l'interaction détritivore-litière est principalement contrainte par la résistance de la litière. Les contraintes liées au phosphore jouent également, mais cet effet est limité. Différentes espèces de détritivores réagissent différemment à ces contraintes, mais dans l'ensemble, les interactions détritivores-litière sont d'abord contraintes par les propriétés de la litière, puis par les spécificités des détritivores.



Figure 2 : Canal du midi, November 2020. *Platanus* dead leaves fell into the water. They are especially hard to decompose and hinder boat trafficking. During three years, I enjoyed about 400h biking along this canal to go to the laboratory and back.

INTRODUCTION

This introduction aims to present what is decomposition, its place in ecosystems, and the role of the actors of decomposition. Among them, I will focus on the role of detritivores and the parameters influencing decomposition. I will then identify precise knowledge gaps this thesis will address.

1) Decomposition in the ecosystem

a) Definition of decomposition

All living organisms maintain the integrity of their body structure (i.e., they keep a low level of entropy) by consuming energy and molecules from their surrounding environment. At their death, the molecules constituting their body are no longer built, replaced, or repaired. From this point, the destruction of these molecules and of the cells they constitute is thermodynamically favored.

Primary producers (i.e. plants) may be consumed by herbivores, but most of their organic matter (up to 90% in some ecosystems, especially terrestrial ones) dies and enters the process of decomposition (Cebrian, 1999; Cebrian and Lartigue, 2004). The dead organic matter of the ecosystem is called detritus. It can be of microbial (biofilms, bacteria, fungi...), animal (dead body, feces) (Seastedt and Tate, 1981), or vegetal origin (wood, leaves, roots, fruits...). Dead leaves are an especially important source of detritus, as they represent up to 40% of dead matter in terrestrial environments, and most of the allochthonous material in streams (Freschet et al., 2013; Marks, 2019; Webster and Benfield, 1986). Deciduous trees abscise their leaves every year in temperate regions, contributing to the important pool of detritus. Yet, roots should not be underrated as they may represent up to 48% of decomposing matter in forest ecosystems, and are often neglected in studies (Freschet et al., 2013).

Definitions of decomposition and decomposers may differ between authors. For example, Petersen and Luxton (1982) define decomposition as all abiotic and biotic processes, while Gessner (2010) restricts to biotic processes. I propose to define decomposition *sensu lato* as all physical and chemical mechanisms leading to detritus breakdown (fragmentation and alteration of particles and molecules) (Petersen and Luxton, 1982). Decomposition *sensu stricto* can be restricted to biochemical modifications of molecules, especially oxidation, catabolism, and mineralization (Gessner et al., 2010). In this manuscript, decomposition will

be used as in the *sensu lato* definition. Decomposition happens under the direct influence of abiotic mechanisms, microorganisms, and detritivores (Figure 3). Microorganisms and detritivores will be considered as decomposers *sensu lato*. Decomposers *sensu stricto* will restrict to microorganisms (bacteria, fungi). In this manuscript, decomposers will be used as in the *sensu lato* definition. Detritivores are animals trophically relying on detritus.

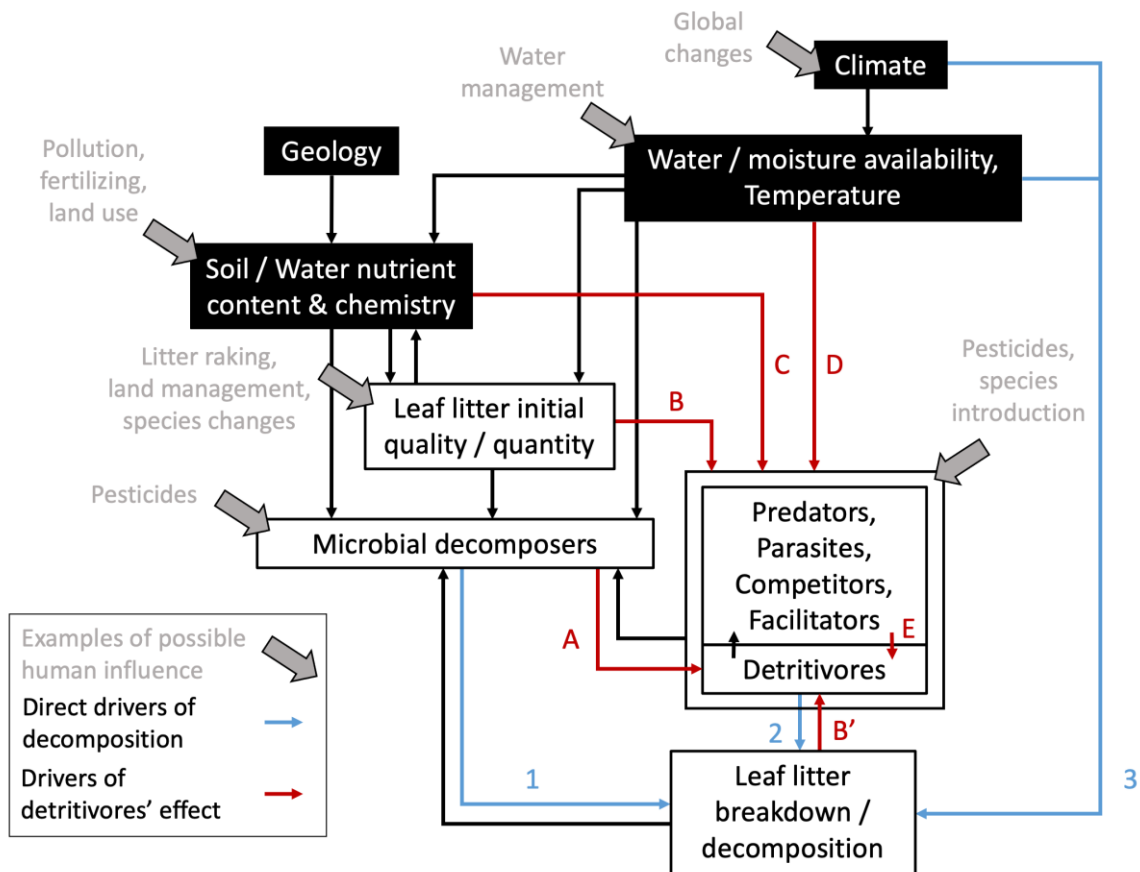


Figure 3: Drivers of leaf litter decomposition. Abiotic parameters are in black boxes. Proximal drivers of decomposition are in blue: (1) microorganisms, (2) detritivores, and (3) abiotic mechanisms (leaching, photodegradation, abrasion). Drivers of detritivores' impact on decomposition are in red: (A) microorganisms, (B) leaf quality and quantity, with the effect of conditioning and a possible retro control (B') as litter quantity and quantity changes with decomposition, (C) soil/water parameters, (D) climate direct and indirect influence, (E) other biotic agents. Examples of possible human influences are in grey. This figure was inspired by Graça et al., 2015.

b) Importance of decomposition for the ecosystem and ecosystem services

Decomposition is a major step of several ecosystem cycles. It is also implied in many ecosystem services (i.e., ecosystem functions that are beneficial for human populations and their activities).

Carbon cycle

Once detritus molecules are assimilated by decomposers, the main catabolic reaction in presence of oxygen is the cellular respiration. Organic matter is consumed with O_2 , which produces CO_2 and H_2O (Figure 4). Through this reaction, chemical and thermic energy are produced. This energy is used by decomposers for their metabolism. In anoxic conditions (without oxygen), other, less efficient metabolic reactions happen such as fermentation or denitrification. It produces incomplete mineralization and other byproducts (e.g. CH_4) (Swan et al., 2021).

With incomplete mineralization, organic molecules are partly shortened and oxidized and can turn into complex and stable molecules (e.g. humus (Prescott, 2010)). Humus (complex organic molecules) is a major component of soils. It influences soil structure and water retention capacity.

The quantity of mineral carbon (CO_2 , CH_4) produced by decomposition and the rate of its release in the atmosphere depends on the rate and conditions of decomposition. Understanding the mechanisms at play is then of critical importance to have a better understanding of the carbon cycle in a context of global warming. Soils have the potential to store carbon (Prescott, 2010) or to release it as in permafrost or peatlands (Turetsky et al., 2007).

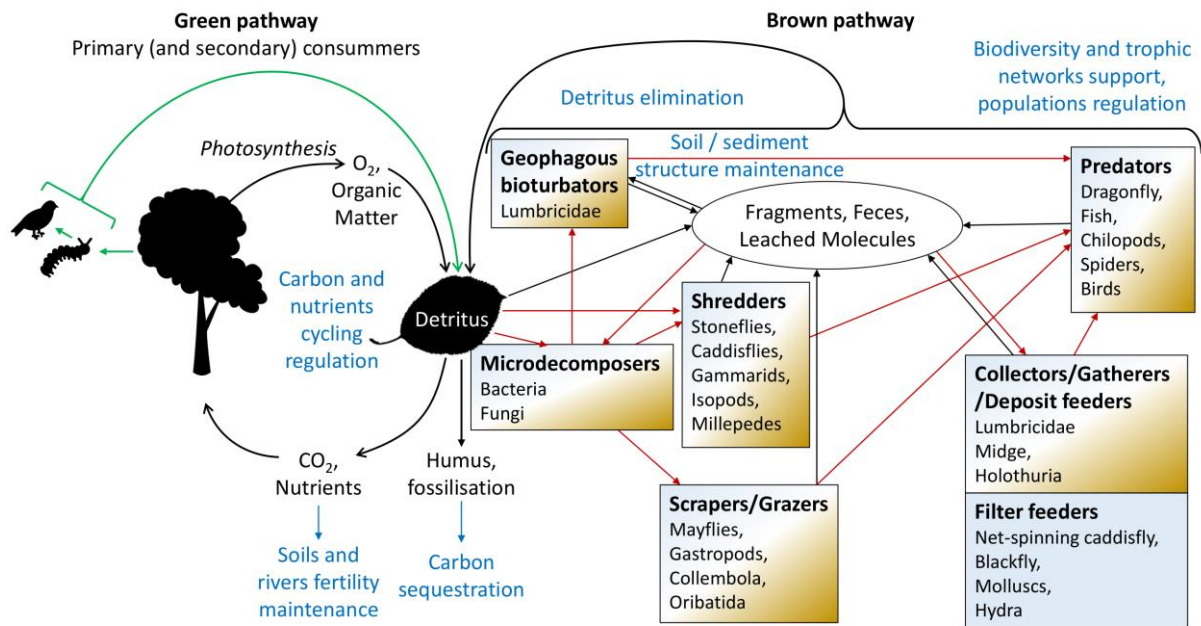


Figure 4: Decomposition and the brown trophic pathway: a major ecosystem process implying many actors. Feeding groups of organisms implied in the brown pathway are presented in boxes with examples of taxa. Brown and blue boxes indicate that the feeding group contains soil and aquatic organisms. Blue boxes indicate that the feeding group contains exclusively aquatic organisms. Red arrows represent trophic relationships implied in the decomposition process. Associated ecosystem services are indicated in blue. Parasites and symbionts were not represented because of their high ecological diversity.

Nutrient cycles

Through decomposition, the elements that constitute dead organisms are ultimately released from the tissues, cells, and molecules they were part of. Besides C, O, and H, living organisms are composed of a variety of elements (Serner and Elser, 2002; Zhang et al., 2022): N, Ca, P, K, S, Cl, Na, Mg, Si, Fe, Zn, Cu... In water and soil, they are typically found as charged molecules (NO_3^- , NH_4^+ , PO_4^{3-} , Ca^{2+} , Na^+ , Mg^{2+} , K^+). These elements are then soluble in water and available for other organisms. In a review, Sayer (2005) presents the consequences of “litter raking”, a common habit of European farmers in the XVIIIth and XIXth centuries. Litter raking consists in collecting dead leaves and using them for animal bedding and as a field fertilizer. By comparing forests where litter raking was common, and nearby forests where it was very limited or non-existent, it is possible to infer the potential consequences of this practice on the ecosystem. In forests where litter raking happened for more than 50 years,

trees were only half the size of similar trees in similar forests but where litter raking never happened. In these forests, soil nitrogen content was lower by more than 40% (and K, Mg, and Ca by more than 30%). When litter is exported, the elements in leaves are exported as well, which limits plant growth. This example highlights the role of decomposition in the nutrient cycle (Figure 4).

Energy fluxes: the “brown pathway”

By constituting a food resource, litter is the basis of a trophic network. Litter is consumed by decomposers and these decomposers may themselves be a trophic resource for other consumers. This trophic network based on detritus material is called the “brown path”, as opposed to the “green path” which starts with the consumption of living primary producers (Krumins et al., 2013; Moore et al., 2004) (Figure 4).

Green and brown pathways differ in the quality of their basal resources. Detritus are generally considered as resources of low quality, with low nutritive content, and a high proportion of refractory molecules (Li et al., 2021; Martinson et al., 2008; Moore et al., 2004). Ultimately, decomposers may be consumed by predators of a third or more trophic level. These predators may rely on both brown and green trophic pathways (Krumins et al., 2013). Litter also acts as a habitat for most soil species (Sayer, 2005).

In aquatic ecosystems, studies testing the impact of litter removal have been conducted for 4 years (Wallace et al., 1999, 1997). It showed that litter removal negatively impacts invertebrate abundance and biomass. In streams where litter was removed, benthic organic matter concentration was lower, total invertebrate abundance decreased by 90%, and biomass by 80%. As a consequence, secondary production decreased by 80% and impacted predators as a bottom-up effect. Litter removal also impacted the species diversity of shredders, collectors, and predators. In contrast, the fauna of moss-covered bedrock substrate was not impacted, suggesting dependence on different foodwebs, not related to litterfall in the short term. In forests, litter raking also leads to lower abundances of detritivores and non-detritivores invertebrates (Sayer, 2005). Litter quantity, quality, and diversity then affect the abundance and diversity of upper trophic-level organisms, from bacteria to predators (Moore et al., 2004).

By consuming detritus, detritivores also quickly remove feces and dead bodies. Without them, decomposition may be much more slowly and animal detritus may be used by other animals, sometimes leading to diseases for human and non-human populations (Dirzo et al., 2014). The case of allochthonous dung beetles processing cattle feces in Australia singularly illustrates the role that detritivores can have in terms of ecosystem services (Doubé, 2018).

Top-down and bottom-up processes then influence decomposition rates, shape ecosystem communities, and rely on high biodiversity (Duffy et al., 2007; Ewers et al., 2012; Lagrue et al., 2015; Mancinelli and Mulder, 2015). Several ecosystem processes and ecosystem services are associated to decomposition processes. Decomposition processes are themselves under the influence of several drivers.

c) Drivers of decomposition

In aquatic and terrestrial ecosystems, decomposition is directly driven by physicochemical mechanisms (leaching, photodegradation, abrasion...), microbial and animal decomposers. Abiotic transformations, microbial metabolization, and detritivores' impacts are themselves under the influence of other biotic and abiotic factors such as climate, detritus quality, and biotic interactions (Figure 3). Distal and proximal drivers of decomposition have been identified as being similar in aquatic and terrestrial environments.

Effects of the abiotic environment

The climate explained 60-70% of decomposition variability in terrestrial global studies (Parton et al., 2007; Wall et al., 2008), and about 30% in a terrestrial meta-analysis (Zhang et al., 2008). Yet, climate parameter comprises several covariables such as litter species identity, decomposer species identity, latitude, altitude, temperature, rainfall, and so on (Figure 3).

Abiotic decomposition happens through several physicochemical reactions (blue arrow n° 3 in Figure 3). Photodegradation, through the energy of light, breaks down molecules, decreasing litter mass. In plant material, it especially affects molecules such as lignin (Austin and Ballare, 2010; Austin and Vivanco, 2006). When put in contact with water (rain, melting snow, running or standing water), hydrophilic molecules (mostly carbohydrates and

polyphenols for leaf litter (Suberkropp et al., 1976)) are dissolved. This phenomenon called leaching can be responsible for up to one-third of initial dry leaf litter mass loss (Allan and Ibañez Castillo, 2009; Taylor and Bärlocher, 1996). Mechanical fragmentation can also happen through abrasion, especially in stream ecosystems (Cristiano and Di Sabatino, 2023).

Temperature strongly influences the kinetics and the equilibrium of chemical reactions. Decomposition is then expected to increase with temperature. Yet, studies found a wide range of effects of high temperatures, from accelerating (Follstad Shah et al., 2017) to slowing down decomposition (Figueroa et al., 2021; Landeira-Dabarca et al., 2019). Especially, a high temperature may be associated with a dry environment, impairing biochemical activity (Aerts, 2006). Moisture is especially important in terrestrial environments (De Smedt et al., 2018). Some detritivores living in dry desertic environments even bury litter resources, keeping it in a relatively moist environment which favors microbial reactions (Sagi et al., 2021). Temperature can also strongly influence detritivores. It increases their metabolism up to a given threshold (Ehnes et al., 2011) and by doing so, litter consumption. Yet, Réveillon et al. (2022) showed that an increase in temperature can lead to an energetical mismatch in *Gammarus fossarum* (aquatic Crustacean), as energetical needs (metabolism) increased faster than energetical intakes (i.e. litter consumption). This could have important consequences on body growth, as well as on population and ecosystem dynamics.

Water or soil pH, and oxygenation are also important parameters influencing decomposition. Low pH and/or oxygenation values impair biochemical activities, detritivores activity, and reduce overall decomposition (Boyero et al., 2016; Moore and Basiliko, 2006; Yue et al., 2022). Under abiotic conditions, decomposition is reduced, and fermentations produce CH₄ or ethanol rather than CO₂.

Detritus identity and quality

Different litter items (leaves, roots, wood, feces, dead bodies...) decompose very differently (see Bonanomi et al. (2021) for a leaf-roots comparison, Špaldoňová and Frouz (2019) for a leaf–feces comparison, and Seastedt and Tate (1981) for a study about the decomposition of arthropod bodies).

For plant litter and especially leaf litter, leaves from different plant species decompose at very different rates. Herbaceous leaves tend to decompose easily, while coniferous leaves tend to decompose slowly (Webster and Benfield, 1986). Describing litter material with traits proved very useful. Traits are individual and measurable characteristics (morphological, physiological, phenological, behavioral...) that can explain the effect or the response of the individual on/to its biotic and abiotic environment (Pey et al., 2014; Violle et al., 2007). Several plant traits have been identified as being closely correlated to decomposition rates. For example, Carbon-Nitrogen ratio (C:N), P content, and Specific Leaf Area (SLA) are often found to be good predictors of decomposability. Nitrogen content explains litter choice and consumption by detritivores (Ohta et al., 2016; Pey et al., 2019). Meta-analyses showed that the effect of detritivores on the field becomes significant when the C:N ratio is above 20, and that climate and litter C:N explain most of the fauna effect (Frouz et al., 2015; García-Palacios et al., 2013). Cellulose, lignin, tannins, phenols, and litter toughness also decrease food consumption by decomposers (Coq et al., 2010; Pey et al., 2019; Walpola et al., 2011; Zimmer et al., 2002). Lignin is a complex molecule especially difficult to catabolize. It can only be metabolized by some specialized fungi species (white and brown rot Basidiomycota fungi) (Floudas et al., 2012; Kirk and Farrell, 1987). Some repulsive molecules such as camphor can also influence the consumption of a given litter by detritivores (Dudgeon et al., 1990).

Decomposition rates can be highly variable between leaves of the same species as traits show high interspecific variability (Lecerf and Chauvet, 2008). Surprisingly, some studies found that green leaf traits better predict decomposition than litter traits (especially N content) (Bakker et al., 2011; Cornwell et al., 2008). Authors often refer to the notion of litter quality. Even though there is no precise definition of quality, litter quality is commonly linked to its decomposition rate or consumption rate. Litter quality then depends on its nutritional (i.e., elemental) content and its potential to be consumed by decomposers. Litter of low quality is often qualified as refractory.

Microorganisms: rulers of decomposition sensu stricto

Microorganisms (blue arrow n° 1 in [Figure 3](#)) constitute *decomposers sensu stricto*. Even though they are most of the time invisible, bacteria and fungi are the first and often most important decomposers *sensu lato* (Bani et al., 2018). In streams and soils, fungi biomass is dominant over bacteria on plant litter, but the fungi/bacteria ratio decreases with

decomposition (Bray et al., 2012; Marks, 2019). These microorganisms can already be present in or on the dead tissues when the detritus item falls on the ground or in the water, but they also come from the surrounding environment (Hayer et al., 2022; Marks, 2019). Bacteria and fungi can cut down molecules with exoenzymes they secrete out of their cells (Štursová et al., 2020). Some fungi of the *Agaricomycota* taxon are especially important as they are the only organisms able to substantially decompose lignin, with specific peroxidases (Floudas et al., 2012) and the use of free radicals (Cragg et al., 2015). This taxon notably contains white and brown rot fungi.

Throughout decomposition, microorganisms modify detritus' physical and chemical characteristics. By breaking lignin, cellulose, and other structural molecules, they decrease litter toughness (Danger et al., 2012; Motomori et al., 2001). By metabolizing tissues, especially carbon (mineralizing it into CO₂), but keeping other nutritional elements for themselves, they increase the overall (litter + associated microorganisms) relative elemental ratios of detritus, such as C:N or C:P ratios (Danger et al., 2012). This transformation process is called microbial conditioning.

Detritivores: rulers of decomposition sensu lato

Detritivores are animals (metazoa) eating or grazing on detritus and/or eating microorganisms on detritus (blue arrow n° 2 in Figure 3). This definition excludes protists (polyphyletic unicellular eukaryotes feeding on bacteria) that are sometimes considered detritivores even though they are not metazoans (Ribblett et al., 2005). On average, detritivores increase decomposition rates by 30-50% and even more in some aquatic field studies (Allan and Ibañez Castillo, 2009; Follstad Shah et al., 2017; García-Palacios et al., 2013; Yue et al., 2022; Zhang et al., 2015). Detritivores directly accelerate decomposition by consuming, fragmenting, moving, and modifying detritus. They also indirectly influence decomposition by interacting with microbial decomposers (David, 2014; Marks, 2019). Detritivores also chemically influence the path of the organic matter they ingest. Indeed, studies showed that some refractory compounds such as condensed tannins almost completely disappear in feces and that the conversion of litter into feces accelerates carbon cycling (Coulis et al., 2009; Joly et al., 2020).

Detritivores can be classified according to their size between micro- (< 0.2 mm; e.g. Nematoda), meso- (0.2 < 4 mm; e.g. Acaria, Collembola), and macro- (4 < 80 mm; Annelidae, Mollusca, Isopoda, Myriapoda, most Insecta) detritivores. Megafauna (> 80mm) typically comprises vertebrates. They are also classified according to their habits of consumption. Xylophagous detritivores are specialized in eating dead wood. They often have a specific microbiota, allowing them to feed on such recalcitrant food (Breznak, 1982). Coprophagous detritivores such as dung beetles consume feces. Some necrophagous animals, such as *Sarcophagidae* Diptera, or vultures, are specialized in eating carrion (Dirzo et al., 2014). Among saprophagous detritivores relying on plant litter, we commonly distinguish several feeding groups (Marks, 2019; McCary and Schmitz, 2021) (Figure 4):

- Some detritivores feed on coarse (> 1mm) particles of litter, breaking it down in the process. They have a quite low assimilation rate of the litter resource. The fragmentation process and their egesta create smaller particles which increase the surface that is accessible to microorganisms. They are called *shredders*.
- Other, often smaller, detritivores scrap or graze on the litter surface. They mainly consume microorganisms, periphyton, and biofilm on the litter. They are called *scrappers* or *grazers*.
- Some aquatic detritivores catch fine particles in the water flow. They are called *filter feeders* and are exclusively aquatic organisms.
- Others consume fine (> 0.5 μm , < 1 mm) surface deposits on or in the soil/sediment. They are referred to as *collectors*, *gatherers*, or *deposit feeders*.
- Geophagous organisms consume soil. They rely on the organic matter that is present in the organo-mineral layers of the substrate.

The terms “shredders”, “scrappers” and “collectors” are mainly used in aquatic ecology but can easily be applied to soil ecology (e.g. McCary and Schmitz, 2021) where no specific term exists to describe them.

Detritivore identity is a key parameter to better understand their influence on decomposition. For example, microarthropods seem to have a lesser impact than macroarthropods (Kampichler and Bruckner, 2009). Detritivorous bioturbators and shredders appear to have a higher impact on decomposition than scrappers (McCary and Schmitz, 2021). Detritivorous bioturbators hold a special place among detritivores as they play a fundamental

role in decomposition by consuming large quantities of litter and moving organic matter down in the soil (McCary and Schmitz, 2021; Patoine et al., 2017). They physically, biologically, and chemically modify their environment, thus indirectly influencing decomposition (Brown et al., 2000). Yet, even though they are key actors of decomposition, their influence can be highly variable and difficult to predict (Allan and Ibañez Castillo, 2009; Follstad Shah et al., 2017; García-Palacios et al., 2013; Yue et al., 2022; Zhang et al., 2015).

Biotic interactions within the brown trophic network

Here, I will point some biotic interactions without being exhaustive in presenting associated mechanisms and methodological approaches.

First, microorganisms have numerous and intricate relationships with detritivores (Figure 3). Microorganisms are the main actors of detritus conditioning. They participate in transforming refractory litter into palatable one (Bärlocher and Kendrick, 1975; Danger et al., 2012; M. A. S. Graça and Cressa, 2010). To disentangle the mechanisms through which microorganisms increase detritivore consumption, Zimmer et al., (2003) tested whether leaf-colonizing microorganisms would increase *Porcellio* (Isopoda) consumption through (1) increasing the nutritive value of leaf litter, (2) increasing the digestibility of leaf litter, (3) serving as indicators of the high-quality nature of the leaf litter. Their findings supported the third hypothesis, without excluding the first two ones.

Microorganisms also constitute the digestive microbiota of detritivores. As such, they play a major role in digestion and assimilation. For example, tannins tend to be detoxified during the digestive process of *Glomeris marginata* (Myriapoda) (Coulis et al., 2009). In isopods, the oxidation of phenols is mainly due to endosymbiotic bacteria in the hepatopancreas (Zimmer, 1999). In asellidae but not in gammarids, the use of antibiotics induced a reduction of phenol oxidase and cellulase activity (Zimmer and Bartholmé, 2003). Some detritivores have specific digestive enzymes of their own, and the overall digestive capacity is due to a complex interaction between the host and its microbiota genomes (Bredon et al., 2020; Cragg et al., 2015). In turn, detritivores can directly (e.g. through consumption) or indirectly (e.g. through detritus fragmentation or fecal pellets production) influence litter-colonizing microorganisms (David, 2014; Hanlon and Anderson, 1980; Marks, 2019).

Detritivores may have facilitative or competitive effects when put together. It is especially expected that when put together, individuals from different feeding guilds (shredders, scrappers) would have facilitative effects (Heemsbergen et al., 2004; Marks, 2019; Patoine et al., 2017) and that food limitation would lead to competition (Fugère et al., 2012; McKie et al., 2009). Invasive species can also lead to new competition and changes in detritivores' communities (Jochum et al., 2022). Yet, the interplay between biodiversity and decomposition are far from being completely understood (Coulis et al., 2015).

Lastly, predators or parasites can also influence detritivores either directly by reducing their abundance or modifying the community (Bouchon et al., 1998; Duffy et al., 2007; Ewers et al., 2012), or indirectly by modifying their behavior (Lagrué et al., 2015). For example, the bacteria *Wolbachia* induces a feminization of isopod populations (Bouchon et al., 1998). Lagrué et al. (2015) showed that the presence of predators reduced the feeding activity of detritivores and induced a shift to predator-free habitat patches in non-armored detritivores.

The relative importance of drivers

Some studies suggest that the importance of climate was over-estimated to the detriment of litter traits in terrestrial environments (Bradford et al., 2016; Cornwell et al., 2008). Indeed, the climate also influences the vegetation, microorganisms, and detritivore species that can be found in each region. It is then difficult to disentangle direct climate effects (temperature and humidity effect) from other indirect effects (e.g. litter traits will depend on plant species that depend on climate) (Graça et al., 2015). In a meta-analysis, Zhang et al. (2015) revealed that detritivores' effect on decomposition is first explained by temperature, then precipitation, then litter phosphorus, nitrogen, and lignin content. In the classical Hierarchical Model of Decomposition built in the 1990s, the climate is the first parameter controlling decomposition, especially at large (continental) scales (Lavelle et al., 1993). Yet, the fact that there could be more variability in decomposition rate for different litter under a given climate, than for a given litter under different climate influences (Cornwell et al., 2008) led to the Dynamic Decomposition Model (García-Palacios et al., 2021). This model states that climate, litter quality, and decomposers can have various relative importance in time and space. This model also underlines the similitudes in decomposition control processes between aquatic and terrestrial ecosystems.

Decomposers and decomposition can also be affected by human activities. For instance, pollutants such as pesticides (Rasmussen et al., 2013; Sabater et al., 2018; Schoffer et al., 2020) or microplastics (Ockenden et al., 2022) negatively impact decomposers. Land use change can also affect macroarthropods populations and their role in decomposition dynamics (Christel et al., 2021; Sabater et al., 2018).

Conclusion (EN)

To conclude, decomposition is a major process of ecosystems. It is an important step in many geochemical cycles. Most species, whether they are autotrophic or heterotrophic, directly or indirectly rely on it. A lot of ecosystem services directly or indirectly depend on it. Decomposition is driven by physicochemical processes, microorganisms, and detritivores. These drivers are, in turn, driven by biotic and abiotic variables such as climate and litter quality. Litter quality is commonly described by litter nutritional traits. It influences litter consumption by microorganisms and detritivores. Detritivores are key actors as they accelerate and influence the path of decomposition. They are represented by a large diversity of animals interacting with all actors of brown trophic networks. Their influence is highly variable and lacks functional understanding and predictability.

Conclusion et transition (FR)

En conclusion, la décomposition est un processus majeur des écosystèmes. Il s'agit d'une étape importante dans de nombreux cycles géochimiques. La plupart des espèces, qu'elles soient autotrophes ou hétérotrophes, dépendent directement ou indirectement de ce processus. De nombreux services écosystémiques dépendent également directement ou indirectement du processus de décomposition. La décomposition est due à des mécanismes physico-chimiques, à des micro-organismes et des détritivores. Ces acteurs sont, à leur tour, influencés par des variables biotiques et abiotiques telles que le climat et la qualité de la litière. La qualité de la litière est généralement décrite par ses caractéristiques nutritionnelles. Elle influence la consommation de la litière par les micro-organismes et les détritivores. Les détritivores sont des acteurs clés car ils accélèrent et influencent le processus de

décomposition. Ils fragmentent les litières, les ingèrent et les digèrent. Ils en assimilent une partie et en rejettent une autre, notamment sous forme de fèces. Ils représentent une grande diversité d'animaux interagissant avec tous les acteurs des réseaux trophiques "bruns". Leur interaction avec les micro-organismes et les litières est particulièrement complexe. L'influence des détritivores est donc très variable, fonctionnellement mal comprise, et peu prévisible. Une façon de mieux comprendre leur influence est de mieux comprendre le réseau détritique dans lequel ils s'inscrivent. Ce réseau peut notamment être étudié en se concentrant sur les interactions bipartites détritivore – litière. Ces interactions peuvent être décrites par les traits fonctionnels de chaque acteur. Les traits fonctionnels sont supposés pouvoir expliquer la présence ou l'absence d'une espèce dans un environnement donnée, ainsi que sa capacité à interagir avec un autre acteur du réseau. En particulier, si les traits des deux acteurs influencent fortement l'interaction, on s'attend à ce qu'une concordance entre les traits régule l'interaction. Cette thèse visera donc à mieux comprendre les interactions trophiques entre détritivores et litières, en (1) construisant un cadre conceptuel de ces interactions, basé sur la littérature déjà existante et (2) en identifiant les règles de l'interaction basées sur les traits des détritivores et des litières. L'objectif (2) s'appuiera sur le cadre conceptuel défini précédemment (1).

2) Knowledge gaps, questions, and method

This second part identifies the knowledge gaps this thesis will tackle. Knowledge gaps will be addressed through precise questions. Each chapter constituting this thesis will address one or more questions by testing key hypotheses.

a) Understanding decomposition: historical approaches

Decomposition has been historically studied through two main approaches (Brussaard, 2012). The first one can be considered a biogeochemical approach. It consists in studying the process of decomposition through matter and energy fluxes in the ecosystem. It tackles several questions about the dynamic of decomposition, its place in the ecosystem, and its contribution to upper trophic levels (Cebrian, 1999; Four et al., 2019). Yet, it rarely considers the actors of decomposition and neglects the precise role of each decomposer. The second approach consists in studying decomposer species and their interaction with detritus. It is a biological approach. It tries to understand what shapes communities, or the influence of biotic and abiotic filters (Fernández et al., 2015; Frainer and McKie, 2015). Yet, it rarely investigates the influence of species on processes at the ecosystem scale. Here, we will focus on the precise influence of detritivores on plant litter.

These approaches traditionally use a taxonomic identification of species. Yet, taxonomical identity is not necessarily linked to the functionality of species. Ecosystem processes depend more on species functionality and complementarity than on species number and taxonomic identity. For example, Heemsbergen et al. (2004) showed that detritivores' interspecific dissimilarity, and not species number, predicted litter decomposition. Plus, the taxonomy of detritivores is sometimes very difficult to handle because of the vast diversity of organisms and because some taxa lack a rigorous classification or because they are difficult to identify (especially for larvae or juveniles individuals that lack sexual parts (Blower, 1985; Decaens et al., 2008; Tachet et al., 2010)).

These historical approaches did not allow to precisely quantify and predict the role of detritivores in decomposition despite their crucial influence. Today we still lack predictive power about the effect of detritivores and we can explain only a quarter to a third of the variability of their effect at the ecosystem level (Boyero et al., 2016; Zhang et al., 2015).

b) Understanding trophic network rules

First attempts to bridge “biochemical” and “biological” approaches were conducted on plants, by describing species with functional traits. It allowed to explain the impact of plant communities on the ecosystem (Lavorel and Garnier, 2002). Yet, taking into account several trophic levels with multiple interactions prevents applying this method to complex networks that include animals (Gravel et al., 2016). To understand ecosystem processes that are driven by multiple species from different trophic levels, it may be useful to understand the underlying trophic networks functioning (Gravel et al., 2016; Schleuning et al., 2015). The functioning of a trophic network depends on (1) the structure of the network characterized by the presence and the abundance of co-occurring network species (nodes identity and nodes size). The presence and abundance of species can depend on biotic and abiotic filtering (Belyea and Lancaster, 1999; Decaëns et al., 2008). The functioning of networks also depends on (2) the feasibility and the strength of the interaction between each pair of actors (links and links width between nodes). Trait-based approaches allowed to investigate the underlying mechanisms ruling trophic networks by taking into account the functional characteristics of species (Bartomeus et al., 2016; Gravel et al., 2016; Schleuning et al., 2023, 2015). Some traits rule species filtering and help to infer network structure. Other traits rule species interactions and help to infer network organization and functioning. Trait-based approaches may then contribute to filling the gap between “biogeochemical” and “biological” approaches (Marjakangas et al., 2022; Schleuning et al., 2015). Yet, until now, studies investigating detritivore-litter interactions with functional traits mainly focused on litter traits and especially on litter chemical traits. Such studies rarely consider interaction traits between litter and detritivore and rarely connect functional descriptions of the community to network structure.

It was hypothesized that the feasibility and strength of the interaction between two actors may be explained and predicted not only by single traits of both actors but also by a match between these traits (Bartomeus et al., 2016; Laigle et al., 2018; Pearse et al., 2013; Schleuning et al., 2015, [Figure 5](#)). A famous historical example is the match between Darwin’s finches’ beak size and fruit size explaining the outcome interaction: birds with large beaks tend to eat large fruits (Price, 1987). Regarding detritivore-litter interactions, Brousseau et al. (2019, 2018) showed through a field approach that invertebrates traits spatially correlate with prey

and predators (e.g. prey cuticle toughness with predator mandible strength) and that detritivores' mandibles shape spatially correlates with litter traits. Yet, apart from a few examples of field correlations, no study tried to apply trait-matching approaches to detritivore-litter interactions.

Using trait-based approaches to explain ecosystem functioning is a challenging task. Yet, identifying traits ruling bipartite interactions is a first step. Inferring these rules should help to scale up at the network level.

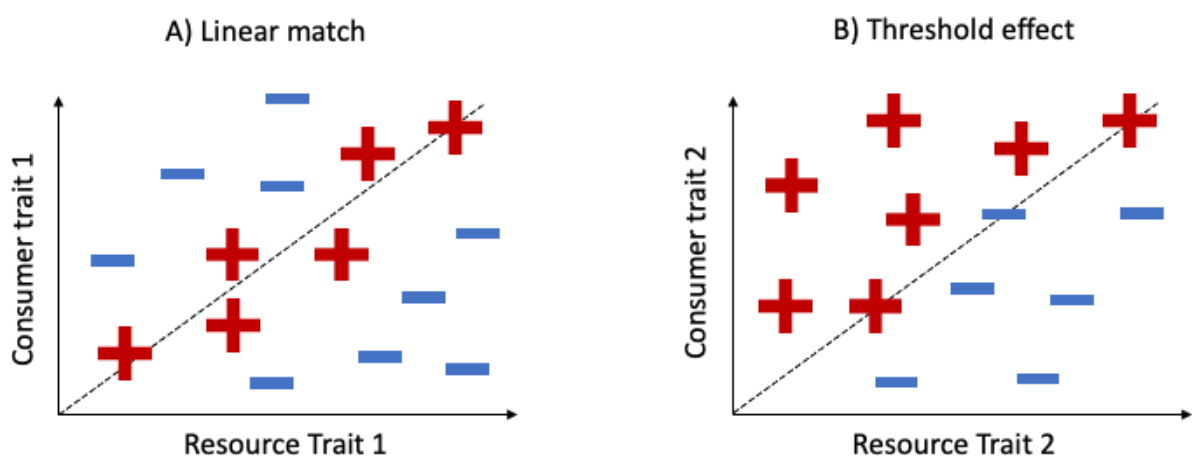


Figure 5: Examples of different trait-matching interactions. A) Example of a linear matching relationship. A laboratory trait-matching approach showed that there is a linear relationship between grasshoppers' incisor strength and plant toughness, explaining the consumption rate of plants by grasshoppers (Ibanez et al., 2013). In short, grasshoppers with strong mandibles eat tough plants and vice versa. Here, the traits “mandible strength” and “plant toughness”, as well as their interaction, are important to explain the outgoing trophic interaction. B) Example of a match with a threshold effect. Observations of pollination events revealed that trait-matching can apply with threshold constraints: when the proboscis of the pollinator insect is shorter than the depth of the flower nectar holder, the interaction does not happen (Stang et al., 2007).

d) Questions, Hypotheses

This thesis aims to tackle one main objective and to help answer several questions.

Main objective: Better understand the trophic interactions between detritivores and detritus

Objective I: Build a conceptual framework for detritivore-litter interactions

Question 1a: Which constraints may drive detritivore-litter interactions? (Chapter I)

Question 1b: Which traits may be associated with these constraints? (Chapter I)

Question 1c: Which detritivore and litter traits may match to better explain detritivore–litter interactions? (Chapter I)

To understand detritivores' impact on decomposition, we need to have a clear understanding of what could drive and influence the interactions between detritivores and detritus. This need for a conceptual framework has already been answered for other trophic interactions such as prey-predators interactions (e.g. Wootton et al., 2023), or plant-herbivore interactions (Pearse et al., 2013). Yet, detritivore-detritus interactions need a specific framework as detritus are dead organic matter and do not react to the interaction as animal prey or living plants do. For example, detritus have no defense mechanisms other than residual chemical compounds or structural attributes (Dudgeon et al., 1990; Nakamura et al., 2022). Detritus are also changing over time with decomposition. Initial leaf litter, for example, is considered mainly unpalatable for detritivores. Consumption is the cornerstone of detritivore–litter interactions as it initiates litter fragmentation by detritivore handling, and transformation by detritivore metabolism once ingested (David, 2014; Marks, 2019). Different constraints may then apply differently over time, impairing or allowing consumption. A conceptual framework for litter–detritivore interactions should then identify which kind of constraint may impact interactions and at which step of the interaction (detection, ingestion, assimilation...) they may stand. For each constraint, we also need to identify which traits play a role and which detritivore and litter traits could match to explain the interaction (Figure 5).

Objective II: Identify trait-based rules of the interactions between detritivores and detritus

Question 2a: Which constraints mostly influence detritivore-detritus interactions? (Chapter II)

Question 2b: Which detritivore and litter traits rule these constraints? (Chapter II, III, and IV)

Question 2c: Can trait-matching help to better explain detritivore-detritus interactions? (Chapter II, III, and IV)

Detritivores rely on a particularly poor resource. Leaf litter has generally low nutrient content (i.e. high C:N and C:P ratios), and low carbohydrates, lipids, and protein content compared to green leaves (Li et al., 2021; Simon et al., 2018). It also generally has high refractory compound content such as lignin, tannins, and phenols (Li et al., 2021; Rosenfield and Müller, 2020; Sariyildiz and Anderson, 2005). Detritivores present a large range of body masses and diverse morphological and functional attributes (mandibles, antennae sizes and shapes, digestion capacities, macroelement content...) (Staden et al., 2011; Zhang et al., 2022; Zimmer and Bartholmé, 2003, [Figure 10](#), [Figure 11](#)). Under the null assumption that all detritivores can interact with the full range of litter, no constraint should impact the interaction ([Figure 7](#), hypothesis H0). Yet, under the assumption that litter constraints and detritivore capacities and needs may impact the interaction, we can expect some constraints (e.g., mechanical, elemental) to predominate over others and to be associated with key litter and detritivore traits. These constraints can lead to a gradient of interaction specificity from a high importance of litter constraints (with an over importance of litter traits) to highly specialized diet niches (with both detritivore and litter traits at play) ([Figure 7](#), hypotheses H2 and H3).

Emerging from a trait-based perspective (Schleuning et al., 2023), a trait-matching approach seems promising to understand bipartite interaction rules that may depend on an interaction between both consumer and resource traits (Ibanez et al., 2013). Yet, it has never been formally applied to saprophagous detritivores apart from a few field correlation studies (Brousseau et al., 2019; Raymond-Léonard et al., 2019). The importance of trait-matching should depend on the specificity of the interaction between detritivores and litter. If detritivore taxa are totally or partly specialized in consuming a given range of litter, we can expect trait-matching to be important in explaining the interactions ([Figure 7](#), hypothesis H2 or H3). If detritivores are generalist and opportunistic consumers, we can expect trait-matching not to apply to the interaction ([Figure 7](#), hypothesis H0 or H1).

Question 3: What is the temporal dynamic of the underlying trait-based rules? (Chapter III)

Detritus traits are drastically changing over time and seasons, due to physical and microbial conditioning (Nilsson, 1974; Wickings et al., 2012). We will then investigate whether those changes have consequences on trait-based rules and the outcoming interaction. If detritivores are limited by some specific constraints that change with time through decomposition, we can expect the interaction to be possible within a given range of litter conditioning (Figure 7, hypotheses H1, H2, and H3).

Question 4: Do trait-based rules have consequences at the community scale? (Chapter IV)

Detritivores have limited dispersion capacities (Auger et al., 2023; Chatelain and Mathieu, 2017; Gongalsky and Persson, 2013). Individuals generally have to cope with the locally available litter. Field studies show that detritivore communities are influenced by litter. For example, detritivore population biomass can be influenced by litter chemistry (Ott et al., 2014). Macrodetrivore species richness may also increase with litter diversity (David et al., 2023). Different detritivore reactions or adaptations to a given local litter quality could have consequences at the community level. First, detritivore body chemistry may change according to the local litter resource chemistry (non-strict homeostasis hypothesis). Second, some detritivore species with the lowest chemical needs may better cope with low-quality litter (low nutrient content) than other species (Figure 7, hypothesis H3). Under these two assumptions, we can expect trait-matching to have consequences at the community level. We can then expect to observe a match between detritivore community chemistry and litter chemistry. On the opposite, if these assumptions do not apply, or if other constraints predominate (e.g., environmental filtering), or if detritivores show different reactions or adaptations (food complementation or compensation), no elemental match between detritivore and litter should arise.

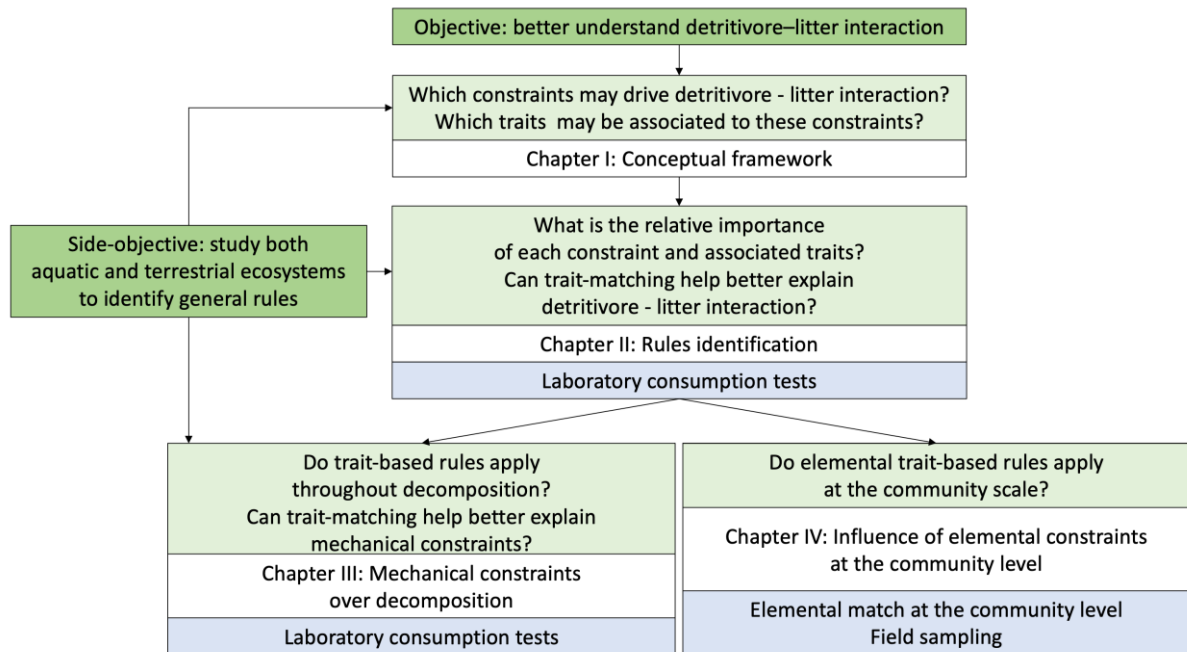


Figure 6: Conceptual architecture of this thesis. Objectives are in dark green boxes. Questions are in light green boxes. Chapters tackling these questions are in white boxes. Experimental approaches are in blue boxes.

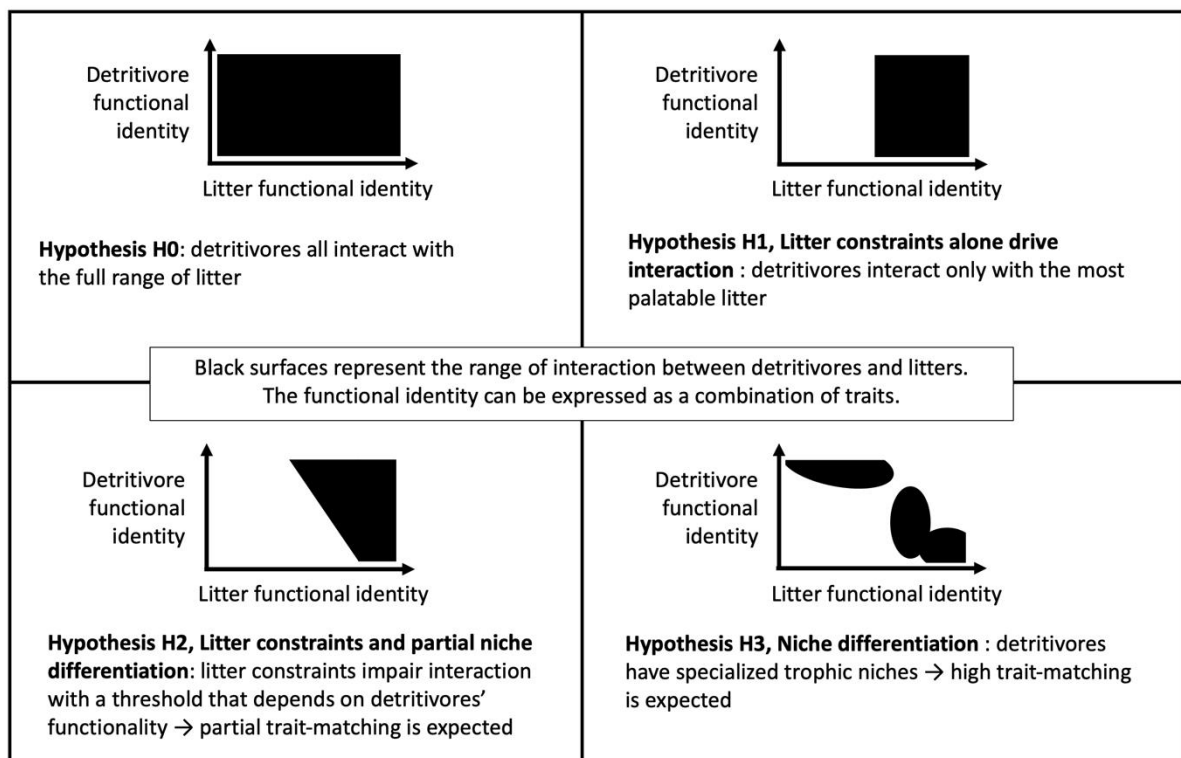


Figure 7: Key hypotheses of how detritivores and litter could interact.

e) Models, material, and methods

Studying both aquatic and terrestrial ecosystems

Decomposition in aquatic and terrestrial environments is traditionally studied separately, by experts belonging to two different communities of researchers. Yet, these two ecosystems are more similar than they seem, and they share common environmental drivers of decomposition processes. Despite early calls to study them with a common approach (Wagener et al., 1998), and the construction of common theoretical frameworks (Gessner et al., 2010; Krumins et al., 2013), inter-ecosystems studies started to be conducted only recently. They brought empirical confirmation that decomposition in aquatic and terrestrial ecosystems has much in common (Four et al., 2019; García-Palacios et al., 2016; Handa et al., 2014; Rota et al., 2022). Studying these two ecosystems at once allows us to identify consistent mechanisms and generic rules that do not depend on one ecosystem in particular.

Studied taxa

Experimentally, we mostly focused on arthropod macrodetritivores. Macrodetrivores have the largest impact on decomposition, compared to other detritivores (Kampichler and Bruckner, 2009; McCary and Schmitz, 2021). Earthworms do not only depend on litter as they also depend on soil organic matter (David, 2014). Plus, focusing on arthropods allowed us to have uniform experimental setups (e.g., earthworms require large quantities of soil in microcosms) and to measure comparable traits (e.g., mandible size). We studied a diversity of the most common lifeforms of arthropod macrodetritivore in temperate regions. It included Crustaceans (aquatic Amphipoda and terrestrial Isopoda), Insecta (aquatic larvae of Plecoptera, Tipula, and Trichoptera), and Myriapoda (Glomerida, Polydesma, and Diplopoda). Detritivores were captured in la Montagne Noire, a forested massif east of Toulouse for Chapter II. For Chapter III, they were captured in Oak-Hornbeam forests southwest of Toulouse (Fabas and Mauboussin forests in Cassagnabère-Tournas (31420) and Saint-André (31420), respectively). For Chapter IV, we used multiple pairs of sites in different pedo-climatic regions of France (Pyrenean piedmont, Montagne Noire, Luberon, Vosges, Normandie).

Detritivores sampling

In Chapter IV, detritivore communities (identity and abundance of each morphospecies) were characterized by quantitatively sampling detritivores. For this, we extracted soil blocs of 25x25x25 cm³, including litter, and sort-handed all macrofauna individuals. Several blocs were extracted and sorted on each site. The community of each site was then first characterized by the identity and the abundance of detritivore morphospecies.



A) Example of quantitative sampling. A soil bloc of 25x25x25 cm³, including litter, was extracted and all macrofauna individuals were hand-sorted. May 2021, Montagne Noire, France.



B) Example of sight-hunting on the soil. In favorable conditions, many individuals are visible in a few cm². At least 14 *Polydesmus* are visible in this picture. Can you find them all? June 2021, Auzeville-Tolosan, France.



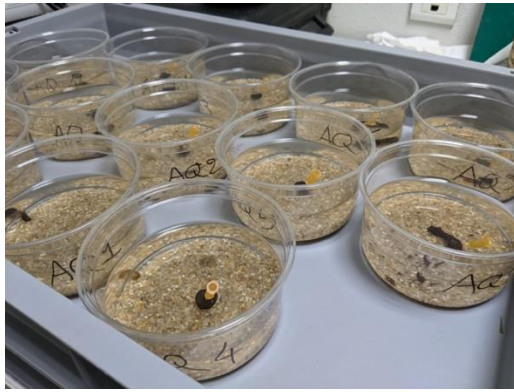
C) Example of sight-hunting in a stream. We are searching for individuals between dead leaves. November 2021, Montagne Noire, France.

Figure 8: Field techniques to sample detritivores.

Laboratory consumption tests

Laboratory consumption tests of a single litter by a single detritivore individual in a microcosm are a powerful means of identifying trophic interaction rules. Choice trials allow to test for consumption preferences while no-choice consumption tests allow to test for consumption capabilities (Dray et al., 2014). No-choice consumption tests allow one to focus on rules constraining or allowing consumption. As detritivores are alone in a microcosm under controlled conditions, it also allows to remove variability due to abiotic and biotic influence apart from microorganisms' effect (Coulis et al., 2015). Detritivores also do not have to search for their food, which removes the influence of detection constraints (spatial constraints in Chapter I) (Crespo, 2011; Erktan et al., 2020). For these reasons, we used no-choice consumption tests in Chapters II and III. Detritivores were acclimated and starved for a few days before the tests so that non-feeding strategies would be energetically too costly. Consumption tests happened in small plastic boxes with clean sand and water, in the dark at 10°C, and lasted no longer than 4 days. For Chapter II, we wanted to assess the fundamental rules constraining litter consumption. We then used litter species that were all unknown to detritivores to minimize bias. Likewise, we conditioned litter in artificial and controlled conditions. On the contrary, for Chapter III the objective was to follow the natural process of leaf decomposition. We then used litter species that detritivores were used to, conditioned in the natural conditions of their habitat of origin.

Few studies tried to explain the consumption of detritus by detritivores using both litter and detritivore traits. Detritivore quantitative traits are especially understudied, except for body mass (Brousseau et al., 2019; Raymond-Léonard et al., 2019).



A) Microsomes for no-choice feeding trials of aquatic detritivores. A needle maintains the discs that would otherwise be floating.



B) Microsomes for no-choice feeding trials of terrestrial detritivores.



C) *Potamophylax* sp. (Caddisfly larvae) with oak leaf discs. A needle maintains the discs that would otherwise be floating.



D) *Cylindroiulus* sp. (Diplopoda) with Robinia leaf discs.

Figure 9: Individual no-choice consumption tests for aquatic and terrestrial detritivores.

Detritivore traits measurement

Dry body mass is a trait that is widely and almost systematically used to describe animal species (Green et al., 2022). According to the Metabolic Theory of Ecology (Brown et al., 2004), basal metabolic rate scales positively with body mass according to a $\frac{3}{4}$ power law. Under the assumption that total energy expenditure correlates with basal metabolic rate and that consumption fills energetical needs, body mass can be considered as a proxy for consumption linked to energetical needs. Detritivore body mass was measured to the nearest 0.1 mg. For Chapters II and III, fresh body mass was measured on all individuals. Dry body mass was also measured afterward on half individuals that were freeze-dried. A linear regression between fresh and dry body mass was then used for each taxon to estimate the dry body mass of

individuals that were only fresh-weighted. For Chapter IV we only used dry body mass from individuals that were dried at 45°C for 4 days.

To estimate detritivore biting force in Chapters II and III, we used a mechanical model. Head width is empirically correlated to the strength of masticatory muscles (Clissold, 2007; Rühr et al., 2022; Wheeler and Evans, 1989). The strength of adductor muscles (whose contraction close mandibles) is proportional to the strength transmitted to the tip of the mandible. The proportionality coefficient depends on mandible shape, more precisely on the ratio between mandible width (i.e. the distance between the insertion of the adductor muscle and the axis of rotation of the mandible, identified by condyles), and mandible length (i.e. the distance between the mandible tip and the axis of rotation of the mandible, identified by condyles) (Clissold, 2007). We then measured head width (H_w), mandible length (M_L), and mandible width (M_w) on several individuals conserved in 70% ethanol and dissected under a stereomicroscope equipped with a digital camera (Olympus SZX10) to determine morphological traits to the nearest 0.01 mm (Figure 11). Those metrics were used to calculate an index of biting force (F) at the taxon level:

$$F = \frac{H_w M_w}{M_L}$$

To estimate the capacity of detritivores to open mandibles and grab a piece of leaf litter, we measured mandible gape for Chapter II (Brousseau et al., 2019). Mandible gape was considered as the maximal opening of mandibles. We then measured this parameter to the nearest 0.01 mm on several individuals conserved in 70% ethanol and dissected under a stereomicroscope equipped with a digital camera (Olympus SZX10) to determine a mean value at the taxon level.

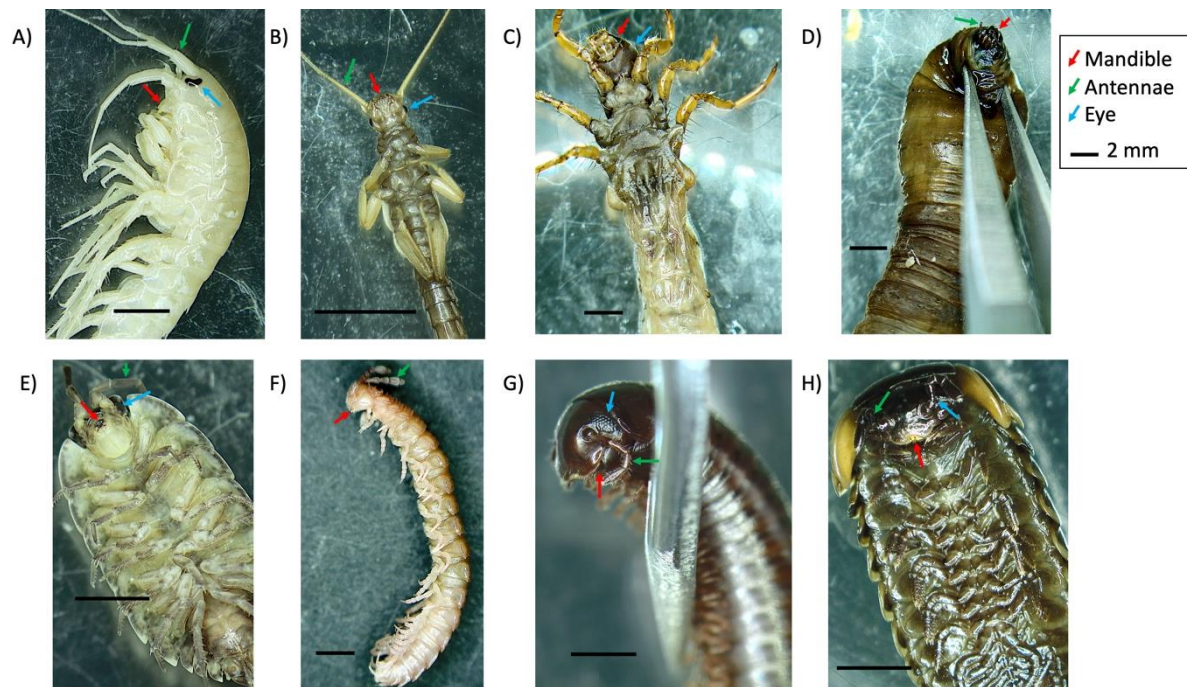


Figure 10: Anterior morphology of some detritivore taxa. All images are oriented so that the head is on top. This figure illustrates the diversity of detritivore morphologies (Shape, soft-hard tissues, number of legs, antennae, eyes...). A) *Gammarus fossarum*, side view. B) *Nemoura* sp., ventral view. C) *Potamophylax cingulatus*, ventral view. D) *Tipula* sp., ventral view. E) *Porcellio monticola*, ventral view. F) *Polydesmus inconstans*, side view. G) *Cylindroiulus londinensis*, side view. H) *Glomeris marginata*, ventral view. C, D, and F pictures were taken by Lola Estabes.

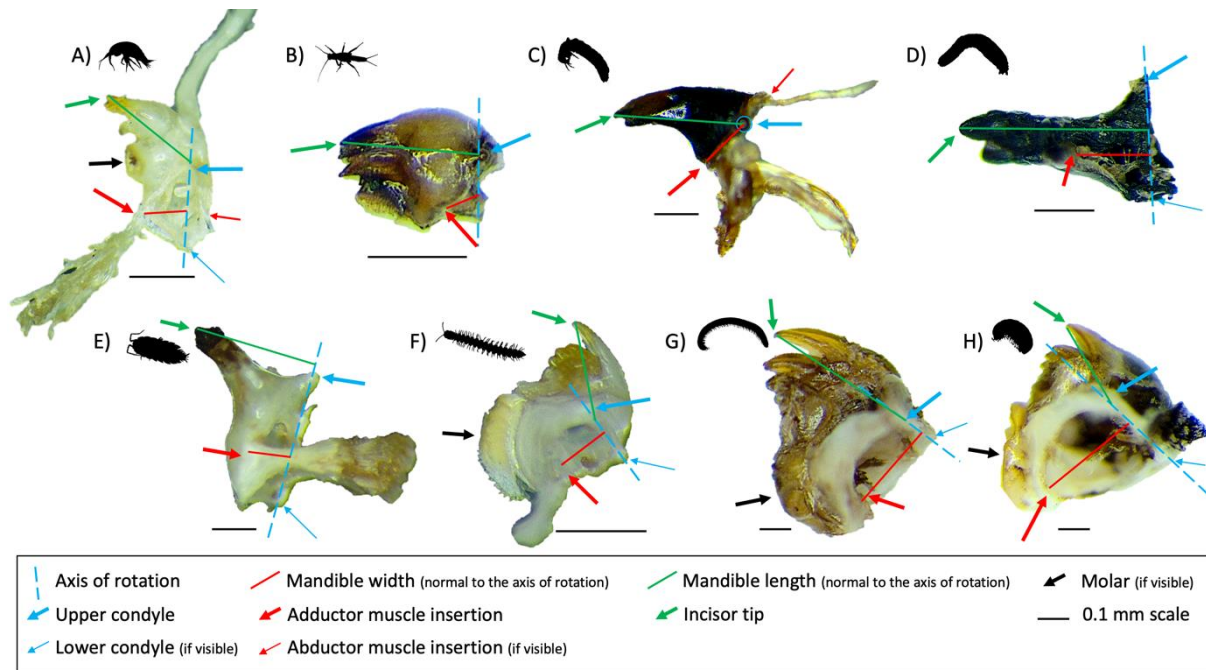


Figure 11: Mandible morphology of some detritivore taxa. All images were oriented so that the upper condyle is on top, with incisors pointing to the left. For uniformity, images were arranged so that all mandibles appear as right mandibles (some are mirror images). Mandible length and width position is indicated but, in most pictures, the distance is biased by perspective. On each mandible, several measures have to be made from different points of view to have a proper estimation of mandible length and width. This figure illustrates the diversity of mandible shapes in macrodetritivores. A) *Gammarus fossarum*. A palp is standing above the mandible, while adductor muscles (whose contraction close mandibles) stand down. B) *Nemoura* sp. C) *Limnephilinae*. Here, the axis of rotation is normal to the photograph. Mandible length and width are perfectly measurable, without perspective bias. The adductor (and abductor, whose contraction open mandibles) muscles are clearly visible. D) *Tipula* sp. E) *Porcellio monticola*. The adductor muscles are clearly visible. F) *Polydesmus inconstans*. G) *Cylindroiulus londinensis*. H) *Glomeris marginata*. B, D, F, G, and H pictures were taken by Lola Estabes.

To estimate detritivore needs in different elements, we measured detritivore body content in carbon (C), nitrogen (N), phosphorus (P), calcium (Ca), and potassium (K) (Chapter II). We also measured magnesium (Mg) content for Chapter IV. Detritivores were starved for 24h to purge their digestive tract and placed in a freezer. They were then cleaned with miliQ

water and dried at 45°C for 4 days. Several individuals of the same taxa were pooled to ensure sufficient analysis material. They were then ground into powder with several silica spheres, using a bead mill (FastPrep-24™ Classic Instrument). Carbon and nitrogen content was then estimated by analyzing 5.000 – 10.000 mg of powder with a Total nitrogen and Organic Carbon analyzer (TOC L, Shimadzu) by the LEFE Platform for physical and chemical analyses (PAPC, Univ Toulouse UPS, INPT, CNRS). For P, K, Ca, and Mg analysis, 4.500 – 5.500 mg of powder was digested by 0.5 mL of 63-67 % nitric acid for one night at 95°C in a white room with over-pressurization to avoid contamination. Depending on the initial volume of each sample, 10 or 15 mL of milliQ water was added the next morning. Samples were then analyzed with an Induced Coupled Plasma – Mass Spectrometer (ICP-MS) by the Fast Bio-analyses of Trace Elements platform (FBil, Univ Toulouse UPS, INPT, CNRS). Control (without powder) and reference samples (Certified Reference Material: river prawn PRON-1 and dogfish liver DOLT-3) were used to ensure the quality of the measurements for each element. C, N, P, K, Ca, and Mg content was expressed as a percentage of element mass relative to the sample dry mass.

Litter traits measurements

To estimate leaf litter physical resistance, we measured litter toughness as the strength needed to punch through the limb (Graça et al., 2005). We used a digital force tester (CS225 Series, Chatillon®) to measure the strength (± 0.1 N) needed to punch a 2.2-mm steel rod to penetrate through a leaf disc. Toughness was then expressed as penetration pressure (kPa) by dividing the maximal strength applied by the area of the rod tip. The measure was repeated on several leaf discs of the same litter.

Limb thickness was measured to the nearest 0.001 mm with a Helios-Preisser® digital micrometer, avoiding main veins. The measure was repeated on several leaf discs of the same litter.

To estimate litter content in different elements, we measured the proportion of carbon (C) and nitrogen (N) (Chapter III), as well as phosphorus (P), calcium (Ca), and potassium (K) (Chapter II), and magnesium (Mg) (Chapter IV). Litter was analyzed following the same procedure as for detritivores (see above). It was cleaned, dried, ground, and a sub-sample of the powder was analyzed for C and N content, while another sub-sample of the powder was digested with nitric acid and analyzed with an ICP-MS. We also used control and reference

samples (Certified Reference Material: apple leaves NIST-1515, peach leaves NIST-1547, and lichen IAEA 336) to ensure the quality of the measurements for each element for the ICP-MS. C, N, P, K, Ca, and Mg content was expressed as a percentage of element mass relative to the sample dry mass.

CHAPTER I

TRAIT-MATCHING BETWEEN DETRITIVORES AND DETRITUS, A CONCEPTUAL FRAMEWORK TO UNRAVEL CONSUMPTION RULES IN A CONTEXT OF DECOMPOSITION

Prologue (EN)

Detritivores' contribution to decomposition can be extremely variable and still lacks understanding. One way to better understand detritivores' contribution to decomposition is to better understand the detrital trophic network, especially detritivore-litter interactions, and their rules. This chapter aims to build a conceptual framework of detritivore-litter interactions at the individual level. We will focus on the functionally coherent context of saprophagous detritivores fragmenting plant detritus. We will focus on consumption as an integrated process of the interaction. Based on the existing literature, we will identify different constraints driving litter consumption by detritivores. We will identify which traits may match to explain the interaction. This knowledge will help to design precise experimental studies aiming to identify constraints ruling detritivore-litter interactions (Chapter II) (Figure 6). Such experiment will also aim to assess the role of different traits and the weight of trait-matching.

Prologue (FR)

La contribution des détritivores à la décomposition peut être extrêmement variable et reste mal comprise. Une façon de mieux comprendre la contribution des détritivores à la décomposition est de mieux comprendre le réseau trophique détritique, et en particulier les interactions entre les détritivores et la litière, ainsi que leurs règles. Ce chapitre vise à construire un cadre conceptuel des interactions entre les détritivores et la litière au niveau individuel. Nous nous concentrerons sur le contexte fonctionnellement homogène des détritivores saprophages qui fragmentent les débris végétaux. Nous nous focaliserons sur la consommation en tant que processus intégré de l'interaction. Sur la base de la littérature existante, nous identifierons différentes contraintes régissant la consommation de litière par les détritivores. Nous identifierons quels traits peuvent être en concordance pour expliquer l'interaction. Ces connaissances aideront à concevoir des études expérimentales précises visant à identifier les contraintes qui régissent les interactions entre les détritivores et la litière (Chapitre II) (Figure 6). De telles expériences viseront également à évaluer le rôle des différents traits et le poids de l'appariement des traits.

Trait-matching between detritivores and detritus, a conceptual framework to unravel consumption rules in a context of decomposition

Théo Marchand¹, Antoine Lecerf¹, Pierre-Marc Brousseau², Matthieu Chauvat³, Michael Danger⁴, Estelle Forey³, Tanya Handa², Mickael Hedde⁵, Florence Maunoury-Danger⁴, Mathieu Santonja⁶, Benjamin Pey¹

¹ Laboratoire écologie fonctionnelle et environnement, Université de Toulouse, CNRS, Toulouse, France

² Département des Sciences Biologiques, Université du Québec à Montréal, Montréal, Québec H2X 1Y4, Canada

³ Université Rouen Normandie, INRAE, ECODIV USC 1499, F-76000 Rouen, France

⁴ Université de Lorraine, CNRS, LIEC, 57000 Metz, France

⁵ Eco&Sols, Université Montpellier, CIRAD, INRAE, Institut Agro, IRD, Montpellier, France

⁶ Université Aix Marseille, Avignon Univ, CNRS, IRD, IMBE, Marseille, France

Abstract

From soil to freshwater ecosystems, decomposition can be conceived as the outcome of interactions between organic matter detritus and decomposers. Detritivores' contribution to decomposition is significant but sometimes extremely variable. A way to better understand and predict their contribution is to study the structure and functioning of detrital trophic networks. It could be done through a trait-matching approach on pairwise interactions. For detritivores, trophic interactions mainly rely on detritivore-detritus (including associated microbes) or predator-detritivore interactions.

Here, we present a conceptual framework which describes pairwise trophic interactions between saprophagous detritivores and plant detritus based on existing literature. We focus on detritus consumption by detritivores as a main part of the trophic interaction. We argue that the feasibility and the strength of the consumption of a detritus item by a detritivore individual is governed by trait-matching rules acting on five complementary facets: (1) a spatial match rule regarding the encounter (2) a mechanical match rule regarding the ingestion, (3) a digestive match rule regarding assimilation, (4) an energetic match rule regarding the fulfillment of metabolic needs, and (5) an elemental match rule regarding the fulfillment of chemical element needs in adapted proportions.

To illustrate the holistic aspect of this framework, we propose a reinterpretation of the contrasted patterns of "compensatory feeding" observed in the literature. Another asset of the framework is that it can be applied at any time and could thus integrate the time variability of trait-matching constraints throughout the whole decomposition process. We finally outline the conceptual, methodological, and analytical challenges emerging from this framework. Understanding the trait-matching rules acting at different facets of the trophic interaction between saprophagous detritivores and detritus will allow to better predict the resulting consumption, the resulting trophic network, and its role in the ecosystem.

This framework also suggests an original definition of a saprophagous detritivore as an animal which consumes plant detritus as its traits match the traits of its resource, passing through the five main filters of the five before-mentioned facets.

Keywords: trophic interactions, trait-matching, plant detritus, plant litter, detritivore, consumption

Introduction

Decomposition can be defined as the gradual transformation of dead organic matter that is ultimately mineralized with release of CO₂ and nutrients (Petersen and Luxton, 1982). It is the second most important ecosystem function maintaining life on Earth after primary production (Gessner et al., 2010). Detritus refers to the different types of dead organic matter which differ in terms of physical attributes such as size, biochemical quality, and hence, the type of interactions with organisms. From soil to freshwater ecosystems, decomposition can be viewed as 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 physico-chemical environmental parameters (global or local, *e.g.*, climate, soil or water properties), detritus parameters, and microbial and animal actors drive decomposition.

In order to better understand the link between biodiversity and ecosystem function, studying the structure and functioning of networks' interactions may be particularly useful (Gravel et al., 2016; Schleuning et al., 2023). One approach is based on pairwise interactions of the network, through a trait-matching approach in order to connect functional community structure description to network structure (Gravel et al., 2016; Schleuning et al., 2015). With this perspective, decomposition can be viewed as the direct or indirect result of interactions, mainly trophic, between highly diverse resources (*e.g.* litter detritus or carrion), consumers (*e.g.* fungi, bacteria, animals) and their regulators (*e.g.* predators, pathogens) under the control of a spatio-temporal abiotic gradient (Gessner et al., 2010; Krumins et al., 2013; Wagener et al., 1998).

Most animal processing of detritus is performed by a very diverse and countless number of invertebrates, called detritivores. They can be defined as any invertebrate animal which contributes to decomposition by feeding on detritus or by grazing on microbial decomposers (fungi, bacteria) associated with detritus (Brussaard, 1998; Marks, 2019). Detritivores can have direct effects on decomposition (*e.g.* assimilation) or indirect effects through regulating microbial activities (*e.g.* by regulating microbial biomass by grazing microbes on litter, or by fragmenting litter detritus becoming more available for microbial colonization) (Brussaard, 1998; David, 2014; Marks, 2019). Decomposition rate was shown to be higher when detritivores are present, increasing decomposition rate up to roughly 50%

(García-Palacios et al., 2013; Handa et al., 2014). However, this contribution is also highly variable and remains to be elucidated (García-Palacios et al., 2013; Tonin et al., 2021).

In our proposed conceptual framework, we advocate that the contribution of local detritivore communities (alpha diversity scale) to decomposition mainly depends on the structure and functioning of the detrital trophic network. For detritivores, pairwise trophic interactions mainly rely on detritivore-detritus (including associated microbes on detritus) or predators-detritivores interactions. We first argue that co-occurrence and abundance of detritivore individuals or detritus items indirectly influence network structure and functioning. Co-occurrence is a prerequisite of any interaction and impacts directly trophic network structure while abundance may be involved in per component interaction (Canard et al., 2012). Co-occurrence and abundance of individuals or detritus items may partially depend on certain environmental filters not directly involved in the detrital trophic interaction acting at several levels, from meta-community level to individual level. A great body of concepts already exist in the literature to address non detrital-trophic assemblage rules (Belyea and Lancaster, 1999; Boyero et al., 2012; Decaëns et al., 2008). Co-occurrence and abundance of individuals or detritus item may also depend on the trophic network functioning itself. For instance, top-down control such as predator trophic cascades (e.g. Mancinelli and Mulder, 2015) or bottom-up control (Brousseau et al., 2019, 2021; Marjakangas et al., 2022) can occur and modify the size and composition of trophic levels.

We also suggest that the detrital trophic network structure and functioning may directly depend on the feasibility and strength of pairwise interactions between detritivore individuals and detritus items. Such pairwise interactions can be explained and predicted by trait matching rules (Gravel et al., 2016). Predator-detritivore interactions in a trophic networks perspective have been largely studied (Mancinelli and Mulder, 2015), sometimes through the prism of trait-matching (Brousseau et al., 2018), showing the strength of this approach to establish generic interaction rules. On the other hand, despite valuable scarce studies exploring detritivore and detritus traits (Brousseau et al., 2019; Coq et al., 2018; Raymond-Léonard et al., 2019), no trait-matching framework exists for detritivores and detritus interactions yet.

Here we present a conceptual framework based on existing knowledge on detritivores. It aims to understand and study pairwise detritivore-detritus trophic interactions at the individual (detritivore) and item (detritus) level, through the prism of trait-matching. We

scope our conceptual framework on saprophagous detritivores fragmenting detritus, i.e. mechanically fracturing such as cutting, scratching, grinding (e.g. with their mandibles for arthropods, gizzard for earthworms, radula for gastropods). We also focus on particulate detritus originating from plants (e.g leaf litter, dead wood) as plants are the main generator of detritus (Moore et al., 2004). Finally, we focus on the detritus consumption by saprophagous detritivores as a main part of their trophic interaction with litter. Consumption is the cornerstone of the effect of fragmenting saprophagous detritivores. It notably initiates breakdown of large particles of detritus by fragmenting them and transforms them by detritivore metabolism once ingested (incorporated in tissue, respired, excreted, egested) (David, 2014; Marks, 2019).

A holistic and time-dynamic trait-matching framework at the individual detritivore and detritus item level

We chose to build our framework at the individual level as intraspecific detritivore consumption variability has been demonstrated to be substantial compared to interspecific one (e.g. (Fontana et al., 2019; Rota et al., 2022)). We advocate that the feasibility and strength of the interaction are governed by five complementary but distinct trait-matching facets. These facets cover all of individual biological processes which could directly or indirectly influence the consumption of a detritus item by a detritivore individual: 1- spatial match between a detritivore and detritus, by indirect (random match) and/or direct (detritus detection by detritivores) mechanisms, 2- biomechanical match between detritivore mouthparts and detritus, 3- match between digestion abilities of a detritivore and detritus chemical deterrents, 4- match between detritivore metabolism and detritus energy content and finally 5- elemental match between a detritivore and detritus (Figure I.1). As the first two trait-matching facets occur before litter ingestion, we advocate that they govern both the feasibility and strength of detritus consumption (see examples in the following section). The last three facets mainly influence strength of the interaction, as they occur after litter ingestion. We advocate that our conceptual framework presents two main assets. The first asset is that our framework is holistic as it covers all the facets of individual biological processes which could influence directly or indirectly the detritivore consumption of litter.

Secondly, our framework can be applied at any time and could thus integrate the time variability of trait-matching constraints throughout the whole decomposition process.

The following section formally describes each facet one by one. Finally, the last section presents how the two before-mentioned assets could improve understanding and prediction of current knowledge of detritivore consumption at the detritivore individual level. It also points the current conceptual and methodological challenges to overcome to make our framework fully efficient and predictive.

Formal description of the five trait-matching facets

In the current literature, saprophagous detritivore trophic interactions are often studied at a species level rather than at an individual level. We therefore use examples of trophic interactions at a species level to indirectly support and illustrate our individual centered conceptual framework. We considered that trophic interactions at a species level can be seen as the range of trophic interactions of individuals. Furthermore, we illustrate each facet by concrete detritivore-detritus existing studies. When no specific example was available, we used illustrations coming from other close biological models.

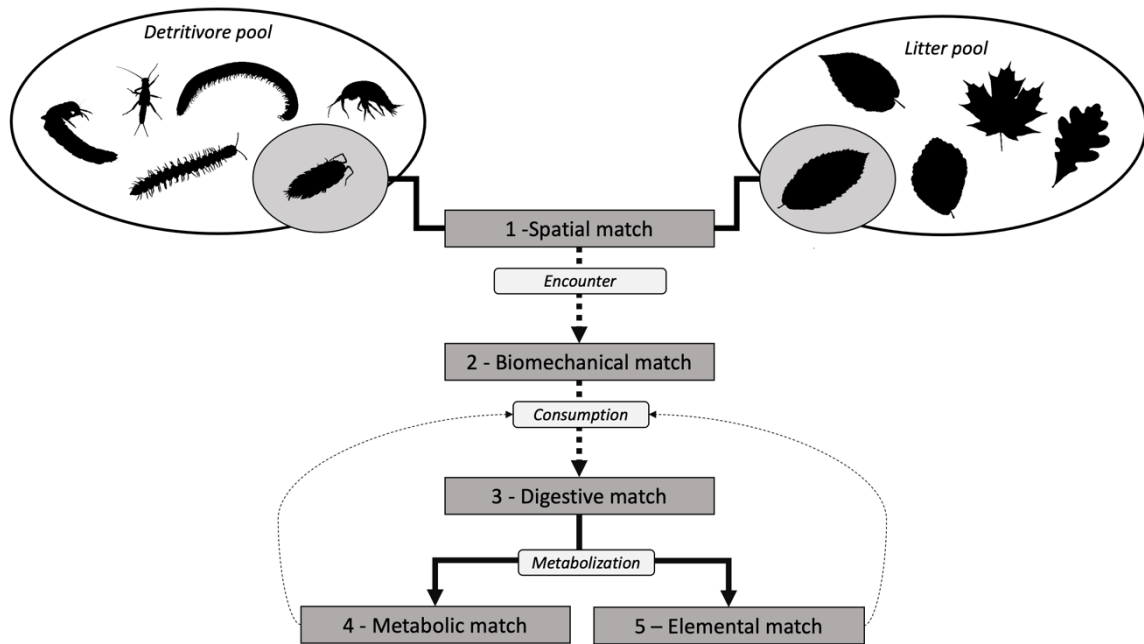


Figure I.1: Conceptual framework of pairwise trait-matching interactions between a given detritivore and a detritus item. Dark shaded boxes represent trait-matching facets. Pale boxes with text in italic represent mechanisms of the trophic interaction. A thick dotted arrow indicates that the trait-matching facet could govern both the feasibility and strength of the interaction. A complete arrow indicates that the trait-matching facet mainly governs the strength of the interaction. Finely dotted arrows indicate retrocontrol of trait-matching facets on detritus consumption.

i) Spatial match: litter detection and selection

Detritivores rely heavily upon 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). Study 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 centimeters comparatively to surface detritivores due to pore size and soil hydration state

(Auclerc et al., 2010; Erktan et al., 2020). In aquatic environment, the distinction between olfaction and taste to detect and select food is vaguer (Crespo, 2011; Zacharuk, 1980), but the propagation of chemical cues in water is well preserved at great distances from the source compared to terrestrial environment (Murlis et al., 1990).

Regarding the compounds that attract detritivores at distance, volatile organic compounds (VOCs) and CO₂ seem particularly involved. For example, Moursi (1961) reported that Collembola sense and direct their movement towards CO₂ sources associated to microbial activity, while Staaden et al. (2011) demonstrated that Collembola differentiate fungi using olfactory cues. However, only few studies identified the 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 attraction, at distance, of the earthworm *Eisenia fetida* to the fungi *Geotrichum candidum*. Additionally, and even if their volatility are low, other compounds including amino acids, fatty acids, sugar or alcohols has been reported to attract, at distance, soil detritivores (Brückner et al., 2018; Salmon and Ponge, 2001). For example, Brückner et al. (Brückner et al., 2018) showed that *Cheloribates* sp. (fungivorous Oribatid mite) was highly attracted by the alcohol 1-octen-3-ol produced by fungi.

Interestingly, despite detritivores possessing olfactory receptors, several studies performed in both aquatic and terrestrial systems pointed random individual movements followed by a food choice only based on gustatory cues (Motyka et al., 1985; Tuck and Hassall, 2004). This food selection has been reported to depend on the nutritional status of the litter (Swan and Palmer, 2006) as well as on microbial colonization improving the nutritional quality of these litter (M. A. S. Graça and Cressa, 2010; Motyka et al., 1985).

No previous study was performed with a trait matching approach between detritivorous traits involved in olfaction or taste and detritus 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 behavioral responses associated with the detection of chemical cues (e.g. shift from non-directional (random or search strategy) to directional (target-oriented) movements, (Auclerc

et al., 2010)). Detritus traits involved in olfaction are VOCs or CO₂, while those involved in taste are nutrient content or microbial-associated chemicals.

ii) Match between mouthpart abilities and litter mechanical properties

Once a given detritivore decides to ingest a detritus item, the next filter is the ability for the individual to ingest the detritus. This ability may be controlled by mechanical constraints.

The mechanical interactions between the detritivores and their detrital resources can imply different actions (cutting, grinding, scratching) and organs (mandibles, chelicera, radula). Although each action and mouthpart types involve a different biomechanical processing, the overall principle remains the same, namely the ability for a detritivore to manipulate the resource and be strong enough to pass through its 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 thickness is a well-recognized matching trait for herbivore caterpillar (e.g. (Bernays, 1998)). Danger et al. (2012) also pointed out that litter thickness acts differently depending on detritivore body size. Small *Lucifera* were not impacted by leaf litter thickness as they just scraped the surface, whereas bigger shredders had to cut through the whole limb. Nonetheless, leaf thickness was shown to covary positively with the mandibular gape 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 thickness and detritivores consumption rate (Canhoto and Graça, 1995; Ponge, 1991), but it was unclear if this was due to a direct limitation imposed on mandibular gape.

Leaf toughness represents the physical resistance of the leaf to puncturing, tearing and rasping/scratching (Padilla, 1989; Sanson et al., 2001). Tougher leaves can represent a defense against herbivory (Malishev and Sanson, 2015) that can also impede the consumption by detritivores. In the case of arthropods, the mandible of scratcher can include apical tooth that are missing in cutters (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 include elements such as zinc and silica in the structure of the mandible (Laiolo et al., 2021) which allow eating tougher leaves, but proper allometry to include such aspect are still missing. Although less studied, the presence of trichome or spicules on leaves could also limit the consumption of the litter by detritivores. Experimental evidences are scarce but recently Nakamura et al. (2022) demonstrated that high densities of silicious trichomes reduced meso- and macrofauna impact on decomposition.

The radula of Gasteropoda consist of a thin cuticular sheet with embedded rows of teeth and 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 did attract 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. The main biomechanical constrain is thus the match between the size of particles and their mouth size. However, earthworms possess gizzard, which could be functionally assimilated to arthropod mouthparts.

The trait-match between mouthpart force and leaves toughness was tested on 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-match was not experimentally tested with detritivores, the covariation in mandibular force and litter leaves toughness was observed in forest ecosystems (Brousseau et al., 2019).

iii) Match between digestion abilities and detritus digestibility

Once ingested, food is partially digested. The quantity of nutrients that is assimilated depends both on the digestion processes and on detritus digestibility.

Matches between consumed items and digestion abilities is of utmost importance for individual fitness and animals basically rely either on endogenous enzymes or on their microbiota in digestion. Detritus like woody vegetation may be composed of 75% or more refractory (i.e., resistant to digestion) cell wall material not eligible to rapid digestion with endogenous enzymes. Due to plant nutrient remobilization and soluble compounds leaching, nitrogen and phosphorus concentration decrease significantly from green leaves to leaf litter (Li et al., 2021). Likewise, soluble sugar content is more than five times lower in leaf litter compared to green leaves, while lignin proportion increases by 25% in multiple tree species (Li et al., 2021). They thus generally have very low N and P concentrations and a large proportion of hardly decomposable structural carbon compounds (Martinson et al., 2008; Moore et al., 2004). This low-quality resource makes assimilation constraints especially high. Detritivores, therefore evolved multiple strategies to match their physiological requirements regarding the rather refractory materials they rely on for their diets. Basically, there is a continuum of species called “feeders” that assimilate nonrefractory materials and pass the refractory ones mainly undigested, and “digesters” which extract considerable energy from refractory materials (Abe and Higashi, 1991). Differences in enzymatic activities between detritivores species may reflect these different strategies. For example, the millipede *Polydesmus angustus* showed more gut extracts activity towards polysaccharides than those of the woodlouse *Oniscus asellus* (Beck and Friebe, 1981). Similarly, different carbohydrase activities were observed between two sciarid fly larvae (*Plastosciara falcifera* and *Bradysia confinis*) (Deleporte and Charrier, 1996). Bärlocher and Porter (1986), found that while all three detritivore species *Gammarus tigrinus*, *Tipula caloptera*, *Hydropsyche betteni* were able to digest starch and laminarin, *Tipula* was the only one able to hydrolyze proteins of microbial-unconditioned maple leaves mostly due to an alkaline gut pH. 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 utilization of plant structural polysaccharides was significantly increased following the ingestion of fungal (*Penicillium* sp.) cellulase by the woodlouse *Trachelipus rathkei* (Kukor and Martin, 1986). Furthermore, it is known that leaves subjected to leaching which removes several refractory compounds like phenolics and tannins, as well as microbial conditioning, are preferred by detritivores compared to “unconditioned” or “unleached” leaves (see David (2014) and

citations therein). Zimmer (2002) showed that litter consumption by isopods depends both on litter traits (especially C:N ratio and phenolic concentrations) and isopod species, terrestrial isopods being better adapted than semiterrestrial ones to phenolic concentrations found in their daily resources.

iv) Match between metabolism and litter energy content

Once assimilated, detritus molecules are used by the consumer organism to gain energy through catabolism. Energy content of the assimilated food should then meet metabolic requirements.

Plant detritus are energetically extremely poor, with very low nutrient content (Li et al., 2021). Besides the low energy content of detritus, the low digestibility of plant litter places detritivores at the bottom of the pyramid of assimilation efficiency. A systematic analysis of energetic traits of aquatic and terrestrial arthropods yielded to a mean energy assimilation efficiency of 16% for detritivores, around threefold lower than the value estimated for herbivores (Lang et al., 2017). Beside this low assimilation efficiency, feeding rate can greatly vary across detritivores; for instance, 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 energetical situation can explain the variability in feeding rates.

Lang et al. (2017) demonstrated no significant difference between trophic groups in mass-corrected metabolic rate, suggesting that detritivores generally cope with the low digestibility of their resource by increasing ingestion rate rather than by lowering their energy demand. The existence of compensatory feeding strategy (i.e. when some detritivore species exhibit greater ingestion rate on low than high quality litter) would support this idea (Cruz-Rivera and Hay, 2000; Danger et al., 2013; Mas-Marti et al., 2015; Ott et al., 2012), even though this strategy is not systematic in detritivores (Evans-White and Halvorson, 2017; Fenoy et al., 2021; Hättenschwiler and Bretscher, 2001). Interestingly, Ehnes et al. (2011) found that some detritivores had lower respiration rates than the linear model's predictions, using a smaller dataset than Lang et al. (2017). This would indicate that some detritivore taxa do have a lower metabolism as a different strategy to cope with their poor alimentary resource. The existence of different energetical strategies is also pointed by Fenoy et al. (2021) who

identified different abilities to maintain energetic reserves when exposed to detritus of different qualities, depending on the detritivore species. Different energetical strategies could result from different metabolic needs. For example, differences in metabolism linked to reproduction or sex-specific behavior (e.g. mate-guarding) can lead to differences in energy requirements and in detritus selection (Rota et al., 2018). Depending on the development stadium, the importance of detritus quality can also change. Juveniles can have specific requirements due to energetical needs for growth and rely on specific resources (Crenier et al., 2017).

Findings of Rota et al. (2018) also point out differences in foraging strategy between large and small detritivores. In their study, small individuals of an aquatic detritivore species were found to spend more time feeding on leaf litter than large ones. The trend for longer inactivity period in bigger individuals compared to small ones should reflect the energetic costs of the maintenance of large body mass. Therefore, it is plausible that 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 may be viewed as a matching trait that makes detritivores adapt to the low energy content of plant litter.

v) Elemental 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 composed of the same essential chemical elements associated into their body in variable amounts. Ecological stoichiometry corresponds to an approach of ecology specifically taking into account the balance between consumers' elemental requirements and elements availability in their resources (Sturner and Elser, 2017). Any elemental imbalance arising between consumers' 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 it can be extended to other essential elements such as calcium, sodium, or magnesium, for example (e.g. Ott et al., 2014).

Elemental constraints are especially important since most detritus available in ecosystems – at least those produced by plants – are extremely nutrient depleted. To overcome these constraints, detritivores – as well as herbivores – generally exhibit low element requirements/high C:N:P ratios, when compared to carnivorous taxa (Cross et al., 2005; Martinson et al., 2008). Yet, due to the low N and P contents of detritus, detritivores also need to adopt different strategies to cope with potential elements limitation. One way to reduce elemental imbalances of detritivores is to consume more resources until they obtain enough of the most limiting elements: the before-mentioned compensatory-feeding mechanism (Jochum et al., 2017). Another strategy is to select for the most element-rich patches of the detritus, these detritus being generally quite heterogeneous in terms of elemental contents (Grimmett et al., 2012), and/or to complement their detrital resources by a sufficient amount of other element-rich resources (Crenier et al., 2017).

One of the current limitation 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)). Yet, using detritivores C:N:P contents as a proxy of their elemental requirements leads to neglecting the metabolic and biochemical costs necessary for processing and assimilating their diet. To estimate the real elemental requirements of a consumer, one can evaluating its Threshold Elemental Ratios (TER, i.e. the ratios at which the nutrient limitation of consumers growth switches from one element to another; (Frost et al., 2006)). Secondly, it is necessary to investigate if and how much these elemental – and metabolic – requirements depend on the 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, these parameters partly depending on the other detritivore-detritus matching facets. As current ecological stoichiometry focuses on elemental stoichiometry, we mainly considered the elemental match via the prism of elemental stoichiometric. However, consumers also have to fulfill requirements for essential fatty acids, specific proteins, and essential amino acids (Anderson et al., 2017). This complementary approach also must be considered for detritivore-detritus interactions.

Assets of the framework and remaining challenges to assess trait-matching rules

i) Assets of the framework

To illustrate the holistic asset of our framework, we propose to reinterpret contrasted patterns of compensatory feedings. Compensatory feeding is defined as an increase of detritivore consumption rate when the nutritive quality of food is limited to compensate for animal needs (Cruz-Rivera and Hay, 2000; Hättenschwiler and Bretscher, 2001; Jochum et al., 2017). However, the underlying mechanisms behind the mismatch between low nutritive quality of litter and detritivore needs were not always addressed. When addressed, mechanisms were assessed through several relevant approaches, i.e. *via* the prism of the digestive, metabolic, elemental, biomechanical or spatial matches between litters and detritivores which mirror our five matching facets (e.g. De Oliveira et al., 2010; Hättenschwiler and Bretscher, 2001; Jochum et al., 2017; Mas-Marti et al., 2015; Ott et al., 2012; Tuck and Hassall, 2004). To our knowledge, two main drawbacks however stayed and limited the understanding and prediction of these underlying mechanisms. First, no literature study addressed explicitly and simultaneously all the matching facets necessary to approach all the individual biological processes which could operate during detritivore consumption of litter. If authors sometimes mentioned other facets than those they explicitly studied, they did not address them directly them and mention them in the discussion parts, see for instance Walpola et al. (2011). One other major drawback is a methodological one: if a large majority of studies evoked some of the matching facets between detritivores and litters, they did not systematically test for trait-matching between litter and detritivore traits, as detritivore traits were generally poorly informed. We would then describe a notable example to illustrate the way how these drawbacks can impede our understanding of compensatory feeding. In a first laboratory experiment, Hättenschwiler et al. (1999) observed compensatory feeding of beech litter (*Fagus sylvatica*) with low N concentration (grown under elevated CO₂ atmospheric conditions) by the isopod *Porcellio scaber* compared to control beech litter with higher N content. In another laboratory experiment, Cotrufo (1998) however did not observe compensatory feeding of litter with low N concentration by *Oniscus asellus* (also grown under elevated CO₂ atmospheric conditions) compared to ash control litter. Differences of compensatory feeding between these two isopods in similar situations with low N

concentration have to be enlarged by considering all the trait matching facets of our framework.

Another asset is that our framework is time dynamic. Throughout the decomposition process, some detritivores and litter traits could change over time. It is particularly pronounced for detritus traits (Wickings et al., 2012) but can also apply to some detritivore traits (e.g. the metabolism changes with seasonal temperature) (Nilsson, 1974). Such changes could modify at each time the trait-matching constraints which rule feasibility and strength of detritivore-detritus interactions. It could ultimately modify the detritivore consumption of detritus and so a part of their contribution to the decomposition process. Our framework shed light on the need to assess trait-matching rules temporal evolution across complete decomposition process to allow a better comprehension and prediction of the detritivore contribution to decomposition.

ii) Conceptual challenges

Our framework is not designed to fully understand and predict saprophagous detritivore consumption and assess its effect on decomposition. In a way, it can be seen as a conceptual tool to define the fundamental trophic niche of an individual which can locally be modulated (“realized niche”) by adaptations to the local detrital resource, by abiotic constraints, or by interaction with another than detrital trophic network components. Our framework must then be connected to the whole detrital trophic network and replaced in the context of a changing environment with changing abiotic constraints which can drastically modulate fundamental detritivore-detritus pairwise interactions. For instance, our framework does not take directly into account competition or facilitation for the detrital resource between detritivore individuals and communities (e.g. (Rota et al., 2018; Zimmer et al., 2005). Furthermore, our framework does not consider all detritivores. We expect that our framework needs specific conceptual adjustments to correctly include all facets of social insects’ trophic interactions (ants, termites). We also expected that another specific framework is needed for detritivores which do not fragment detritus (e.g., phagocytosis for protists or piercing mouthparts of some Collembola). In addition, our individual-centered conceptual framework did not directly consider individual autocoprophagy. We propose to implicitly consider autocoprophagy when assessing digestive, metabolic, and elemental trait matching rules of

coprophagous detritivores. Finally, our framework was thought for plant detritus, although other detritus such as carrion and dung are crucial for some other detritivores.

Finally, moving from a pairwise vision of detritivore-detritus trait-matching to a complete trophic network is far from easy. Such challenges have been mentioned previously (see for instance Gravel et al. (2016)) and they clearly stated that there is currently no clear answer to this issue. However, they advocated that the assessment of pairwise trait-matching rules is a promising avenue to infer interactions at a network level and contribute to the understanding of trophic network dynamics. In this perspective, our proposal has to be viewed as a first step to initiate the description of detritivore-detritus trophic interaction in trophic networks via the assessment of trait-matching rules.

iii) Methodological challenges

Demonstrating the existence of each trait-matching facet and test for the relative importance of all five facets hinder methodological challenges.

A first methodological step is to select relevant interaction traits for both detritivores and detritus. The trait choice must be done according to the considered trait-matching facet that is studied, and the underlying mechanisms. Trait choice is a twofold challenge as covariation of traits among a detritivore or among a detritus could make it hard to connect a pairwise trait to a unique trait-matching facet. For instance, detritivore body mass which could be used in the energy match is often highly correlated to other morphological traits such as mandibular traits (Rühr et al., 2022).

Table I.1 presents a non-exhaustive but illustrative description of detritivore-detritus matching traits currently used in the literature. It is representative of the fact that trait-matching is rarely considered in current studies. Identifying traits and addressing their relevance to explain trait-matching rules is a next challenge to test for the relevance of the proposed framework.

Table I.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 detritus trait, theoretically involved in a same matching facet.

	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 content	Ott et al., 2012
	Metabolism, body mass, energetic storage	Litter content	Fenoy et al., 2021
Elemental match	C:N	C:N	Frainer et al., 2016; García and Pardo, 2015; Ohta et al., 2016; Tagliaferro et al., 2021
	C:P	C:P	Frainer et al., 2016; García and Pardo, 2015; Ohta et al., 2016; Tagliaferro et al., 2021
	N:P	N:P	Frainer et al., 2016; García and Pardo, 2015; Tagliaferro et al., 2021

A second methodological challenge is to differentiate between “realized” and “fundamental” trophic niche. For this, we advocate using complementary experimental approaches. Using correlative approaches between detritivore and detritus interaction traits at a field scale (e.g. Brousseau et al. (2019)) allows to characterize realized trophic niche and to identify potential trait-matching. Mesocosm approaches at a field scale, in which detritivore and detritus interaction traits could be manipulated (e.g. see Hättenschwiler and Gasser (2005) in which litter traits only were manipulated) allows for a more precise investigation of underlying mechanisms. Finally, we also recommend laboratory consumption or preferences tests in which detritivore and detritus interaction traits could also be manipulated.

In experimental approaches, we believe that trait manipulation can be done to facilitate the assessment of trait matching rules. It can be done for a number of litter traits (e.g. chemical composition can be modified by conditioning in an enriched medium (Danger et al., 2013), toughness can be reduced by chemical hydrolysis (Bärlocher and Kendrick, 1975)). Yet, it is difficult to modify only one trait, without affecting others (conditioning will modify altogether detritus toughness, chemistry, palatability...). Traits of detritivores are especially difficult to manipulate (with the exceptions of removing organs such as antenna, or modifying the microbiota with by starvation (Bredon et al., 2021) or with antibiotics (Zimmer and Bartholmé, 2003)).

iv) Analytical challenges

In an analytical perspective, one way to test trait-matching is using the RLQ and the 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 for 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 allows to characterize actors only at the species, and not at the individual level. Rohr et al., (2016) provide a different and elegant approach based on the probability of a link in the network to happen. This probability is expressed using as the sum of a *matching* term based on traits influencing matching between two nodes (i.e., Mandible size and toughness

of food), 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 using two complementary approaches. Unlike in other interaction networks (predation, parasitism), interactions between detritivores and plant detritus are rarely discrete (one item (e.g., one leaf), is rarely entirely consumed by one individual). Consequently, it is difficult to describe those interactions through a qualitative binary approach. Fortunately, most analyses can be adapted to quantitative datasets (Dray and Legendre, 2008).

Most of the methods presented here are susceptible to be used for predicting new interactions and the position of a new node in the network (Ibanez, 2012; Rohr et al., 2016). Pearse et al. (2013) suggested using both traits and phylogeny to predict new plant-herbivore interactions. Traits and phylogeny can be included in a matching-centrality model to assess both constrained simultaneously (Brousseau et al., 2018).

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 entry datasets to train the models.

Conclusion

Reasons why some animals have evolved toward detritivory are probably linked to the ubiquity and abundance of plant detritus in many habitat types (Cebrian, 1999). Plant detritus is reported to improve the physical environments of detritivores, for instance through moisture retention in forest floor and attenuation of predation owing to complex habitat structure. In contrast, plant detritus is perhaps the worst-quality food to animals, suggesting that trophic adaptation is a core component of detritivore fitness and evolution.

Resource competition triggers trophic specialization, which should result in adaptive divergence in foraging traits among co-existing species. However, there is mixed evidence in support of trophic niche partitioning among detritivores. Most detritivores tend to select higher quality detritus patches 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).

Overall, we can suggest an original definition of a saprophagous detritivore arising from our conceptual framework. A detritivore is an animal which consumes detritus (including associated microbes) as its traits match the traits of its resource, passing through five main filters (the five facets of our framework) on the way to the interaction.

Authors contribution

BP initiated the paper. BP, AL, and TM launched the study. BP and TM are the main contributors. All authors participated in writing parts of the paper according to their area of expertise. The final version included in this manuscript was not reviewed by co-authors. They cannot be accountable for any mistake in this version.

Conflicts of interest

Authors declare they have no conflict of interest.

Epilogue (EN)

Here, we identified five different constraints driving consumption. Spatial constraints rule the detection and choice of a litter item by a detritivore. Biomechanical constraints rule the ability of detritivores to process and ingest a given litter. Digestive constraints rule the amount of nutrients that is assimilated. Metabolic constraints control the allocation and the fulfillment of metabolic needs. Elemental constraints control the allocation and the fulfillment of elemental needs. Many detritivores and litter traits may match to explain litter consumption, depending on which constraints mainly drive the interaction. From this conceptual framework, we can define a detritivore as an animal which consumes detritus (including associated microbes) as its traits match the traits of its resource, passing through five main filters (the five facets of our framework) on the way to the interaction. We will now rely on this conceptual framework and test its relevance (Figure 6). We will investigate the relative importance of several constraints and identify the weight of associated traits. In Chapter II we will focus on biomechanical *versus* elemental constraints. Each constraint will be described by several pairs of detritivore and litter traits. The weight of the match will be investigated.

Épilogue (FR)

Dans ce chapitre, nous avons identifié cinq contraintes différentes régissant la consommation. Les contraintes spatiales contrôlent la détection et le choix d'un élément de litière par un détritivore. Les contraintes biomécaniques régissent la capacité du détritivore à traiter et ingérer une litière donnée. Les contraintes digestives régissent la quantité de nutriments assimilés. Les contraintes métaboliques contrôlent l'allocation et la satisfaction des besoins métaboliques. Les contraintes élémentaires contrôlent l'allocation et la satisfaction des besoins en éléments. De nombreux traits des détritivores et de la litière peuvent être en concordance pour expliquer la consommation de litière, en fonction des contraintes qui gouvernent principalement l'interaction. A partir de ce cadre conceptuel, nous pouvons définir un détritivore comme étant un animal qui consomme des détritits (associés à des microorganismes) tant que ses traits sont en concordance avec ceux de sa ressource. Cette concordance lui permet de passer à travers cinq principaux filtres, les cinq facettes de notre

cadre. Nous allons maintenant nous appuyer sur ce cadre conceptuel et en tester la pertinence (Figure 6). Nous étudierons l'importance relative de plusieurs contraintes et identifierons le poids des traits associés. Dans le chapitre II nous nous concentrerons sur les contraintes biomécaniques par opposition aux contraintes élémentaires. Chaque contrainte sera décrite par plusieurs couples de traits des détritivores et des litières. Nous testerons l'importance de la concordance des traits.

CHAPTER II

LITTER CONSUMPTION BY MACRODETRITIVORES DEPENDS MORE ON MECHANICAL THAN ON ELEMENTAL CONSTRAINTS

Prologue (EN)

Leaf litter presents a high mechanical and elemental heterogeneity that depends on plant identity and on physical and microbial processing over the course of decomposition. Litter consumption by detritivores is known to depend on metabolic and elemental constraints but the importance of mechanical constraints is yet unknown. Building on the conceptual framework presented in Chapter I, this second chapter aims to investigate the relative importance of some constraints (Figure 6). We will avoid the influence of spatial constraints by focusing on bipartite interactions in microcosms. We will take metabolic constraints into account with detritivore body mass reflecting metabolic needs according to a power law relationship derived from metabolic theory predictions. Digestive constraints will be considered integrative of the interaction. We will mainly test for the relative importance of biomechanical *versus* elemental constraints, associated with key traits. Selected detritivore and litter traits are expected to match. The weight of the match will be investigated. If detritivores are diet-specialized, we expect trait-matching to strongly influence consumption (Figure 7, hypothesis H3).

Prologue (FR)

La litière foliaire présente une grande hétérogénéité mécanique et élémentaire qui dépend de l'identité des plantes ainsi que des processus physiques et microbiens au cours de la décomposition. On sait que la consommation de la litière par les détritivores dépend de contraintes métaboliques et élémentaires, mais l'importance des contraintes mécaniques demeure inconnue. S'appuyant sur le cadre conceptuel présenté dans le chapitre I, ce deuxième chapitre vise à étudier l'importance relative de certaines contraintes (Figure 6). Nous éviterons l'influence des contraintes spatiales en nous concentrant sur les interactions bipartites dans des microcosmes. Nous prendrons en compte les contraintes métaboliques en utilisant la masse corporelle des détritivores qui reflète les besoins métaboliques. Les contraintes digestives seront considérées comme intégratives de l'interaction. Nous testerons principalement l'importance relative des contraintes biomécaniques par rapport aux contraintes élémentaires, associées à des traits clés. On s'attend à ce que les traits sélectionnés des détritivores et de la litière concordent, et nous testerons l'importance de

cette concordance. Si les détritivores sont spécialisés dans leur alimentation, nous nous attendons à ce que la concordance des traits influence fortement leur consommation (Figure 7, hypothèse H3).

Litter consumption by macrodetritivores depends more on mechanical than on elemental constraints

Théo Marchand¹, Lola Estabes¹, Benjamin Pey¹

¹ Laboratoire Écologie Fonctionnelle et Environnement, Université de Toulouse, CNRS, Toulouse, France

Abstract

Ecosystem functions greatly depend on trophic interactions between consumers and their resources. Resource consumption depends on ingestion, digestion, and allocation processes. Three constraints act on these processes. Mechanical constraints are expected to influence ingestion, while metabolic and elemental constraints are expected to influence allocation. Leaf litter are resources presenting a high mechanical and elemental heterogeneity that depends on plant identity and on physical and microbial processing over the course of decomposition. Litter consumption by detritivores is known to depend on metabolic and elemental constraints but the importance of mechanical constraints is yet unknown.

After accounting for metabolic constraints on consumption rate, we tested the relative importance of mechanical and elemental constraints in explaining litter consumption rates by detritivores. For this, we exposed 16 leaf treatments (8 leaf species either just leached or leached and microbially conditioned) to 4 aquatic and 5 terrestrial detritivore taxa in laboratory no-choice consumption experiments. We investigated two mechanical constraints: grabbing and fragmenting the resource, by measuring suitable couples of mechanical traits for both litter and detritivores. We also investigated four elemental constraints related to N, P, K, and Ca contents in both detritivores and litter. For each constraint, we also tested if trait matching significantly contribute to explain consumption.

Our analysis revealed that both mechanical and elemental constraints are influencing mass-independent consumption rate but that mechanical constraints predominate over elemental constraints. Litter fragmentation, studied through litter toughness and detritivore biting force, was especially important to explain consumption rate. Elemental constraints were dominated by P constraints. Trait-matching had very weak importance and was significant only for P constraints.

Our findings highlight the importance of mechanical constraints for litter consumption by detritivores.

Keywords: trait-matching, detritivores, litter, consumption rate, trophic interaction, traits, nutrients, toughness

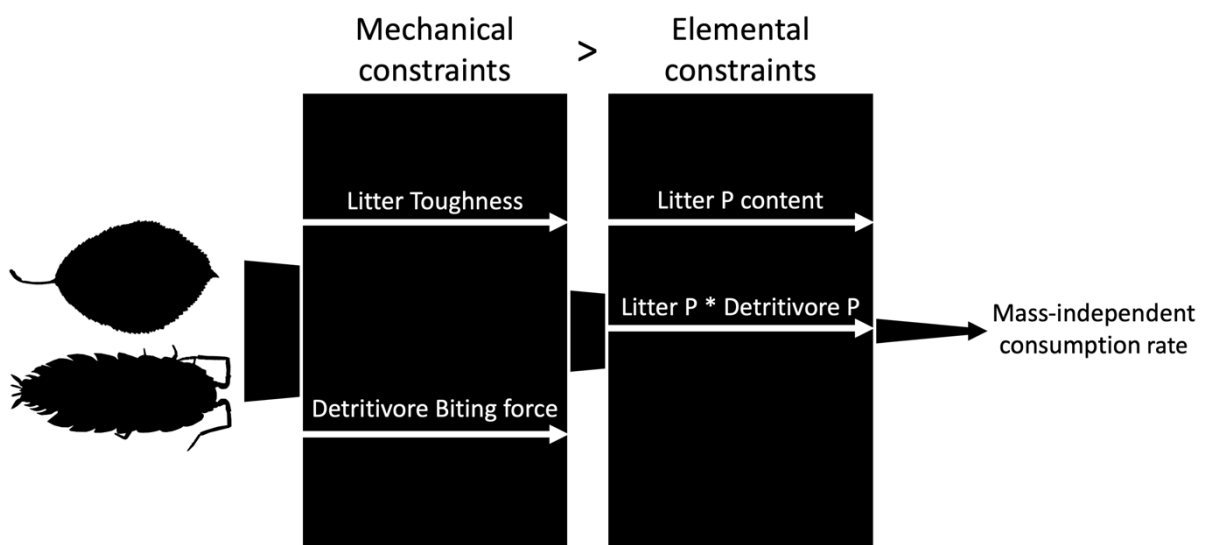


Figure II.0: Graphical abstract. Mass-independent consumption rate depends more on mechanical than on elemental constraints. Mechanical constraints are best explained by litter toughness and detritivore biting force. Nutritional constraints are best explained by litter phosphorus (P) content and by a match (represented by the asterisk) between litter P and detritivore P content.

Introduction

Ecosystem functions greatly depend on trophic interactions between consumers and their resources (Hines et al., 2015; Schmitz et al., 2018; Thompson et al., 2012). A way to better understand feeding interactions including animals is to describe the trophic network by functional metrics (e.g. functional traits) (Gravel et al., 2016; Schleuning et al., 2023). Wootton et al., (2023) notably built a modular theory of trophic interactions for co-occurring species. According to this framework, consumers must go through several steps ruling resource location, decision to feed, attack, and consumption. Specifically, resource consumption theoretically depends on ingestion, digestion, and allocation processes. The feasibility and the strength of each step of the pairwise consumer-resource interaction could be explained and predicted by some traits of both the consumer and the resource (Gravel et al., 2016; Schleuning et al., 2015; Wootton et al., 2023). It was notably hypothesized that trophic interactions could be explained not only by traits of consumers and resources alone, but also by a match between those traits (Bartomeus et al., 2016; Laigle et al., 2018). The modularity of Wootton's framework lies in fact that the relative importance of the different steps could change regarding of the type of interaction (e.g., predation, detritivory).

Consumption rates are limited by different constraints. First, ingestion of a resource by a co-occurring consumer partly depends on mechanical constraints. These constraints impact the handling time, i.e. the time needed for a consumer to handle and ingest its resource (Ott et al., 2012). A longer handling time will result in a lower consumption rate. For instance, a match between carabid beetle biting force and prey cuticular toughness successfully predicted trophic interactions (Brousseau et al., 2018). Chemical deterrents such as toxic, repulsive or unpalatable molecules (e.g. tannins, lignin) can also modulate the ingestion rate (David, 2014; Wootton et al., 2023). Second, allocation of digested resource can be divided into allocation of energy and elements. As a consumer has to fulfil its demands for survival, growth, and reproduction, consumption rate is expected to depend on consumer's metabolic rate which is linked to body mass (Brown et al., 2004; Rall et al., 2012), and on resource's energy content (Neu et al., 2023). Yet, repeated observations of deviations from predictions based on an energy-metabolic approach, led to the conclusion that energetical constraints are far from entirely driving consumption rate (Pawar et al., 2012; Rall et al., 2012; Rota et al., 2018). Lastly, as a consumer also must meet its demands in elements, consumption

rate is also expected to depend on both consumer and resource nutrient composition. Ecological stoichiometry theory predicts that consumers will perform better with resources having elements in similar proportions as in their own body (Sterner and Elser, 2017). An outcome of this prediction is that a trophic interaction will depend on the match between consumer's need and resources' content of one or more elements that may be in limiting concentrations in their resource (Danger et al., 2013; Frost et al., 2006; Sterner and Elser, 2017).

Macrodetritivores are defined as invertebrate animals larger than 2 mm which mainly contribute to decomposition by feeding on detritus which mainly came from plant (hereafter called litter) (Brussaard, 1998; Marks, 2019). They thus contribute to numerous associated ecosystem services (Mancinelli and Mulder, 2015). Litter presents a high mechanical and elemental heterogeneity. This heterogeneity partly depends on the plant identity. It is further enhanced by physical and microbial agents during decomposition, decreasing litter toughness, transforming chemical deterrents, and increasing nutrient concentration over time (Brousseau et al., 2019; Danger et al., 2012; David, 2014). While elemental constraints are well studied, mechanical constraints are largely under considered (Clissold, 2007; Evans-White and Halvorson, 2017; Motomori et al., 2001). Several experiments suggested that mechanical constraints could predominate over elemental ones, but such experiments were not always designed to test it formally and if so, they focused on litter traits only (Foucreau et al., 2013; M. A. S. Graça and Cressa, 2010; Walpola et al., 2011).

Under the assumption that elemental constraints drive litter consumption by detritivores, we expect one or a few elements to be limiting consumption rates. Although all organisms are composed of approximately 25 elements, the vast majority of studies focused on C, N and P elements, with a focus on C and N (Sterner and Elser, 2017). Yet, other macroelements have rarely been investigated in the context of detritivore consumption. For example, K and Ca are crucial common elements (metabolic cofactors and tegument components) with C, N and P (Peñuelas et al., 2019; Zhang et al., 2022). Under the assumption that mechanical constraints limit food ingestion, consumption rate should be explained by traits reflecting mechanical constraints. Two main mechanical constraints have already been

identified for detritivores handling leaf litter. First, grabbing the limb of the leaf should depend on limb thickness and mandible maximal gape (Brousseau et al., 2019). Second, punching through the limb, cutting, and shredding it should depend on the ability of mandibles to break leaf litter mechanical resistance. A detritivore should be able to punch through the limb if its biting force exceeds litter toughness (Brousseau et al., 2019; Ibanez et al., 2013; Raymond-Léonard et al., 2019). However, their effects on consumption have not been extensively tested. Scarce existing studies suspected litter toughness to impair consumption (Motomori et al., 2001; Patoine et al., 2017)

Previous literature based on litter traits solely indicates that mechanical constraints can overcome elemental ones (M. A. Graça and Cressa, 2010; Motomori et al., 2001; Patoine et al., 2017). Furthermore, detritivores are considered as being prone to feed on the most conditioned litter (which were subjected to physical and microbial processing agents), i.e. on the resource with highest quality and lowest constraints (Danger et al., 2012; Evans-White and Halvorson, 2017; Frainer et al., 2016; M. A. Graça and Cressa, 2010). Yet, as conditioning increases litter quality, competition could lead to niche partitioning. For instance, some species would exploit litter at an earlier stage of decomposition (Cummins et al., 1989), or differently exploit litter (grazing from surface vs fragmenting the whole limb) (Danger et al., 2012). Under the assumption that detritivores are rather generalists and opportunistic consumers relying on a large variety of resources, we expect functional trait identity of detritivores and/or litter to separately explain litter consumption by detritivores (e.g., litter toughness impacts all detritivores similarly). On the contrary, under the assumption that detritivores are diet-specialized, we expect that a match between detritivore and litter traits will mainly explain litter consumption (e.g. detritivores with strong mandibles will consume tough leaves) (Brousseau et al., 2018; Ibanez, 2012; Neu et al., 2023).

Our study aimed to test for the relative importance of mechanical constraints over elemental constraints in explaining litter consumption by detritivores. For this, we compared the consumption rates of a large variety of leaf litter by several detritivore taxa representative of aquatic and terrestrial ecosystems in laboratory no-choice consumption tests. Leaf litter was chosen to have a large range of mechanical and elemental trait values. After considering

metabolic constraints on consumption rate by using a power-law correlation with detritivore body mass, we investigated two mechanical constraints: grabbing and fragmenting the litter. For this, we measured suitable couples of mechanical traits for both litter and detritivores. We also investigated four elemental constraints related to N, P, K and Ca contents in both detritivores and litter. Constraints relative to C content were not investigated as they are expected to be linked mainly to metabolic constraints. For each constraint, we also tested if trait matching drives a significant part of litter consumption by detritivores.

Material and methods

Experimental design

We performed leaf litter consumption tests by offering one of 16 different leaf litter types to one of 9 macrodetritivore taxa (four aquatic and five terrestrial species). We selected 8 leaf litter species with a large range of mechanical and elemental trait values to cover a wide spectrum of potentially different constraints. Each leaf litter species was then either just leached, or leached and microbially conditioned before being offered to detritivores. This ensured enlarging the range of initial mechanical and elemental litter traits values while limiting the content of chemical deterrents. Detritivore taxa were chosen to be representative of coarse lifeforms commonly encountered in aquatic and terrestrial ecosystems. As we aimed to assess fundamental rules of pairwise interactions between detritivores and litter, we tested the consumption of a single litter by a single detritivore individual at the time. We also offered litter species that detritivores could not encounter in their natural habitat. We thus sampled litter in a geographical site (Canal du Midi: Toulouse, 31000 and Ramonville-Sainte-Agne, 31520, France) distant from the geographical sites where we sampled detritivores (Montagne Noire, France). We performed a total of 576 consumption tests, corresponding to 144 detritivore-litter pairs: 9 detritivores taxa * 16 litter treatments (8 leaf litter species * 2 litter conditioning treatments (leaching or leaching plus microbial conditioning)) * 4 replicates. Replicates spread out from week to week and were associated with corresponding control tests without detritivores (Appendix, [Table S.II.3](#)). We performed a total of 128 control tests without detritivores: 16 litter treatments (8 litter species * 2 litter conditioning treatments (leaching or microbial conditioning)) * 2 ecosystem types (aquatic or terrestrial) * 4 replicates.

We performed consumption tests in microcosms made of clean plastic containers with 50 g of clean sand in the dark at 10°C. For aquatic detritivores, we added 200 mL of water collected from their stream. For terrestrial ones, we sprayed 5 mL of tap water on the sand. We starved detritivores for 3 days prior to the consumption test. In each microcosm we placed one individual (assigned randomly) and 5 discs of one litter treatment (litter species * conditioning treatment) that were previously freeze-dried, weighted, and rehydrated in tap water for 1 h. Tests were stopped when consumption visually reached 75% of initial discs surface and did not last more than three days. At the end of the consumption tests, remaining discs fragments larger than 1 mm were collected, freeze-dried and weighted. When one individual died during the first 24 h of the test, we immediately replaced it with a new individual. When the individual died later during the test, we repeated the consumption test the week after, with corresponding control treatments. At the end of consumption tests, detritivores were starved for 24 h, and were weighted (aquatic animals were gently blotted with paper towel). We converted fresh body mass into dry mass using a linear relationship established for each taxon (See Macrodetritivores' section). For each detritivore taxon, we conserved half of the individuals in 70% ethanol for dissection and we froze the other half for chemical analyses. All weight measurements were determined at the nearest 0.1 mg.

Leaf Litter

We collected dead leaves at abscission from October to November along the Canal du Midi (Toulouse, 31000, and Ramonville-Sainte-Agne, 31520, France) from a limited number of individuals (≤ 5) for each species. We used 8 tree species belonging to 8 different families, namely *Ailanthus altissima* (Simaroubaceae), *Robinia pseudoacacia* (Fabaceae), *Juglans regia* (Juglandaceae), *Carpinus betulus* (Betulaceae), *Acer platanoides* (Aceraceae), *Prunus avium* (Rosaceae), *Quercus petraea* (Fagaceae), *Platanus xhispanica* (Platanaceae). Leaves were air-dried and stored in the dark until being leached with tap water during 24 h. We then cut 1-cm diameter leaf discs with a cork-borer. Some leached discs were microbially conditioned. They were incubated in a mix of decomposing dead leaves until they were visually microbially colonized (soft and discolored). For aquatic conditioning specifically, we collected 50 L of stream water and dead leaves from the same stream where we collected aquatic individuals. We added Fertiligène Naturen® fertilizer (NPK: 3 – 2 – 5) at 0.5 mL.L⁻¹. We left it three days in

a greenhouse with constant oxygenation for microorganisms' development. We then filled tanks with filtered (63 μm) water and placed one fine-mesh bag of monospecific litter discs of each litter species per tank with constant oxygenation. For terrestrial conditioning, we collected dead leaves from Montagne Noire forest soil (beech, chestnut, hazelnut) and grinded it with a garden shredder. We left it three days in a green house after humidification with the same fertilizer at $0.5 \text{ mL}\cdot\text{L}^{-1}$. We then placed monospecific leaf discs in a fine-mesh bag of each litter species between two layers of fragmented litter in each tank. Tanks were regularly humidified with the same fertilizer.

To test for mechanical constraints of grabbing and fragmenting litter, we measured thickness and toughness on 8 discs from controls, respectively. We measured limb thickness to the nearest 0.001 mm with a Helios-Preisser® digital micrometer, avoiding main veins. We measured litter toughness as the penetration pressure (kPa) needed for a 2.2-mm diameter steel rod to penetrate through a leaf disc. We used a custom-made penetrometer, such as described in Graça et al. (2005), fitted to a digital force tester (CS225 Series, Chatillon®) measuring force to the nearest 0.1 N. To test for elemental constraints, we quantified nitrogen (N) content using a Total nitrogen and Organic Carbon analyzer (TOC L, Shimadzu) on three replicates of 20 mg. We quantified phosphorus (P), potassium (K) and calcium (Ca) content with an Induced Coupled Plasma – Mass Spectrometer (ICP-MS) on three replicates of 5 mg.

Macrodetritivores

We collected macrodetritivores in la Montagne Noire, a metamorphic forested massif east of Toulouse (France) (Appendix, [Table S.II.1](#) and [Table S.II.2](#)). We hand-captured aquatic detritivores from February to March in a stream mainly boarded by beech, hazelnut and chestnut trees. We hand-captured terrestrial detritivores in April in a site dominated by ash. We identified all taxa to the lowest taxonomic level, mostly species. Only Plecoptera and Tipula larvae were identified to the genus, *Nemoura* and *Tipula*, respectively (Tachet et al., 2010). Case-bearing Trichoptera larvae were identified as *Potamophylax cingulatus* (Stephens, 1837) (Waringer and Graf, 2011), and Amphipods as *Gammarus fossarum* (Koch, 1835) (Tachet et al., 2010). Terrestrial detritivores were either Isopods (*Philoscia affinis* (Verhoeff, 1908) and *Porcellio monticola* (Lereboullet, 1853)) (Oliver and Meehan, 1993; Vandell, 1962) or Diplopods (*Cylindroiulus londinensis* (Leach, 1815), *Polydesmus inconstans* (Latzel, 1884),

and *Glomeris marginata* (Villiers, 1789)) (Blower, 1985; David, 1995). At the laboratory we sorted them by taxon and left them 1 – 3 days in the dark at 10°C for acclimatation before being starved.

We performed dissections on at least 5 individuals per taxon, from several random experimental conditions, under an Olympus SZX10 stereomicroscope equipped with a digital camera. To assess the ability of detritivores to overcome litter thickness constraints, we measured mandible gape (maximum opening of mandibles) to the nearest 0.01 mm. To assess biting force as the ability to overcome litter toughness, we measured head width (H_w), mandible length (M_L , distance between the incisive tip and the axis of rotation which was identified with condyles), and mandible width (M_w , distance between the adductor muscle insertion and the axis of rotation) to the nearest 0.01 mm (Clissold, 2007). We used these metrics to calculate an index of biting force at the taxa level (F , (Brousseau et al., 2018; Wheater and Evans, 1989)):

$$F = \frac{H_w M_w}{M_L}$$

To assess metabolic constraints, we converted detritivore fresh body mass into dry mass using a linear relationship established for each taxon with individuals both fresh- and freeze-dry-weighted ($n \geq 30$, $p < 0.001$, $R^2 \geq 0.57$). To assess elemental constraints, four pools of at least four individuals for each detritivore taxon (resulting in a total of four analytical replicates per taxon) were grinded into powder and analyzed following the same procedure as for litter samples. For *Nemoura* alone, only two pools were analyzed due to the very small body weight of this taxon.

Data analyses

To illustrate mechanical and elemental trait profiles variations of litter and detritivores used in the experiment, we performed two PCA on leaf litter traits and detritivores traits separately.

We calculated individual rate of litter consumption (C in $\text{mg}\cdot\text{d}^{-1}$) as follows:

$C = \frac{M_f - M_i \cdot \frac{M_{fc}}{M_{ic}}}{\Delta t}$, where M_f and M_i are the final and initial mass (mg) of litter discs offered to detritivores, respectively. M_{fc} and M_{ic} are the final and initial mass (mg) of corresponding litter discs in control conditions, respectively. Δt is the test duration.

To take into account the effect of detritivore body mass on individual consumption rate, we built a log-log linear model with all consumption rate values above 0.001 mg.d⁻¹. This threshold was based on visual analysis of the data and removed 91 quasi-null observations. The exponential coefficient allowed to compute mass-independent rate of litter consumption (C_i in mg.mg^{-1-c}.d⁻¹) as follows: $C_i = C.B^c$, where B is the individual body mass, and c is the estimate for the effect of body mass in the log-log linear model.

To assess which part of the variability in mass-independent consumption rate was explained by the origin ecosystem type (aquatic or terrestrial), detritivore taxon, litter species, and microbial conditioning treatment (aquatic, terrestrial, or no conditioning), we fitted a linear mixed model (*lmer* function from *lme4* package) ($\ln(C_i) \sim 1 | \text{Ecosystem/Detritivore taxon/Conditioning/Leaf species}$) following the procedure by Messier et al. (2010). As advised by Messier et al., we used bootstrap ($n = 500$) to precisely estimate the variability effects. To assess how much of data variability could be explained by trait-matching, we performed a linear model explaining mass-independent consumption rate by the interaction of detritivore taxa and litter treatment ($\ln(C_i) \sim \text{Detritivore taxon} * \text{Litter treatment}$).

To test if replicates had an influence on consumption rate, we performed a mixed model explaining $\ln(C_i)$ with “Replicate week number” as a fixed factor (Appendix, Table S.II.3), and the identity of each detritivore taxon – litter treatment pair as a random factor ($\ln(C_i) \sim \text{Replicate week number} + (1 | \text{Detritivore taxon} - \text{Litter treatment pair})$).

We then tested (1) which of the five above-mentioned constraints best explain mass-independent consumption rate, and (2) for each constraint, whether trait-matching can help better explain mass-independent consumption rate. Rohr et al., (2016) suggested the use of matching-centrality models to investigate the influence of single traits and of a match between consumer and resources traits on trophic interactions. We built six different pairs of models: two of them (I) are related to mechanical constraints (grabbing and fragmenting the

litter by detritivores) and four of them (II) are related to elemental constraints (N, P, K and Ca contents in both detritivores and litter). Within each pair of models, a model with corresponding detritivore trait and litter trait, and a “matching term” reflecting the match between those two traits, was compared to a reference model with both traits but without the matching term. We computed matching terms of the form $(X - Y)^2$, where X and Y are standardized (scaled) detritivore and litter traits, respectively (Brousseau et al., 2018; Rohr et al., 2016). Log transformations were applied when necessary. We considered a matching term to have a significant influence if it was significant in the first model and if the first model was significantly better (assessed with an ANOVA and by comparing the Akaike Information Criterion (AIC) values) than the reference model. In a second step, we aimed at identifying the traits and matching terms of all of the five constraints which best explain consumption rate. For this, we built a final model (III) by combining the best model (I) reflecting mechanical constraints with the best model (II) reflecting elemental constraints. We performed a step-wise selection to remove non-significant variables. As we expected non-linear relationships between mass-independent consumption rate and traits, we only used Generalized Additive Models (GAM) with the *gam* function (Brousseau et al., 2018; Rohr et al., 2016). We used the lowest smoothing parameter ($k = 3$) to avoid over-fitting (Brousseau et al., 2018; Crawley, 2012). Residuals distribution of all models was visually checked. To assess the relative importance of each variable in a model, we compared the deviance explained by the model with the deviance explained by the same model from without the variable (Crawley, 2012). All analyses were performed with R version 4.0.3.

Results

Leaf litter

Litter toughness varied over a 17-magnitude range across the whole dataset (from 38 kPa for *Ailanthus* with aquatic conditioning, to 656 kPa for *Quercus* without conditioning, Appendix, Table S.II.4). Litter thickness varied between 0.044 mm for *Ailanthus* with aquatic conditioning, to 0.17 mm for *Platanus* with aquatic conditioning. N, P, and K content varied between 0.57, 0.03, and 0.05 % (for *Platanus* without conditioning for the three elements) to 2.86, 0.11, and 0.81 % (for *Ailanthus* with aquatic conditioning, *Ailanthus* with aquatic conditioning, and *Juglans* without conditioning), respectively. Ca content ranged from 1.69 %

(*Carpinus* without conditioning) to 8.44 % (*Juglans* with terrestrial conditioning). Conditioning decreased litter toughness by 42 ± 4 % (mean \pm se value). It only slightly affected litter thickness, decreasing it by 9 ± 4 %. Conditioning increased N, P, K, and Ca content by 37 ± 7 %, 29 ± 8 %, 24 ± 18 %, and 14 ± 5 %, respectively. Litter mean consumption rate varied from 0.07 (*Platanus* without conditioning) to 2.96 mg.d⁻¹ (*Ailanthus* with terrestrial conditioning). Conditioning considerably increased consumption rate (by 250 ± 85 %). The first two axis of PCA on litter traits (Figure II.1A) represented 76.4 % of variability. Litter treatments are quite well scattered along the first axis (49.7 % of variability) which can be interpreted as an axis of “litter quality” with more recalcitrant litter (typically *Platanus* and *Quercus*) on the left, and more palatable litter (*Ailanthus*) on the right. The conditioned litter is always more on the right-hand side than the unconditioned litter from the same species (to the exception of *Juglans* with terrestrial conditioning). A-posteriori mass-independent consumption rate vector is closed to the first axis, pointing to the right, consistently with the above-mentioned interpretation of “litter quality”.

Macrodetritivores

Mortality was low over the entire experiment (< 3%). Mean dry body mass ranged from 1.0 (*Nemoura*) to 156.7 mg (*Cylindroiulus*) (Appendix, Table S.II.5). Biting force (*F* index) varied from 0.50 for *Nemoura*, to 2.64 for *Glomeris*. N, P, and K content varied from 4.32, 0.86, and 0.28 % (for *Cylindroiulus*, *Nemoura*, and *Cylindroiulus*) to 10.80, 2.10, and 2.14 % (for *Nemoura*, *Polydesmus*, and *Potamophylax*), respectively. Insect larvae exhibited very low Ca content (from 0.21 % for *Nemoura*, to 0.32 % for *Tipula*) compared to crustaceans and millipedes (from 8.74 % for *Philoscia*, to 17.78 % for *Polydesmus*). Compared to N and K elements, P was the element with the highest $\frac{[\text{Element}]_{\text{Detritivore taxon}}}{[\text{Element}]_{\text{Litter treatment}}}$ ratio for 138 out of 144 detritivore taxon – litter treatment couples. Mean P ratio was 28.3 ± 0.6 over the entire dataset, meaning that P content was on average 28 times higher in detritivores than in the litter. The highest ratio (80.7) was for the P element for *Polydesmus* with *Platanus* without conditioning. K and N only displayed the highest ratio on five (for *Tipula* and *Potamophylax* on *Ailanthus* and *Ailanthus* with aquatic conditioning, and for *Tipula* on *Robinia* without conditioning) and one (*Nemoura* on *Juglans* without conditioning) occasions, respectively. The first two axis of PCA on detritivore traits (Figure II.1B) represented 83.0 % of variability. Detritivore taxa are roughly

grouped by phylogenetic proximity: insect larvae are on the left part of the panel, with high N and K content, and crustaceans are close to the second axis. Two millipedes, *Glomeris* and *Cylindroiulus*, are on the right part of the panel (high body mass and biting force), while *Polydesmus* shows different characteristics.

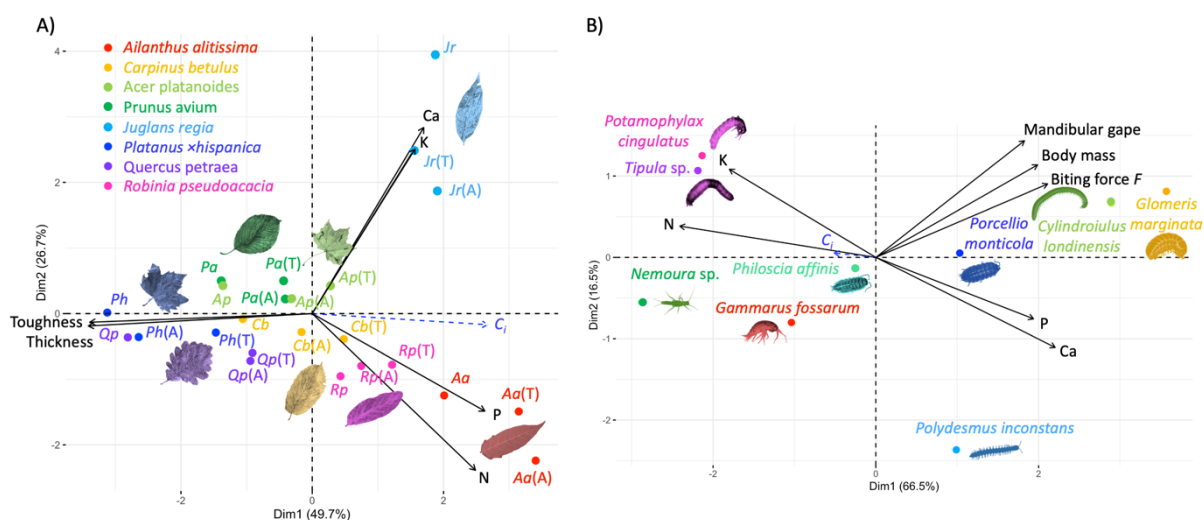


Figure II.1: Principal Component Analysis of (A) litter traits, and (B) detritivore traits. On the left (A) panel, litter treatments are indicated by the first letters of the litter genus and species, with “(A)” if the litter was conditioned in aquatic conditions, “(T)” if the litter was conditioned in terrestrial conditions or without additional letter if the litter is just leached. On each panel, mass-independent consumption (C_i) was added a-posteriori as a supplementary variable (dotted blue arrow).

Sources of variation of litter consumption rate

Mean consumption rate of detritivore taxa varied from 0.15 (*Nemoura*) to 1.44 $\text{mg}\cdot\text{d}^{-1}$ (*Potamophylax*). Mean consumption rate divided by detritivore dry body mass varied from 0.004 (*Glomeris*) to 0.291 $\text{mg}\cdot\text{mg}^{-1}\cdot\text{d}^{-1}$ (*Potamophylax*), meaning that *Potamophylax* daily consumed a mean quantity of litter representing 29% of its body mass (Appendix, Figure S.II.2). Maximum consumption rate per detritivore body mass reached 1.37 $\text{mg}\cdot\text{mg}^{-1}\cdot\text{d}^{-1}$, for a *Potamophylax* individual on *Ailanthus* with aquatic conditioning.

A log-log linear model showed that detritivore body mass weakly but significantly influenced individual consumption rate ($n = 485$, $R^2 = 0.02$, $F_{1,482} = 7.8$, $p = 0.005$). We then

used the estimated coefficient ($c = 0.11$) to correct for the body mass effect and compute mass-independent consumption rate (C_i).

In a model explaining $\ln(C_i)$ with Ecosystem/Detritivore taxon/Conditioning treatment/Leaf species as random nested effects, the ecosystem (aquatic or terrestrial), detritivore taxon, conditioning treatment (aquatic, terrestrial, or just leached), and leaf species explained $< 0.0 \pm 0.0$, 11.6 ± 3.4 , 22.3 ± 4.0 , and 34.3 ± 3.0 % of variability, respectively. Residuals accounted for 31.8 ± 2.7 % of total variability (mean \pm standard error).

In a model explaining $\ln(C_i)$ with Detritivore taxon * Litter treatment, both parameters and the interaction term were significant ($F_8 = 39.0$, $p < 0.001$ for detritivore taxon, $F_{23} = 18.9$, $p < 0.001$ for litter treatment, and $F_{112} = 1.3$, $p = 0.028$ for the interaction term). Detritivore taxon, litter treatment, and the interaction term accounted for 23.5, 32.9, and 11.1 % of the sum of squares, respectively.

In a mixed model with “Replicate week number” as a fixed factor, and the identity of each detritivore taxon – litter treatment pair as a random factor, replicate weeks were significantly influencing $\ln(C_i)$ (Anova: $\text{Chisq}_{10} = 24.1$, $p = 0.007$). Yet, they accounted for only 1.8 % of the total sum of squares.

Trait-based models explaining litter consumption rate

Our analysis revealed that both mechanical and elemental constraints are influencing consumption rate (Table II.1). Concerning mechanical constraints, the best model explaining consumption rate was the model based on litter toughness and detritivore biting force (Deviance explained = 30.8 %). For this model, the matching term did not significantly increase the performance of the model. Consumption rate first decreased with litter toughness (Δ Deviance explained = 20.6 %), the decrease being stronger at low toughness values (below 400 kPa), than at high toughness values (above 400 kPa) where consumption reaches a minimal plateau (Figure II.2A; Appendix, Figure S.II.4). Biting force index F influenced consumption rate with a humped-back relationship, consumption being maximal for F values around 1 (Δ Deviance explained = 10.2 %).

Concerning elemental constraints, the best model was based on elemental P constraints (Table II.1, Deviance explained = 24.9 %). For this model, the matching term

between P content in detritivores and in litter significantly increased the performance of the model (Δ Deviance explained = 1.4 %). Consumption rate first increased, almost linearly, with litter P content (Δ Deviance explained = 19.6 %) (Figure II.2B; Appendix, Figure S.II.5). Detritivore P content influenced consumption rate according to a humped-back relationship (Δ Deviance explained = 2.0 %), consumption being maximal for detritivore P content values around 1.3 %. Lastly, the matching term negatively influenced consumption rate, meaning that consumption rate decreases when the gap between detritivore and litter P content increases (Δ Deviance explained = 1.4 %). To assess the mechanisms behind the influence of the P match on the model, we extracted predicted values of $\ln(C_i)$ for detritivore taxa with highest (2.10 %) and lowest P (0.82 %) contents (Appendix, Figure S.II.5). We then fitted one linear model to each prediction. Predicted consumption rate of detritivores with the highest P content was positively influenced by litter P with a slope coefficient of 2.22 ± 0.05 (mean \pm standard error) ($F_{1,18} = 2038$, $p < 0.001$, $R^2 = 0.99$). On the other hand, predicted consumption rate of detritivores with the lowest P content was positively influenced by litter P with a slope coefficient of 1.42 ± 0.06 ($F_{1,18} = 548$, $p < 0.001$, $R^2 = 0.97$). Only the model accounting for Ca constraints presented potentially concerning residuals distribution due to bimodal distribution of detritivore Ca content. Although not presented we also performed models accounting for putative C constraints which have proven to be very uninformative (Deviance explained < 4 %, data not shown).

For each constraint type, either mechanical or elemental, the best above-mentioned model outperformed the others by a substantial margin (Table II.1, gap in deviance explained of 10.1 % and 9.8 %, for mechanical and elemental constraints respectively).

Table II.1: Generalized Additive Models explaining mass-independent consumption rate with detritivore and litter traits. For each X and Y pair of detritivore and litter traits, pairs of models are compared: one with a matching term $(X - Y)^2$, and one without. ΔAIC is computed as $AIC_{with\ matching\ term} - AIC_{without\ matching\ term}$. A negative ΔAIC then indicates that the model with the matching term is better (more parsimonious) than the same model without the matching term. For each constraint type, models are ordered by decreasing performances.

Constraints	Traits used in the model	p-value of the matching term	Deviance explained with matching term	Deviance explained without matching term	Difference between the two models	
Mechanical	Punching through and shredding the limb	Litter Toughness – Biting force	$F_1 = 1.5$ $p = 0.22$	31.0%	30.8%	$F_{-2,3} = 1.4$ $p = 0.23$ $\Delta AIC = 0.5$
	Grabbing the limb	Litter Thickness – Mandible Gape	$F_1 < 0.1$ $p = 0.98$	20.9%	20.9%	$F_{-1} = 0$ $p = 1$ $\Delta AIC = 2.0$
Elemental	P limitation	Litter P – Detritivore P	$F_1 = 10.6$ $p = 0.001$	24.9%	23.5%	$F_{-1,8} = 5.6$ $p = 0.005$ $\Delta AIC = - 7.2$
	N limitation	Litter N – Detritivore N	$F_1 = 1.2$ $p = 0.28$	15.1%	14.9%	$F_{-1} = 1.4$ $p = 0.24$ $\Delta AIC = 0.6$
	K limitation	Litter K – Detritivore K	$F_1 = 2.4$ $p = 0.18$	13.4%	13.4%	$F_{-0,2} = 0$ $p = 1$ $\Delta AIC = 0.9$
	Ca limitation	Litter Ca – Detritivore Ca	$F_1 = 0.2$ $p = 0.62$	7.0 %	7.0 %	$F_{-1} = 0.25$ $p = 0.62$ $\Delta AIC = 1.8$

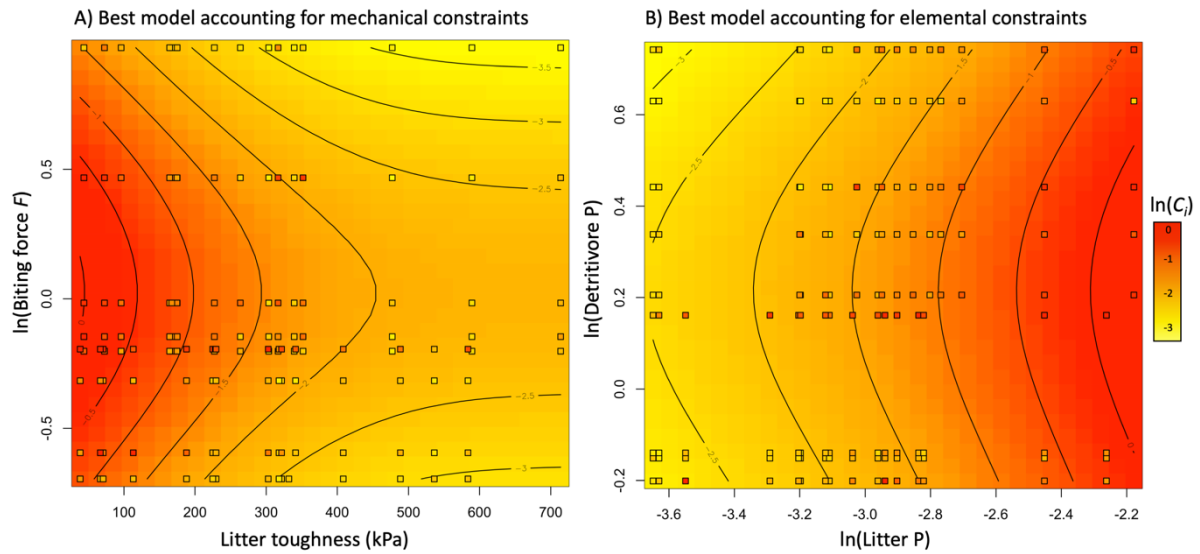


Figure II.2: Visual representation of the best generalized additive models accounting for (A) mechanical constraints, and (B) elemental constraints. Squares represent the mean mass-independent consumption rate (C_i) value ($n = 4$) at each point. On the left panel (A), consumption rate decreases strongly with litter toughness until 400 kPa. Above this toughness value, consumption rate is very limited and depends almost exclusively on biting force. Biting force influences consumption rate according to a humped-back shape relationship with consumption rate being maximal for biting force values around 1 ($\ln(1) = 0$). The model explained 20.9 % of deviance. On the right panel (B), consumption rate mostly depends on litter P according to a positive relationship. Detritivore P content influences consumption rate according to a humped-back shape relationship with consumption rate being maximal for P content values around 1.3 % ($\ln(1.3) = 0.26$). P-matching term effect is not represented but is visible by the non-symmetrical effects of litter and detritivore P contents. The model explained 24.9 % of deviance. See also Appendix, [Figure S.II.4](#) and [Figure S.II.5](#).

The final synthetic model explained mass-independent consumption rate with litter toughness, biting force, litter P parameters, and the P matching term ([Figure II.3](#); Appendix, [Figure S.II.6](#)). Detritivore P parameter was removed because it did not significantly improve the model. The model explained 36.6 % of deviance. Consumption rate was first influenced by biting force (Δ Deviance explained = 8.4 %) according to a similar humped-back shape as in the model accounting for mechanical constraints. Litter toughness was the second explaining parameter (Δ Deviance explained = 5.6 %) with the same negative relationship as in the best

model accounting for mechanical constraints. Consumption rate then linearly increased with litter P content (Δ Deviance explained = 4.2 %). Lastly, the P matching term decreased consumption rate (Δ Deviance explained = 1.4 %), as in the best model accounting for elemental constraints.

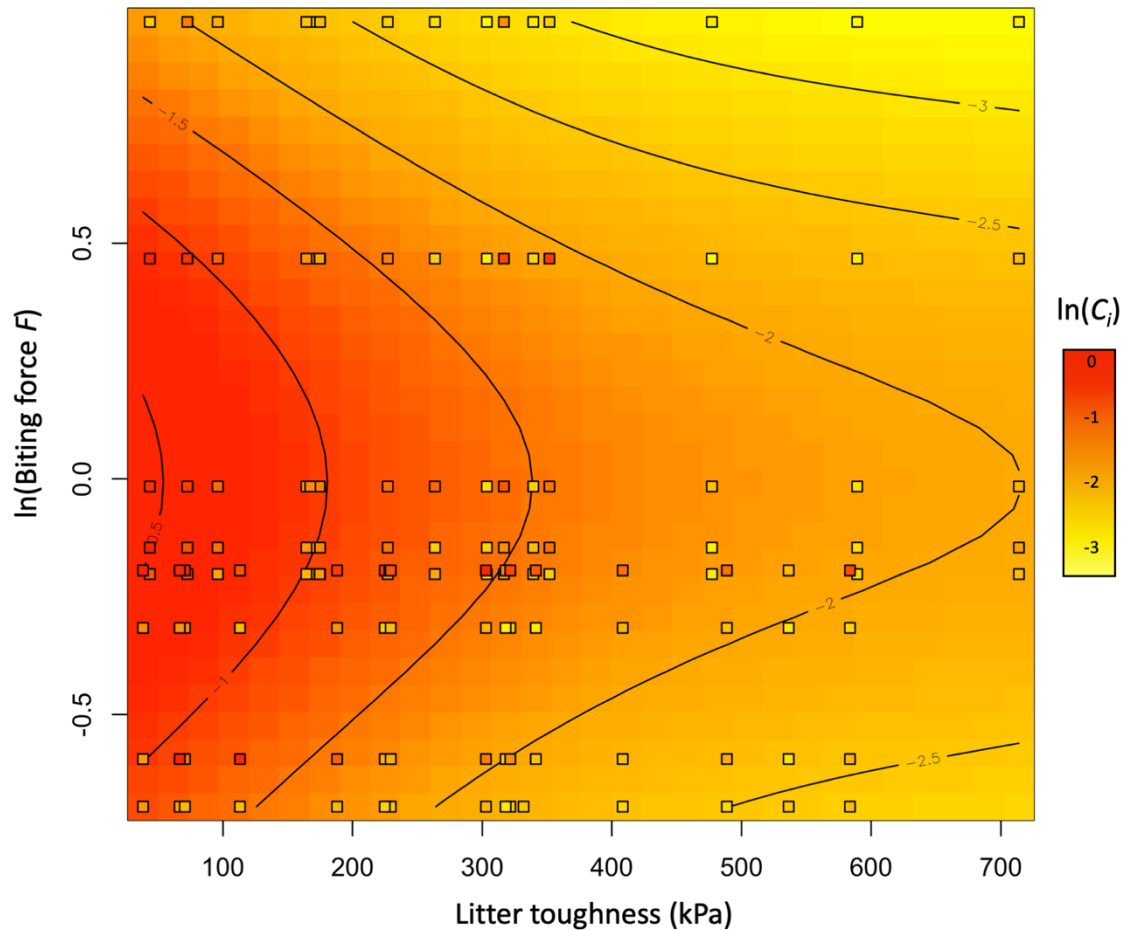


Figure II.3: Final generalized additive model accounting for both mechanical and elemental constraints. The influence of the two first parameters (biting force and litter toughness) on mass-independent consumption rate (C_i) are presented. Squares represent the mean consumption rate value ($n = 4$) at each point. Consumption rate decreases strongly with litter toughness. Biting force influences consumption rate according to a humped-back shape relationship with consumption rate being maximal for biting force values around 1. The differences in predictions with [Figure II.2A](#) are due to elemental constraints. Non-represented variables are litter P content and the P matching term. The model explained 36.6 % of deviance. See also Appendix, [Figure S.II.6](#).

Discussion

In this study, after taking into account the influence of body mass, consumption rate was best explained by mechanical constraints, especially by litter toughness and detritivore biting force. Trait-matching had a very low explanatory power. Only the P-P match significantly improved the model based on P elemental constraints. Overall, the final model explained up to one third of the variability in the data.

In the final model accounting for both mechanical and elemental constraints, mechanical traits explained a higher portion of deviance compared to elemental traits. This indicates that mechanical constraints dominated over elemental constraints in our experiment. This is in line with the consideration that consumers first have to be able to process and ingest the resource before they can assimilate it and feed again in order to match their elemental requirements (Wootton et al., 2023). If mechanical constraints dominate over elemental constraints, we can expect consumption rates of detritivores to be limited by their ability or by the time they need to handle and process their resource. On the contrary, if elemental constraints dominate over mechanical constraints, we can expect detritivores to apply a strategy of compensatory feeding in increasing consumption rate to compensate for a low amount of elements in the resource (Danger et al., 2013; Ott et al., 2012). We did not observe compensatory feeding, thus reinforcing the interpretation of a predominance of mechanical constraints. Those results then support the idea that mechanical constraints drive litter consumption, as hypothesized by other studies (Danger et al., 2012; Foucreau et al., 2013; Motomori et al., 2001; Patoine et al., 2017). Among investigated elements, P content was the first parameter explaining consumption rate before N, K, and Ca contents. The match between detritivore and litter P content was the only matching term significantly improving the explanation of consumption rate. The weak influence of matching terms for both mechanical and elemental constraints makes sense as the interaction between detritivore taxa and litter treatments explained a low amount of consumption rate variability. Accordingly, as litter treatment explained a higher amount of variability than detritivore taxa, litter traits were expected to have a stronger influence than detritivore traits in the models which is consistent with our results.

As in other consumption experiments using both aquatic and terrestrial detritivores, the ecosystem parameter (aquatic vs terrestrial) explained a very low amount of data variability (Rota et al., 2022). Observed patterns can then be considered as being relatively generic across detritivores coming from these two ecosystems. Detritivore body mass had a surprisingly weak effect. The power coefficient of 0.11 that fitted our data strongly deviates from the value of 0.75 that is expected under the metabolic theory of ecology (Brown et al., 2004). A lower coefficient than 0.75 is expected if other traits than body mass drive consumption, thus decreasing the importance of metabolism and body mass effect (Pawar et al., 2012; Rall et al., 2012). As detritivores were starved prior to our consumption tests, the choice of not consuming litter would result in a high energetic imbalance. However, our experiment exposed detritivore taxa to resources with diverse mechanical and elemental constraints that could limit consumption. This would explain in part the low influence of body mass. Finally, as the distribution of replicates over time had a very weak effect on mass-independent consumption rate (1.8 % of total sum of squares), we are confident that it did not change our interpretations.

Litter consumption rate decreased with litter toughness until it reached a horizontal asymptote for toughness values greater than 400 kPa (Figure II.2A; Appendix, Figure S.II.4). This pattern, identified in the first model accounting for mechanical constraints, was found to be very similar in the final model summarizing mechanical and elemental constraints (Appendix, Figure S.II.6). A non-linear influence of resource toughness on consumption rate is expected under the hypothesis that consumers need to break through the resource item to process it, increasing the time they need to handle the resource (Clissold, 2007; Ott et al., 2012). When resource toughness is higher than the critical biting force of consumers, we can expect them to be unable to process food. Consumption should then be minimal. Our data then suggest a critical biting pressure around 400 kPa for the detritivore taxa we tested. This value is of the same order of magnitude as what is found in the few previous studies that investigated ability of detritivores to overcome resource toughness (Danger et al., 2012). The influence of biting force on litter consumption followed an unexpected humped-back shape (Figure II.2A; Appendix, Figure S.II.4). We rather expected a monotonically increasing relationship as consumers with stronger mandibles should spend less time and efforts

handling and processing the food, which should allow them to consume larger quantities in the same amount of time (Ott et al., 2012). This humped-back relationship between consumption rate and the index for biting force could be explained by a trade-off between biting force and other traits limiting consumption. We also expected that a match between litter toughness and biting force would drive consumption rate. It was not the case, which highlights the need to know more about how detritivores mechanically process their food. For example, *Potamophylax* was the taxon with the highest consumption rates, even for the toughest and most recalcitrant litter treatments (Appendix, Table S.II.5). Because of their habit of cutting discs from leaves to make their cast (Waringer and Graf, 2011), they can be expected to have very strong mandible capacities. Yet, they displayed average biting force index values. Other traits such as mandibles sharpness should then be considered as it may also contribute to explain why detritivores cut more or less efficiently through tough leaves (Clissold, 2007).

The predominance of P content over other elements is expected because P is often the most limiting element for a large variety of organisms (Sturner and Elser, 2017). A few studies highlighted the importance of P for detritivores (Danger et al., 2013). In almost all detritivore - litter pairs of our study, P was the element for which content in detritivores was the highest, relatively to litter content. This would indicate that P is most likely the most frequently limiting element. Another argument comes from the study by Frost et al (2006) who computed the C:P Threshold Elemental Ratios (TER) by atoms for many aquatic organisms (i.e. the resource C:P ratio at which consumer growth limitation switches from one element to another). They found that detritivore organisms typically have $TER_{C:P}$ around 1000. As our litter had C:P ratios of 2424 ± 188 ([min - max] = [1014 - 4791]), we are confident that P was a limiting element for detritivores. Consumption is expected to depend on detritivores and litter P proper contents but also possibly on their match. The P match only slightly contributed to consumption in our data. Yet, compared to the model without P matching term, adding the P match led to model predictions that are in line with ecological stoichiometry theory predictions (Sturner and Elser, 2017). This theory predicts that consumers with high elemental requirements will be more impacted by resources of low element content, compared to other consumers with modest requirements (Ohta et al., 2016). Accordingly, in the best model accounting for elemental constraints, the predicted consumption rate of detritivores with high P content (i.e., probably

having highest P requirements) is more negatively impacted by low litter P content, than for detritivores with low P content (i.e., probably having lowest P requirements). Even though we demonstrated the existence of a P match explaining trophic interactions, the underlying mechanisms remain unclear. It seems unlikely that detritivores can taste the amount of P in the resource and adapt their consumption in response. Detritus P content is known to increase with microbial decomposition and with microorganism's biomass (Danger et al., 2012). Detritivores are able to detect the presence of microorganisms (M. A. Graça and Cressa, 2010; Motyka et al., 1985) and consumption rate of detritivores is known to increase in presence of microorganisms (Swan and Palmer, 2006; Zimmer et al., 2003). It would make sense to postulate that the direct influence of microorganism's presence on consumption rate would explain an indirect influence of resource P content. The weakest performance of models based on N content is surprising considering the major importance attributed to litter N content in the literature (Frouz et al., 2015; García-Palacios et al., 2013; Zhang et al., 2015). Yet, as N is often correlated to P (Li et al., 2021) and as N is more systematically investigated than P, this could blur the importance of P over N in past studies. Results about elemental constraints and their relative importance with mechanical constraints should nonetheless be interpreted with caution. Elemental content we measured in our experiment did not reflect biological needs for detritivores or bioavailability for litter. Acute measures of elemental needs (e.g., N content in proteins vs N content in nucleic acids) or of litter elements' bioavailability (e.g., N content in tannins vs soluble N) may change some of the observed patterns and may improve our understanding of elemental constraints.

As a conclusion, we contributed to assess fundamental pairwise trophic rules of interactions by using single detritivore – litter pairs. To be completed, other steps of the interaction must be investigated (e.g., chemical deterrents acting on selection or digestion) to be fully understood and predicted. Furthermore, the low effect of trait-matching on consumption is in line with the assumption that detritivores are generalists and opportunistic feeders, relying on various resources (Crenier et al., 2017; Rubio-Ríos et al., 2023). Contrarily to consumption of dead resources, other trophic interactions (herbivores - green plants, pollinators – flowers, predators – preys) are expected to drive co-evolution between the two actors of the interaction who have to be adapted to their interacting organism (Brousseau et

al., 2018; Ibanez, 2012; Ibanez et al., 2013; Neu et al., 2023). From an ecosystem perspective, these fundamental pairwise rules are expected to be modulated by indirect interactions with other biotic trophic network components (e.g., predation, competition, facilitation) or by abiotic parameters fluctuations.

Authors contribution

BP supervised the study. TM and BP designed the experiment. TM and LE conducted the experiments. TM analyzed the results and wrote the first draft of the manuscript with the help of BP. The final version included in this manuscript was not reviewed by co-authors. They cannot be accountable for any mistake in this version.

Data archiving

Data will be archived on the Dryad depository at the time the paper is accepted for publication.

Conflict of interest

The authors declare that they have no known competing interest.

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Epilogue (EN)

Mechanical constraints appear to be overimportant compared to elemental constraints. Even though litter toughness is understudied, it was the main trait influencing mechanical constraints in this chapter, by impairing consumption with a non-linear effect. Elemental constraints were mostly due to constraints linked to the phosphorus element. Trait-matching was identified only for the phosphorus element, and had a very weak influence on consumption, in line with the mainstream hypothesis that detritivores are rather generalist consumers, with modest specialization (Figure 7, hypothesis H2). Mechanical constraints will be more precisely investigated throughout decomposition in Chapter III, as microbial conditioning strongly decreases litter toughness (Figure 6). The consequences of elemental constraints, and especially of phosphorus limitations will be investigated at the community level in Chapter IV (Figure 6).

Épilogue (FR)

Les contraintes mécaniques semblent être d'une importance primordiale par rapport aux contraintes élémentaires. Bien qu'étant sous-étudiée, la résistance physique de la litière était le principal trait influençant les contraintes mécaniques en limitant la consommation via un effet non linéaire. Les contraintes élémentaires étaient principalement liées aux contraintes de l'élément phosphore. La concordance de traits a été identifiée uniquement pour l'élément phosphore et avait une très faible influence sur la consommation, ce qui correspond à l'hypothèse générale selon laquelle les détritivores sont plutôt des consommateurs généralistes, avec une spécialisation modeste (Figure 7, hypothèse H2). Les contraintes mécaniques seront étudiées de manière plus précise au cours de la décomposition dans le chapitre III, car le conditionnement microbien diminue fortement la résistance de la litière (Figure 6). Les conséquences des contraintes élémentaires, en particulier des limitations liées au phosphore, seront étudiées au niveau de la communauté dans le chapitre IV (Figure 6).

CHAPTER III

MECHANICAL TRAITS

AS DRIVERS OF TROPHIC INTERACTION

BETWEEN MACRODETRITIVORES AND LEAF LITTER

Prologue (EN)

In diverse arrays of consumers foraging on physically heterogeneous resources, the matching between invertebrate mandibular traits and the toughness of resource items is thought to be important in driving pattern of consumer-resource interactions. However, quantified evidence of interspecific differences in detritivore feeding is still scarce. Building on the conceptual framework from Chapter I, this third chapter aims to further investigate how biomechanical constraints, identified as being predominant in Chapter II, apply throughout decomposition (Figure 6). We will test the consumption rate of two contrasted leaf litter species throughout decomposition by different detritivore species, in laboratory conditions. Based on the findings in Chapter II, we expect litter toughness to have a strong and non-linear influence on litter consumption. We also expect detritivore mandible capacities to modulate the influence of litter toughness, resulting in a match between mandible capacities and litter toughness (Figure 7, hypothesis H2 or H3).

Prologue (FR)

Dans diverses populations de consommateurs se nourrissant de ressources physiquement hétérogènes, la concordance entre les traits mandibulaires des invertébrés et la résistance physique de la ressource est considérée comme importante pour influencer les schémas d'interactions entre les consommateurs et les ressources. Cependant, les preuves quantifiées des différences interspécifiques dans l'alimentation des détritivores restent encore rares. Dans la continuité du cadre conceptuel du chapitre I, ce troisième chapitre vise à approfondir l'étude de la manière dont les contraintes biomécaniques, identifiées comme prédominantes dans le chapitre II, s'appliquent tout au long de la décomposition (Figure 6). Nous testerons le taux de consommation de deux espèces de litière de feuilles contrastées au cours de la décomposition par différentes espèces de détritivores, en conditions de laboratoire. Sur la base des résultats du chapitre II, nous nous attendons à ce que la résistance de la litière ait une influence forte et non linéaire sur la consommation de litière. Nous prévoyons également que les capacités mandibulaires des détritivores moduleront l'impact de la résistance de la litière, résultant en une concordance entre les capacités mandibulaires et la résistance de la litière (Figure 7, hypothèse H2 ou H3).

Mechanical traits as drivers of trophic interaction between macrodetritivores and leaf litter

Théo Marchand¹, Benjamin Pey¹, Corinne Pautot¹, Antoine Lecerf¹

¹ Laboratoire Écologie Fonctionnelle et Environnement, Université de Toulouse, CNRS,
Toulouse, France

Abstract

Resource consumption rate by animals drives matter and energy fluxes in ecosystems. Consumption rate is known to depend on consumer energy requirements, resource nutrient content, and resource mechanical properties. In diverse arrays of consumers foraging on physically heterogeneous resources, the matching between invertebrate mandibular traits and the toughness of resource items is thought to be important in driving pattern of consumer-resource co-occurrence. While there is a general agreement on the idea that coexisting taxa are all prone to feed on the most nutritive and softest litter available, variable abilities of detritivores to overcome mechanical resistance of the toughest litter are expected. However, quantified evidence of interspecific differences in detritivore feeding is still scarce.

We aimed to test for the relative importance of mechanical constraints compared to nutritional and energetic constraints to explain variability of litter consumption rate. We especially investigated the nature of the relationship between litter consumption rates and litter toughness. Finally, we tested for a possible match between biting force (as determined with morphometric analyses) and litter toughness.

Leaf litter of two plant species (hornbeam and oak) were exposed in the field to physical and microbial decomposition in aquatic and terrestrial ecosystems in order to produce resources of varying toughness. Leaf litter was offered to 8 macrodetritivores taxa (3 taxa from stream and 5 from soil forest) in non-choice laboratory feeding experiments. Results were analyzed, taking into account expected effects of litter nitrogen content and detritivore body mass on litter consumption rate.

After removing the influence of body mass, litter consumption rates first depended on litter toughness. A sigmoid function was suitable to describe the relationship between mass-

independent consumption rate and litter toughness. Model parameters differed among taxon, suggesting different strategies used by detritivores to cope with mechanical constraints.

Our findings stress the importance of mechanical traits as drivers of litter consumption rate by detritivores. Nonlinear modelling of the relationship between litter consumption rate and litter mechanical resistance helps detect biomechanical thresholds and biological differences. Further research is needed to understand why biting force did not correlate with feeding performance in our study.

Keywords: Resource consumption, Litter decomposition, Detritivores, Leaf litter, Traits, Litter toughness, Mandible

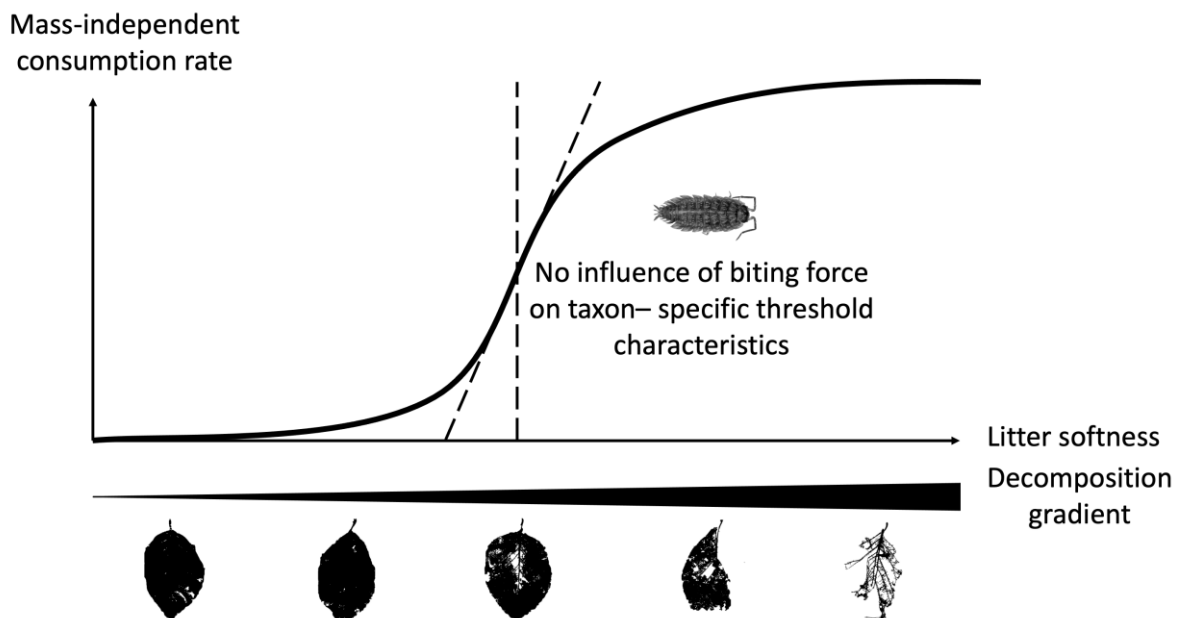


Figure III.0: Graphical abstract. Mass-independent consumption rate depends on leaf litter softness (i.e., the inverse of leaf litter toughness) along a gradient of decomposition, according to a sigmoid relationship. The characteristics of the threshold (inflection point and slope) depend on each detritivore taxon. We found no influence of detritivore traits (biting force) on the characteristics of thresholds.

Introduction

Resource consumption rates by animals drives matter and energy fluxes in ecosystems (Schmitz et al., 2018). Consumer body mass helps explain variation in per capita consumption rate across consumer taxa and trophic levels (Pawar et al., 2012; Rall et al., 2012). According to the Metabolic Theory of Ecology (Brown et al., 2004), metabolic rate scales positively with body mass according to a $\frac{3}{4}$ power law. Under the assumption that resource consumption completely fills metabolic requirements, and the variability of food resource energy content is low, an allometric body mass scaling relationship is expected for the rate of energy intake. However, allometric scaling exponents estimated from empirical datasets often deviates from the $\frac{3}{4}$ power rule (e.g. Pawar et al., 2012; Rall et al., 2012), suggesting that consumer-resource dynamics is not solely controlled by consumer energetics. Further evidence in support to this idea comes from feeding experiments hinting at substantial mass-independent variations in consumption rate (e.g. Raffard et al., 2017; Rota et al., 2018).

Foraging theory predicts that a high resource density is required for animals to achieve optimal consumption rate (Rall et al., 2012). Resource quality also modulates time and effort allocated by consumers to foraging and processing food items. Nutritional resource traits have been the primary focus in research on plant resource exploitation by herbivores and detritivores whereas far less attention has been paid to mechanical traits underpinning resource vulnerability against consumer attacks (Clissold, 2007). It is thus not always clear whether slow resource consumption is a manifestation of consumer avoidance of a poor nutritional quality of the resource (e.g. low elements content and/or high contents of polyphenolics and low-digestible carbohydrates) or if it reflects a mismatch between mouthpart capabilities of the consumer and mechanical attributes (e.g. toughness, thickness, etc.) of the resource (Brousseau et al., 2019; Ibanez et al., 2013). In addition to determine the feasibility domain of trophic interactions, mechanical traits may also influence interaction strength through effects on the handling time (Clissold, 2007) (Box1).

Plant communities produce mechanically and nutritionally heterogeneous leaf litter resources to invertebrate detritivores (Brousseau et al., 2019; Raymond-Léonard et al., 2018). Detrital resource heterogeneity is further enhanced by temporal changes in leaf traits

mediated by physical and microbial agents of litter decomposition, resulting in litter softening and enrichment in nutrients over time (Danger et al., 2012; David, 2014). While there is a general agreement on the idea that coexisting detritivore species are all prone to feed on the most nutritive and softest resource available locally (Danger et al., 2012; Evans-White and Halvorson, 2017; Frainer et al., 2016; M. A. S. Graça and Cressa, 2010), different abilities to handle and process low quality leaf litter may provide the basis for trophic niche differentiation among detritivores (e.g. De Oliveira et al., 2010; Jonsson et al., 2002; Tonin et al., 2018). This idea is supported by spatial covariations between detritivores mandibular traits and leaf toughness and thickness found in forest floors (Brousseau et al., 2019; Raymond-Léonard et al., 2018). Results of some feeding experiments designed to compare effects of mechanical vs. nutritional resource traits also points out a mechanical control of detritivore-litter interaction (M. A. S. Graça and Cressa, 2010; Motomori et al., 2001; Patoine et al., 2017).

There is limited knowledge on the biomechanics of feeding in leaf-consuming detritivores. Mandibular morphology and associated musculature have been shown to determine chewing capabilities of invertebrate predators and herbivores (Clissold, 2007; Püffel et al., 2021; Wheeler and Evans, 1989). The pioneering work of Wheeler and Evans (1989) on predatory beetles has provided a straightforward rationale for calculating biting force based on morphological traits of chewing mouthparts. In addition, insights into the biomechanics of feeding could be gained by assessing resource consumption rate of a given taxon along a gradient of resource mechanical constraints. A sigmoid relationship is expected under the assumption that leaf consumption would arise only when mandibular tip pressure exceeds the fracture point of the leaf material (also see Box1). The inflexion point and sharpness of the transition from low to high consumption rate are likely to inform on mechanical capabilities and foraging mode of consumer taxa. Only a handful of studies have evaluated the relationship between leaf consumption rate by detritivores and leaf toughness and, to our knowledge, none of them have applied non-linear modelling to extract ecologically meaningful parameters (Danger et al., 2012; Foucreau et al., 2013; Motomori et al., 2001; Patoine et al., 2017).

Our study was intended to fill knowledge gaps on the biomechanics of feeding and on the drivers of resource consumption rate and trophic niche differentiation in leaf-consuming

detritivores. We conducted a series of laboratory feeding experiments designed to assess relationships between leaf consumption rate and leaf mechanical resistance for taxonomically distinct macrodetritivores from both aquatic and terrestrial ecosystems. We assessed the relative importance of litter toughness (mechanical constraints), compared to litter N content (elemental constraints) and detritivore body mass (metabolic constraints) in determining litter consumption rate. We expected litter toughness to be at least as much important as litter N content. We expected the relationship between mass-independent consumption rate and litter toughness to be best explained by a sigmoid model (threshold effect) rather than by a linear model. We also aimed to test for a possible match between biting force and litter toughness which could explain mass-independent consumption. To this end, we extracted taxon-specific fitted parameters of toughness-dependent models we built, to confront them to a biting force index of each taxon we built, derived from head and mandibular traits (Wheater and Evans, 1989). We expected that the stronger biting force the taxon has, the more it would be able to consume resistant litters.

Material and methods

Sites and experimental design

Our sampling sites were located in the Pyrenean Piedmont, south of Toulouse (France), an area characterized by a calcareous bedrock and continental climate (Appendix [Table S.III.1](#), [Table S.III.2](#), [Table S.III.3](#)). Plant litter and detritivores were collected in oak-hornbeam forests. For each ecosystem type (low order streams and forest floors), we selected a pair of sites, one dominated by oak (*Quercus petraea*) and another one dominated by hornbeam (*Carpinus betulus*). Hornbeam sites were both located in a hornbeam coppice stand. The terrestrial oak site was a mature even-aged oak forest. As there was no stream crossing it, we selected a nearby stream running along a forest edge dominated by oak trees.

The sites were used to collect the leaf litter and detritivores required to carry out feeding experiments with laboratory microcosms. Leaf litter was collected at abscission, shortly after they fall, and were stored air-dried at room temperature. The sites were also used to expose leaf litter to physical and microbial decomposition in order to produce litter with varying toughness values (Danger et al., 2012). Since we aimed at quantifying the

strength of “realized” interactions between co-occurring macrodetritivores and litters, detritivore individuals collected at a site were only offered the locally dominant leaf litter (either oak or hornbeam) in feeding experiments. Furthermore, the experiments were carried out with partially decomposed leaf litter and detritivores collected in the field at the same time.

Leaf litter

Freshly fallen leaves of oak were expected to be tougher than those of hornbeam and the toughness of both leaf species was expected to gradually decrease with time of exposure in the field. Five grams of air-dried leaves of each species were enclosed in 0.5-mm nylon mesh bags (20x15 cm), thus preventing macrodetritivores to enter the bags. Oak and hornbeam litter bags were incubated at oak and hornbeam sites, respectively. This ensured that the leaf species inside the bags matched dominant leaf species in naturally occurring plant litter.

Litter bags were deployed in the field on autumn 2020. They were arranged in three blocks in each site. In streams, bags were tied up onto iron sticks anchored in the sediments. Terrestrial bags were laid flat onto the topsoil and they were secured with bamboo sticks driven into the soil. At least one litterbag was retrieved from each block at different times to induce gradual change in litter toughness. Assuming that leaf litter disappears faster in streams than in soils, litterbag collection occurred after 54 and 99 days of exposure in the streams and after 82, 111, 152, 236 and 349 days of exposure in terrestrial sites. As hornbeam leaf litter decomposed more rapidly than oak leaf litter, only oak bags were recovered from the terrestrial site at the last sampling date.

Partially decomposed leaves recovered from litter bags were rinsed with tap water to remove exogeneous particles. The leaves were punched with a 10-mm cork borer, avoiding central veins, in order to produce homogeneous food items for detritivores. About 200 discs per sampling date and site were needed to assess litter traits (described thereafter) and perform feeding experiments. We also made *ca.* 300 discs out from undecomposed oak and hornbeam leaves ($t = 0$). As the leaves were stored air-dried, they were allowed to soak water for one hour prior to cutting discs. Leaf discs were freeze-dried, partitioned into sets of five

(except for the first Oak test for which we used sets of four discs, as consumption was very low), and weighed to the nearest 0.1 mg.

We assessed litter toughness by measuring the force needed for a 2.2-mm diameter steel punch to penetrate through a leaf disc laid flat on a perpendicular plane. We used a custom-made penetrometer, such as described in Graça et al. (2005), fitted to a digital force tester (CS225 Series, Chatillon®). This device ensured to reach a high precision (± 0.1 N) when measuring penetration force. Litter toughness was expressed as penetration pressure (kPa), that is the penetration force divided by the cross-sectional area of the rod. Litter softness (kPa^{-1}) was defined as the inverse of penetration pressure. We calculated the average of 15 replicate measurements for each batch of leaf litter (coming from a same site at a same sampling date).

Litter nitrogen (N) content was used as an indicator metric for litter nutritional value assuming that 1) detritivores would experience strong N limitation (Frainer et al., 2016) and 2) contents of other limiting nutrients (e.g. Phosphorus) would positively covary with N content (Li et al., 2021). Three replicates of 3-6 mg per leaf discs batch were grinded into powder by the means of a bead mill (FastPrep-24™ Classic Instrument). The N content was quantified using a Total nitrogen and Organic Carbon analyzer (TOC L, Shimadzu) and values were reported on a dry weigh basis ($\text{mgN}\cdot\text{mg}^{-1}\text{litter}$).

Macrodetritivores

We collected macrodetritivores from natural accumulations of organic debris in the sites where litterbags were placed. We sought to capture enough individuals of several taxa to ensure adequate levels of replication of experimental conditions (i.e., pairs of detritivore taxon and litter batch). However, we did not achieve a fully-balanced design (Appendix, [Table S.III.5](#)) because the structure of detritivore assemblages differed between oak and hornbeam sites and population abundances exhibited large seasonal variations (Appendix, [Table S.III.4](#)). We first conducted a feeding experiment with pre-weighed discs of undecomposed leaf litter (i.e. air-dried leaves used to construct litter bags) and detritivores collected in the field at

litterbag installation. Feeding experiments were repeated whenever litterbags were retrieved from the sites.

Individuals were assigned to coarse taxonomic categories in the field and were then identified at the lowest practicable taxonomic level, mostly genus, based on observations made on dead individuals under a dissecting microscope (Table III.1). We found case-bearing Trichoptera larvae and amphipods (Crustacea) occurring in the two stream sites, and Plecoptera larvae in the hornbeam site only. Amphipods and Plecoptera individuals were both assigned to a single genus, *Gammarus* and *Capnia*, respectively, and Trichoptera individuals to the Limnephilinae genus complex (Tachet et al., 2010). Detritivores from the terrestrial sites were either Isopods (*Philoscia* and *Porcellio*) (Oliver and Meechan, 1993; Vandel, 1962) or Diplopods (*Leptoiulus*, *Cylindroiulus* and *Glomeris*) (Blower, 1985; David, 1995). Other genera (e.g., *Polydesmus*) occasionally encountered were too scarce to ensure gathering sufficient data for assessing patterns of litter consumption rate adequately. Detritivores sorted by taxon and site of collection were held in plastic containers stored in the dark at 10°C. Containers with aquatic taxa were filled with permanently-aerated stream water.

Pre-weighed leaf discs were rewetted for one hour before they were offered to one individual of either detritivore taxon, except *Capnia*. For this small-sized detritivores, we pooled together up to 5 individuals of the same size to ensure accurate quantification of per capita effects on leaf litter. We used 10-cm large plastic containers filled with 50 g of clean sand as experimental units. The sand was sprayed with 5 mL of water to maintain wet conditions required for terrestrial detritivores whereas 200 mL of stream water was added to containers with aquatic taxa. Detritivores were starved for at least 18h prior to the introduction of pre-weighed leaf discs. Terrestrial and aquatic detritivores were allowed to feed over 4 and 2 days, respectively, taking account into differences in feeding rates between ecosystem types. Consumption test could be stopped if disc area had shrunk to 75% of initial leaf area. For each leaf litter species and ecosystem type, we set up five control experimental units without detritivore added to estimate leaf mass loss caused by physical and microbial decomposition. Leaf mass loss in control containers did not exceed 10% of initial mass.

Leaf discs and fragments larger than 1 mm remaining in containers at the end of feeding trials were freeze-dried and weighed to the nearest 0.1 mg. Detritivores from containers were blotted with paper towel before individual wet mass was determined to the nearest 0.1 mg. Wet body mass were converted into dry mass using linear relationship established for each taxon with freeze-dried individuals ($n \geq 12$, $p < 0.001$, $R^2 \geq 0.68$). Half of individuals from each taxon collected at different times were stored in 70% ethanol until needed for quantification of head width (H_W), the length (M_L) and width (M_W) of mandibles. These metrics were used to calculate an index of biting force at the taxon level (F ; Wheater and Evans, 1989):

$$F = \frac{H_W M_W}{M_L}$$

Note that, as H_W (Appendix, [Table S.III.5](#)) is taken as a proxy of the force produced by muscles involved in mandible motion (Wheater and Evans, 1989), the unit for F is not meaningful. A two-dimension graphical representation (F index and dry body mass) depicts morphological differences between dissected individuals of all taxa we used for feeding experiments (Appendix, [Figure S.III.1](#))

Ethanol-preserved individuals were photographed under a stereomicroscope equipped with digital camera (Olympus SZX10) to determine morphological traits to the nearest 0.01 mm. Both mandibles were dissected using forceps and were photographed in suitable positions to determine mandible length and width. Mandible length was determined as the distance between the incisive tip and the axis of rotation which was identified with condyles (Appendix, [Figure S.III.2](#)). The distance between the adductor muscle insertion and the axis of rotation was taken to represent mandible width (Clissold, 2007).

Data Analyses

Because it is convenient to describe resource-mediated constraints on consumer performance by increasing functions (e.g., Monod equation, predator-prey function responses), we used the inverse of toughness (i.e., softness) as a predictor of litter consumption rates in statistical models. Converting toughness into softness made distribution of the data less skewed and more even, which helped obtain accurate parameter estimates from linear and non-linear models.

Our dataset consisted of 291 values of litter consumption rate estimated on 63 pairs of detritivore taxon and litter batch. We calculated mass-specific rate of litter consumption (C_s in $\text{mg}\cdot\text{mg}^{-1}\cdot\text{d}^{-1}$) as follows: $C_s = \frac{M_f - (aM_i + b)}{B\Delta t}$, where M_f and M_i are the final and initial mass (mg) of the leaf discs offered to detritivores, respectively, Δt is the test duration, and B is the final dry body mass of detritivores in the container (mg). The equation term $aM_i + b$ was used to correct initial litter mass for physical and microbial decomposition assessed in control containers, without detritivore. The coefficients a and b are the slope and intercept of the linear regression of final vs initial litter mass in controls ($n = 5$) estimated for each condition (oak and hornbeam leaf discs incubated in terrestrial and aquatic habitats at each time). As the lowest limit of quantification for litter consumption rate was estimated at $0.001 \text{ mg}\cdot\text{mg}^{-1}\cdot\text{d}^{-1}$ (ca. 0.1 mg of litter for the most precise measurements, divided by 100 mg of detritivore body mass for the biggest individuals), smaller values were rounded toward zero. Litter consumption rate was not calculated whenever a detritivore died during feeding experiments. This occurred in 5% of experimental units set up for the study.

To test for the relative importance of traits as drivers of litter consumption rate, we built a linear model to assess effects of litter softness, litter N content and detritivore body mass on mass-specific rate of above-zero litter consumption rate ($C_s > 0.001 \text{ mg}\cdot\text{mg}^{-1}\cdot\text{d}^{-1}$) across the full dataset ($n = 245$). The latter two predictors were intended to represent elemental constraints and energy-mass allometry (Brown et al., 2004), respectively. The dependent variable and all the predictors were log-transformed to linearize the expected power-law relationships and to achieve assumptions of homoscedasticity and normal distribution of residuals.

Further analyses were carried out on mass-independent rate of litter consumption (C_i in $\text{mg}\cdot\text{mg}^{-1-c}\cdot\text{d}^{-1}$) calculated as follows: $C_i = C_s \cdot B^{-c}$, where c was the estimate for the effect of body mass in the linear model. We fitted a random-effects model to assess the contribution of experimental factors (ecosystem type, detritivore taxon, leaf species, and sampling date) to variability of C_i (Messier et al., 2010; Rota et al., 2022). A square root transformation was applied to the data to ensure residual normality and homoscedasticity.

We assumed litter consumption rate (C_i) to change with litter softness (S) following a S-shaped curve with the transitional phase informing on mechanical traits of both the consumer and resource. A three-parameter sigmoid function was fitted to data for each detritivore taxa, using non-linear regression:

$$C_i = \frac{\alpha}{1 + \exp \frac{\beta - S}{\gamma}}$$

α , β and γ are the maximum consumption rate, the softness value at the inflexion point, and a scale parameter, respectively (See Box 1 for more elements about the rationale of this model). To distinguish between smooth versus sharp threshold sigmoid curves, we compared the fit of the sigmoid model with that of a linear model using root mean square error (RMSE) and Akaike Information Criterion (AIC). Parameter estimates of each model by taxon were extracted in order to assess the extent of cross-taxon variability.

Box III.1: Theoretical basis of the model describing consumption rate as a function of litter toughness.

Holling (1959) described *per capita* consumption rate with the following equation: $C_s = \frac{aN}{1+ahN}$ where a is the attack rate i.e. the rate at which the consumer encounters food items. N is the food density and h is the handling time. Under the assumption that $h = k_1 e^{-\frac{k_2}{Toughness}} = k_1 e^{-k_2 * Softness}$ where $Softness = \frac{1}{Toughness}$ and k_1 and k_2 are constants, then:

$$C_s = \frac{aN}{1+aNk_1 e^{-k_2 * Softness}} = \frac{\alpha}{1 + \exp \frac{\beta - Softness}{\gamma}} \text{ where } \alpha = aN, \beta = \frac{\ln(aNk_1)}{k_2}, \text{ and } \gamma = \frac{1}{k_2}$$

In our experimental setup, resource density can be considered as constant and non-limiting. Likewise, the attack rate of a given detritivore taxon can be considered as constant. The handling time then decreases exponentially with resource softness, and consumption of a given litter by a given detritivore depends on litter toughness according to a logistic model describing a sigmoid function. It predicts the existence of a threshold value for softness under which consumption is very limited.

Spearman correlation was used to assess associations between detritivore traits including body mass and mandible traits and parameters of the sigmoid model. All analyses were performed with R version 4.0.3. The `nls2` function were used to fit nonlinear regression model.

Results

Leaf Litter

The mechanical resistance of undecomposed leaf litter of oak and hornbeam was 917 and 389 kPa, respectively. Litter toughness decreased with time spent in the field down to 187 kPa for oak leaves and 95 kPa for hornbeam leaves exposed to terrestrial decomposition. Leaf litter allowed to decompose in streams achieved similar toughness values at the last sampling date (196 and 123 kPa for oak and hornbeam, respectively), despite much shorter incubation times in aquatic (<100 days) than terrestrial (>200 days) ecosystems (Appendix [Figure S.III.4A](#)). Litter toughness varied over a one-order of magnitude range across the whole dataset (69-769 kPa).

Abscised leaves of oak and hornbeam contained 0.72% and 1.03% nitrogen (N), respectively. Litter N content increased with time of exposure in the field up to 1.2% for oak and 1.8% for hornbeam. The highest N content was achieved in the stream for oak and in soil for hornbeam (Appendix [Figure S.III.4B](#)). A positive correlation between litter N content and softness was found across the whole dataset ($R^2 = 0.73$, $F_{1,14} = 37.7$, $p < 0.001$).

Macrodetritivores

We did not determine the consumption rates of undecomposed hornbeam leaf litter by terrestrial detritivores because we were unable to capture individuals at the hornbeam sites in winter at the litterbag installation. For the same reason, consumption rate of undecomposed oak leaf litter by *Cylindroiulus* could not have been determined. Limited availability of detritivores on the field at other sampling dates explained why some treatment combinations were sometimes tested on only one or two experimental units.

There was striking cross-taxon differences in body mass of detritivore individuals collected in the field ([Table III.1](#); Appendix [Figure S.III.5](#)). Mean dry body mass ranged from

0.9 (*Capnia*) to 179.1 (*Cylindroiulus*) mg. Specimens used in feeding experiments also displayed intraspecific differences owing to temporal change in body size (Table III.1; Appendix Figure S.III.5).

The highest mass-specific rate of litter consumption recorded here was $1.33 \text{ mg}\cdot\text{mg}^{-1}\cdot\text{d}^{-1}$, meaning that some individuals ingested more than 100% of their body mass every day (Table III.1). For most detritivore taxa, consumption rates increased with the time the litter resource had spent in the field (Appendix Figure S.III.6). Highest mean mass-specific rate of oak consumption happened for Limnephilinae ($0.24 \pm 0.07 \text{ mg}\cdot\text{mg}^{-1}\cdot\text{d}^{-1}$ at $t = 54$ days). Highest mean mass-specific rate of hornbeam consumption happened for *Capnia* ($0.76 \pm 0.12 \text{ mg}\cdot\text{mg}^{-1}\cdot\text{d}^{-1}$ at $t = 54$ days). Both taxa are stream detritivores, suggesting slower litter consumption by terrestrial taxa. For instance, the highest hornbeam consumption rate of a terrestrial taxa (*Leptoiulus* $0.19 \pm 0.03 \text{ mg}\cdot\text{mg}^{-1}\cdot\text{d}^{-1}$ at $t = 236$ days) was threefold lower than the highest value for *Capnia*.

The biting force index range varied over a 8.6-fold range. Similar values (0.32 – 0.33) were found for *Capnia* and *Leptoiulus* which were positioned at the lower end of the range. Values greater than 2 was found for two terrestrial taxa (*Glomeris* and *Cylindroiulus*), whereas Limnephilinae had the highest biting force among aquatic taxa (Table III.1).

Table III.1: Values of dry body mass, mass-specific rate of litter consumption, and biting force index (F) of each detritivore taxon. Detritivores are ordered by increasing mean body mass, with aquatic detritivores first.

Taxon	Dry body mass (mg)		Mass-specific rate of litter consumption (mg.mg ⁻¹ .d ⁻¹)		Biting force index (F)
Genus (Order)	mean ± se	0.1 – 0.9 quantiles	mean ± se	0.1 – 0.9 quantiles	mean ± se
Only Limnephilinae represents a genus complex and not a genus.					
<i>Capnia</i> (Plecoptera)	0.9 ± 0.1	0.5 – 1.3	0.517 ± 0.099	0.024 – 1.127	0.33 ± 0.01
<i>Gammarus</i> (Amphipoda)	9.3 ± 0.5	5.4 – 13.5	0.021 ± 0.017	0.000 – 0.082	1.01 ± 0.05
Limnephilinae (Trichoptera)	24.2 ± 1.9	8.6 – 41.8	0.141 ± 0.027	0.009 – 0.322	1.65 ± 0.03
<i>Philoscia</i> (Isopoda)	6.7 ± 0.3	3.4 – 9.7	0.048 ± 0.005	0.011 – 0.093	0.76 ± 0.04
<i>Porcellio</i> (Isopoda)	13.2 ± 1.0	3.9 – 20.4	0.025 ± 0.005	0.000 – 0.071	1.05 ± 0.07
<i>Leptoiulus</i> (Julida)	14.1 ± 1.3	8.0 – 21.6	0.073 ± 0.015	0.001 – 0.210	0.32 ± 0.02
<i>Glomeris</i> (Glomerida)	87.1 ± 8.4	25.3 – 165.0	0.019 ± 0.005	0.000 – 0.060	2.75 ± 0.41
<i>Cylindroiulus</i> (Julida)	179.1 ± 15.9	98.2 – 296.9	0.007 ± 0.001	0.001 – 0.013	2.16 ± 0.16

Sources of variation of litter consumption rate

A linear model of log-transformed variables showed that detritivore body mass, the softness and nitrogen content of leaf litter accounted for slightly more than one third of the variability of mass-specific consumption rate ($R^2 = 0.36$, $F_{3,241} = 46.0$, $p < 0.001$, $AIC = 780.6$; [Figure III.1](#)). Litter N content had a non-significant effect ($t_1 = -0.5$, $p = 0.61$) whereas litter softness had a significant positive effect ($t_1 = 3.4$, $p < 0.001$). Given the collinearity among the two litter traits, removing litter softness from the model turns litter N content into a significant predictor of consumption rate ($t_1 = 4.7$, $p < 0.001$). However, the model without litter softness was less parsimonious ($AIC = 790.0$) than the complete model ($AIC = 780.6$) or a model with litter N removed ($AIC = 778.8$), thus hinting at the importance of litter softness as predictor of litter consumption rate.

Outcomes of the complete model sheds light on a strong negative relationship between detritivore body mass and mass-specific consumption rate ([Figure III.1](#)). The estimate for body mass effect (- 0.594) corresponded to the allometric scaling exponent which was subsequently used to calculate mass-independent rates of litter consumption (C_i).

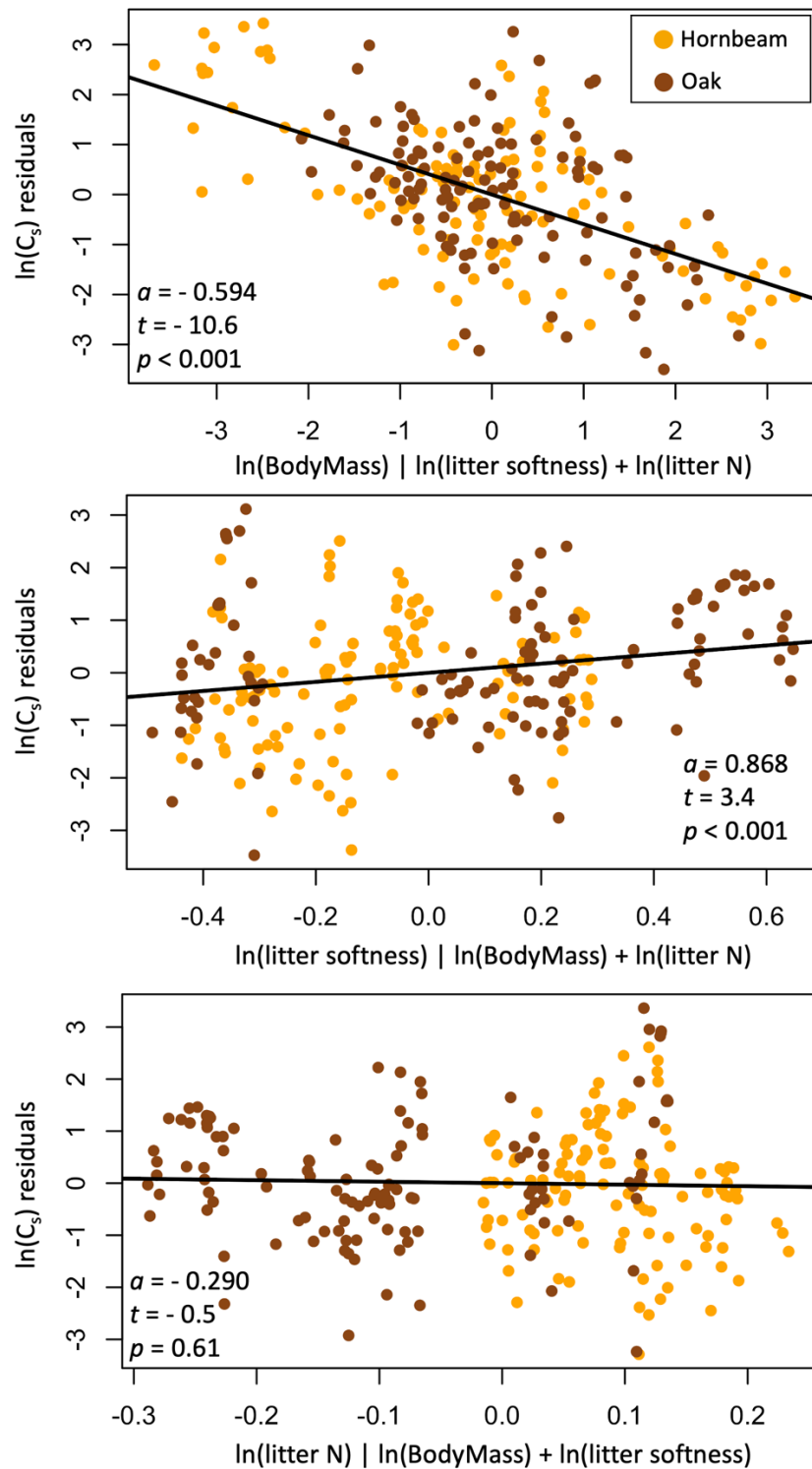


Figure III.1: Partial regression plot. Each panel presents the marginal effect of an explanatory variable (A: $\ln(\text{Body mass})$, B: $\ln(\text{litter softness})$, C: $\ln(\text{litter N})$) on the residuals of mass-specific rate of litter consumption (C_s , $\text{mg} \cdot \text{mg}^{-1} \cdot \text{d}^{-1}$) in the linear additive model. “a” is the estimate of the effect, “t” is the test statistic, and “p” is the type I error rate. Datapoints for hornbeam and oak litters are in orange and brown, respectively.

Cross-taxon variability of litter consumption rate was still apparent after removing body mass effect (Figure 2). A random effects model assessing effects of experimental factors on mass-independent consumption rate shows that detritivore taxon accounted for 14.0% of the total variance in the dataset, with [5.2 – 23.1%] 95% confidence interval. Sampling time was the most important source of variation in mass-independent consumption rate (36.3% [27.0 – 46.3%]) whereas Ecosystem type (7.3% [0.0 – 16.8%]) and Leaf species (<0.1% [0.0 – 0.0%]) were the least important. Residuals accounted for 42.3% [31.9 – 52.7%] of total variability.

Mass-independent rate of litter consumption vs. litter softness

A sigmoid function was used to describe the relationship between mass-independent consumption rate and litter softness for each detritivore taxon (Figure III.2). Although variation around the regression curve is often high, our analysis reveals consistent patterns across detritivore taxa. First, the highest values of mass-independent consumption rate for each taxon were always found for softness level above *ca.* 0.003 kPa⁻¹. In addition, as litter softness got lower, mean consumption rate tended toward zero. Second, mass-independent rate of litter consumption did not increase indefinitely and rather displayed an asymptotic behavior at the upper end of ranges of litter softness. The results for *Glomeris* stood out as an exception since a hump-shaped curve would best represent the relationship between litter softness and consumption rate.

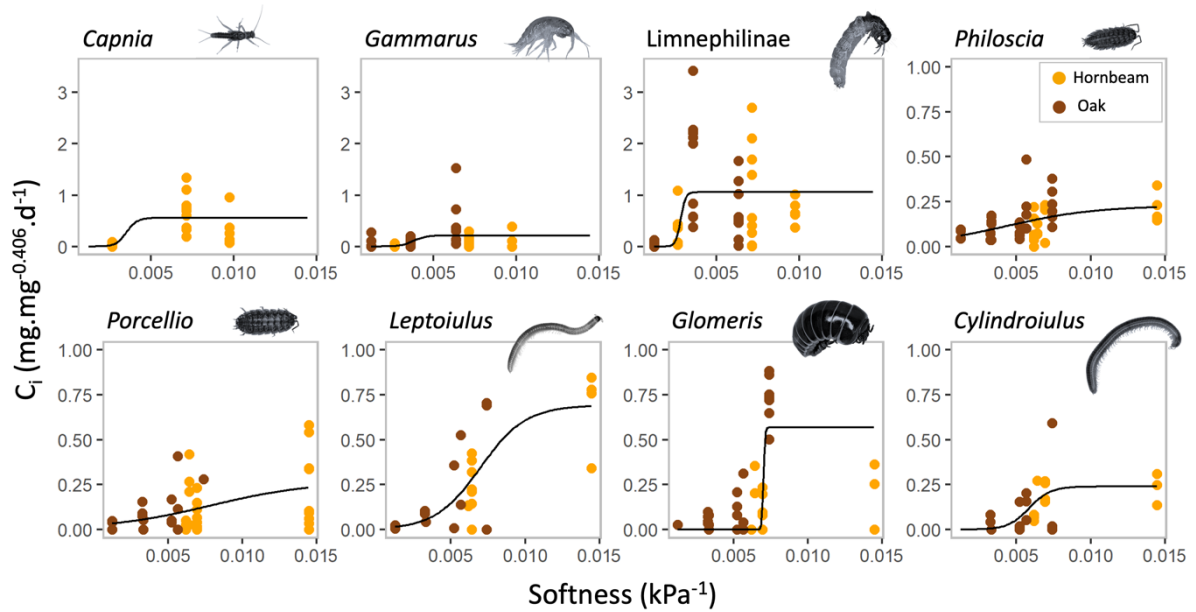


Figure III.2: Mass-independent rate of litter consumption (C_i) for each detritivore taxon with sigmoid model fit. Detritivores are ordered by increasing mean body mass, with aquatic detritivores first. Oak and Hornbeam litters are represented by brown circles and orange circles, respectively. Note that vertical scale is different for aquatic and terrestrial detritivores.

Parameter estimates of the sigmoid models are summarized in Table III.2. The scale parameter (γ) was always statistically indistinguishable from 0 ($p > 0.10$). The softness at inflexion point (β) ranged from 0.0028 to 0.078 kPa^{-1} across detritivore taxa; however, the estimates were significant or marginally significant ($p = 0.054$) for a subset of five taxa (*Gammarus*, *Limnephilinae*, *Philoscia*, *Leptoiulus* and *Cylindroiulus*). Lastly, the maximum consumption rate (α) ranged from 0.22 to 1.06 $\text{mg} \cdot \text{mg}^{-0.406} \cdot \text{d}^{-1}$. The estimates are highly significant ($p < 0.004$) for all but one taxon (*Porcellio*: $p = 0.075$). Maximum consumption rate was much greater in *Limnephilinae* than in any other taxon. The lowest values were found for *Gammarus*, *Philoscia*, *Porcellio* and *Cylindroiulus* (0.22 - 0.27 $\text{mg} \cdot \text{mg}^{-0.406} \cdot \text{d}^{-1}$).

Figure III.2 and parameter estimates for the sigmoid models (Table III.2) highlighted variable width of the transitional phase and variable steepness at the inflexion point of sigmoids. We compared the fit of the sigmoid versus a linear model for each taxon using the differences in RMSE and AIC as criteria. The sigmoid models always produced lower RMSE than linear models ($\Delta \text{RMSE} < 0$; Table III.2). The difference in AIC fell well above zero (< -1.3)

for models for *Capnia*, Limnephilinae, *Cylindroiulus* and *Glomeris* and was almost null or positive for *Gammarus*, *Philoscia*, *Porcellio* and *Leptoiulus*.

Parameter estimates for the sigmoid model were neither correlated with mean body mass ($\text{abs}(\text{Rho}_{\text{Spearman}}) < 0.43$, $p > 0.299$) nor with the biting force index ($\text{abs}(\text{Rho}_{\text{Spearman}}) < 0.36$, $p > 0.389$).

Table III.2: Coefficients of sigmoid models. Δ RMSE computes $\text{RMSE}_{\text{sigmoid model}} - \text{RMSE}_{\text{linear model}}$. Δ AIC is computed in the same way. Negative values mean that sigmoid models have less residuals than linear models. Significant ($p < 0.05$) and marginally-significant ($p < 0.076$) results are displayed in bold.

Taxon	Maximum consumption rate (α)			Softness at inflexion point (β)			Scale parameter (γ)			Δ RMSE	Δ AIC
	Estimate	SE	p	Estimate	SE	p	Estimate ($\times 10^{-3}$)	SE ($\times 10^{-3}$)	p		
<i>Capnia</i>	0.56	0.16	0.003	0.0035	1.82	0.99	0.31	664	1.00	-0.039	-2.32
<i>Gammarus</i>	0.22	0.05	<0.001	0.0038	0.001	0.001	0.37	1.87	0.84	-0.007	-0.29
Limnephilinae	1.06	0.16	<0.001	0.0028	0.001	0.054	0.14	1.15	0.90	-0.076	-6.57
<i>Philoscia</i>	0.23	0.06	<0.001	0.0043	0.002	0.029	3.04	2.00	0.14	-0.001	1.03
<i>Porcellio</i>	0.27	0.15	0.075	0.0078	0.005	0.159	3.41	4.00	0.40	-0.000	2.00
<i>Leptoiulus</i>	0.69	0.10	<0.001	0.0070	0.001	<0.001	1.51	0.94	0.12	-0.003	1.09
<i>Cylindroiulus</i>	0.24	0.07	0.001	0.0059	0.001	<0.001	0.71	0.61	0.26	-0.008	-1.35
<i>Glomeris</i>	0.57	0.10	<0.001	0.0070	0.005	0.216	0.05	3.51	0.99	-0.083	-32.21

Discussion

In this study, litter softness was a consistent predictor of litter consumption rate by detritivores. All detritivore taxa displayed poor abilities to feed on the toughest litter resources, which matches the general expectation that invertebrates do not consume resources whose mechanical resistance exceeds the biomechanical capabilities of their chewing mouthparts (Clissold, 2007). Beyond a critical threshold of litter softness, the release of biomechanical limitation should result in abrupt increase in resource consumption rate until it reaches a plateau. The upper asymptote of sigmoid curves fitted to our data provided reasonable estimates for maximum feeding rates of all but one taxon. The exception was for

Glomeris whose response to litter softness could be best described by a hump-shaped curve. However, caution should be exercised when interpreting the results for *Glomeris* because the decrease in litter consumption rate at high softness values was inherent to a few data points and there was no straightforward explanation for this trend.

There was a striking variability of the maximum rate of litter consumption across detritivore taxa. Limnephilinae outperformed others and consumed litter *ca.* 4-fold faster than the least performing taxon (*Gammarus*, *Philoscia*, *Porcellio*, *Cylindroiulus*). Such a large difference was quite unexpected as the allometric mass correction applied to litter consumption rate is assumed to remove variance in metabolic capacity (McKie et al., 2008). However, recent studies on intraspecific variability in aquatic macrodetritivores have conveyed the idea that body mass allometry fails to capture most of variation in litter consumption rate (Raffard et al., 2017; Rota et al., 2018). It is worth noting here that the exponent of the allometric scaling between detritivore body mass and litter consumption rate estimated here (0.41) was lower than the expected value of $\frac{3}{4}$ (Brown et al., 2004). This mismatch may arise due to behavioral, physiological and/or digestive adaptations of detritivores to cope with the low nutritional quality of plant litter. For instance, low food intake rate may be compensated by high energy assimilation efficiency and/or slow pace of life (and thus low energy expenditure).

Variable shape and parameters of sigmoid functions may unveil fundamental differences in foraging traits across detritivore taxa. Non-overlapping trophic niches may explain why positive complementarity effects sometimes occurred in feeding experiments involving mixed-species assemblages of detritivores (De Oliveira et al., 2010; Jonsson et al., 2002; Tonin et al., 2018). Some investigators have also noticed differences in how detritivores handle their resources as some taxa were observed to bite leaves across the full thickness whereas others tend to feed on the surface of plant litter (Danger et al., 2012; Jonsson et al., 2002; Tonin et al., 2018, Appendix [Figure S.III.3](#)). The latter foraging strategy may ensure sub-optimal exploitation of tough litter, conceivably because scraping the top layers of leaves requires less force than cutting fragments through the full-thickness of leaves. The scraping feeding strategy is thus likely to produce smoothly rising sigmoid curves for the relationship

between litter consumption rate and softness, which was observed here in more than half of detritivore taxa studied here.

The S-shaped relationships between litter softness and consumption rate with sharp threshold suggest that litter exploitation is solely ruled by the matching between the mechanical resistance of litter and the force and sharpness of detritivore mandibles. The softness value at which litter consumption rate switches from low to high (i.e. the inflexion point of sigmoid curves) is thus likely to give a good approximation of the critical pressure required for detritivore mandibles to fracture leaf litter. For sigmoid curves with the sharpest thresholds (Limnephilidae and *Glomeris*), the softness value at inflexion point ranged from 0.0028 to 0.0070 kPa⁻¹, corresponding to estimates of critical biting pressures needed to cut through the limb ranging from 143 to 357 kPa. In comparison, biting pressure greater than 500 kPa can be estimated based on published data of litter toughness and consumption rate of aquatic detritivores reported in Danger et al. (2012). These values for detritivores are *ca.* two orders of magnitude lower than direct measurement of biting pressure made on predacious carabids by Weather and Evans (1989). It is unclear whether this comparison between detritivore and predator invertebrates reveals genuine differences between trophic groups or discrepancies between methods of estimating biting pressure.

Biting pressure can be calculated as the biting force measured by means of gauge-based measurement setups (Rühr and Blanke, 2022) divided by the area of mandible tips assessed through imaging methods (Wheater and Evans, 1989). Both components are difficult to estimate accurately on the smallest invertebrates (e.g. *Capnia*); in addition, existing gauge-based measurement setups do not seem to be suitable for measuring biting force of aquatic invertebrates when kept alive in water. For these reasons, biting force was approximated here by an index calculated from biometric data (Wheater and Evans, 1989). This index did not prove useful to explain taxon-specific response of litter consumption rate to variation in litter softness. This raises the question whether the capability of detritivores to fracture leaf litter is conditioned upon a tradeoff between biting force and sharpness.

As low-digestible fibers are responsible of plant litter toughness (Graça et al., 2005) and negative relationships are expected between fibers and essential nutrients, lack of

consumption of the toughest litter may also be due to avoidance of food with low-nutritional quality by detritivores. This behavior is apparent when detritivores are offered a choice of different food items (M. A. S. Graça and Cressa, 2010; Swan and Palmer, 2006). However, our experiment was designed to minimize the impact of food avoidance on our results as detritivores were forced to feed on a single resource. In addition, detritivores were allowed to starve prior to exposure to leaf litter, so that the choice of not feeding on the offered resource came with plausible unsustainable energetic cost. Reports of compensatory feeding behavior in aquatic and terrestrial detritivores (Danger et al., 2013; Ott et al., 2012) further indicate that detritivore-litter interaction is not systematically impeded at low litter nutrient contents. We therefore believe that reported relationships between litter softness and consumption rates are more likely to reflect biomechanical than nutrient limitations.

To conclude, our findings underscore the importance of mechanical properties of plant litter in controlling feeding performance in detritivores across ecosystem types. This control can be represented by a non-linear model considering realistic mechanical constraints on feeding and yielding ecological meaningful parameters. In addition, we showed that a single set of parameters was insufficient to model the relationship between litter consumption to litter softness across all tested detritivores. Fitting separate sigmoid curves provided quantified evidence of divergent feeding modes among co-existing detritivores. Such interspecific variability was unrelated to body mass, nor the index of biting force inferred based on mandibular traits. This result conveys the idea that other feeding traits are worth considering in further studies on detritivore-litter interaction.

Authors contribution

TM, AL and BP launched the study and carried the fieldwork and laboratory experiments with the help of CP. TM and AL analyzed the data and wrote the first draft of the manuscript with the help of BP. The final version included in this manuscript was not reviewed by co-authors. They cannot be accountable for any mistake in this version.

Data archiving

Data will be archived on the Dryad depository at the time the paper accepted for publication.

Conflict of interest

The authors declare that they have no known competing interest.

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Epilogue (EN)

In line with our expectations, litter toughness (or litter softness) strongly influenced litter consumption, with a threshold effect. This threshold was different for each detritivore taxon. Yet, contrary to our expectations, we did not find any effect of detritivore traits on the characteristics of taxon-specific thresholds. These findings then confirm and precise the importance of litter toughness to explain detritivore – litter interaction. It also confirms, in line with findings of Chapter II, that trait-matching poorly applies to detritivore – litter interactions, especially when considering mechanical constraints (Figure 6). The scarce evidence for trait-matching is in line with the hypothesis that detritivores are rather generalist consumers (Figure 7, hypotheses H0, H1, or H2). The strong influence of litter toughness argues for a limitation of detritivore – litter interaction by litter properties (Figure 7, hypothesis H1). Lastly, the fact that different detritivore taxa exhibit different reactions to litter toughness argue in favor of partial trophic niche differentiation (Figure 7, hypothesis H2), even though the mechanisms of taxon-specificity remain unanswered.

Épilogue (FR)

Conformément à nos attentes, la résistance de la litière (ou sa friabilité) a fortement influencé la consommation de la litière, avec un effet seuil. Ce seuil était différent pour chaque taxon de détritivores. Cependant, contrairement à nos attentes, nous n'avons trouvé aucun effet des traits des détritivores sur les caractéristiques des seuils spécifiques à chaque taxon. Ces résultats confirment et précisent l'importance de la résistance de la litière pour expliquer l'interaction entre les détritivores et la litière. Cela confirme également, en accord avec les conclusions du chapitre II, que la concordance de traits s'applique mal aux interactions entre les détritivores et la litière, notamment lorsqu'on considère les contraintes biomécaniques (Figure 6). La rareté des indices de concordance de traits va dans le sens de l'hypothèse selon laquelle les détritivores sont plutôt des consommateurs généralistes (Figure 7, hypothèses H0, H1 ou H2). L'influence marquée de la résistance de la litière plaide en faveur d'une limitation de l'interaction entre les détritivores et la litière par les propriétés de la litière (Figure 7, hypothèse H1). Enfin, le fait que différents taxons de détritivores réagissent différemment à la résistance de la litière plaide en faveur d'une différenciation partielle des niches trophiques (Figure 7, hypothèse H2), même si les mécanismes de la spécificité taxonomique restent incompris.

CHAPTER IV

LEAF LITTER CHEMISTRY CONTRIBUTES TO SHAPE DETRITIVORE COMMUNITY'S FUNCTIONALITY

Prologue (EN)

Litter resource is nutritionally particularly poor with low macroelement content. Detritivore communities are known to depend on the local leaf litter resource, but it remains to be understood if detritivore chemical composition depends on the locally available litter. This fourth and final chapter aims to investigate whether elemental constraints could result in a match between detritivore community chemistry (i.e., elemental composition) and local litter chemistry (Figure 6). Based on the findings of Chapter II, we especially expect to find a match in phosphorus content. We studied the differences in detritivore community chemistry between pairs of sites differing by their litter. If detritivore species are only limited by their needs in macroelements (especially in phosphorus), we expect detritivore communities to be more diverse on sites with element-rich litter because there are less constraints than on element-poor litter.

Prologue (FR)

Les litières sont des ressources particulièrement pauvres sur le plan nutritionnel, avec une faible teneur en macroéléments. Les communautés de détritivores sont connues pour dépendre des ressources locales en litière de feuilles, mais le fait de savoir si la composition chimique des détritivores dépend de la litière localement disponible reste inconnu. Ce quatrième et dernier chapitre vise à déterminer si les contraintes élémentaires peuvent entraîner une concordance entre la composition chimique (la composition élémentaire) de la communauté de détritivores et la composition chimique de la litière locale (Figure 6). En nous basant sur les résultats du chapitre II, nous nous attendons en particulier à trouver une concordance liée à la teneur en phosphore. Nous avons étudié les différences dans la composition chimique des communautés de détritivores entre des paires de sites ayant une litière différente. Si les espèces de détritivores ne sont limitées que par leurs besoins en macroéléments (en particulier en phosphore), nous nous attendons à ce que les communautés de détritivores soient plus diversifiées sur les sites avec une litière riche en éléments, car il y aura moins de contraintes que sur une litière pauvre en éléments.

Leaf litter chemistry contributes to shape detritivore community's functionality

Théo Marchand¹, Matthieu Chauvat², Estelle Forey², Florence Maunoury-Danger³, Mathieu Santonja⁴, Mickaël Danger³, Philippe Usseglio-Polatera³, David Baqué¹, Frédéric Candaudap¹, Sophia Hansson¹, Frédéric Julien¹, Christophe Laplanche¹, Gaël Le Roux¹, Virginie Baldy⁴, Raphaël Gros⁴, Benjamin Pey¹

¹ Laboratoire Écologie Fonctionnelle et Environnement, Université Paul Sabatier, CNRS, Toulouse, France

² Ecodiv URA/EA-1293, Normandie Université, Université de Rouen, IRSTEA, SFR Scale 4116, UFR Sciences et Techniques, 76821 Mont Saint Aignan Cedex, France

³ Laboratoire interdisciplinaire des environnements continentaux, CNRS UMR 7360, Université de Lorraine, 8, rue du général Delestraint, 57070 Metz, France

⁴ Aix Marseille Université, Avignon Université, CNRS, IRD, IMBE, Marseille, France

Abstract

Addressing the factors responsible for community patterns is a crucial issue as it could help to better understand the relationship between biodiversity and ecosystem functioning, as well as associated ecosystem services. For example, detritivore communities have a major role in decomposition processes and associated ecosystem fluxes. Yet, litter resource is nutritionally particularly poor with low macroelement content. Detritivore communities are known to depend on the local leaf litter resource, but it remains to be understood if detritivore chemical composition depends on the locally available litter. Detritivore macroelement composition is rarely investigated and rarely confronted to litter chemical quality. Furthermore, litter elements other than carbon (C), nitrogen (N), and phosphorus (P) are rarely investigated even though huge differences in other elements (e.g., calcium (Ca), magnesium (Mg)) can occur between detritivore taxa and litter types.

To investigate whether macrodetritivore community chemistry depends on litter chemistry, we sampled pairs of forest sites solely differing by their litter chemical composition.

On each site, we quantitatively sampled litter transformers (Diplopoda and Isopoda) to estimate their abundance. For each morphospecies, we measured mean individual body mass and analyzed their main macroelement content for C, N, P, K, Ca, and Mg. We also analyzed the same macroelements in the dominant litter of each site. We tested if detritivore community taxonomic diversity, chemical diversity, biomass, and abundance were influenced by litter chemistry. We also tested if detritivores were influenced by litter quality at the Order and the morphospecies levels.

At the community level, detritivore chemical diversity was higher on sites with high-quality litter, with changes in P and Mg content. Detritivore Orders were not strongly impacted by litter chemistry. Only abundances tended to be higher on high-quality sites. Morphospecies abundance, body mass, and chemistry showed no differences with litter chemistry.

Our findings indicate that litter chemistry influences the chemical footprint of detritivore communities. This effect is limited and may be due to changes in detritivore abundance. Morphospecies complied with the homeostasis hypothesis, indicating no physiological adaptations.

Keywords: Functional indexes, Population, Morphospecies, Bottom-up effect, Traits, Stoichiometry

















	Hypotheses		Results	
Litter	 Low quality	Macroelement (N, P, K, Ca, Mg) content ↗	 High quality	✓ For N, P, Mg
↓ Morphospecies		Abundance ↗		Trend
		Body mass ↗		✗
		Body chemistry differs		✗
↓ Community		Chemical diversity ↗		✓
		Taxonomic diversity ↗		Trend
		Community and litter chemistry match		Trend for P and Mg
		Detritivores with higher elemental content differ more		✗

Figure IV.0: Graphical abstract. Hypotheses about expected differences in detritivore communities depending on low-quality litter (low element content, on the left) versus high-quality litter (high element content, on the right). The hypotheses depend on the assumption that detritivores growth (body mass), fitness (abundance) and body chemistry are influenced by the local litter quality. Small arrows indicate that the corresponding variable is expected to increase with high-quality litter.

Introduction

During the last decades, community ecology tried to address the factors responsible for observed community patterns. It is a crucial issue as it could help to better understand the relationship between biodiversity and ecosystem functioning, as well as associated ecosystem services (Brussaard, 2012; Diamond, 1975). It was notably addressed whether community structuration is stochastic or governed by assembly rules (Connor and Simberloff, 1979; Diamond, 1975; Ulrich, 2004). In the view of community structuration governed by assembly rules, a great body of literature underlined the role of several environmental filters. These filters may act at different levels of organization (such as biogeographical and historical constraints at the biogeographical level, or biotic interactions at the community level) (Belyea and Lancaster, 1999; Decaëns et al., 2008). To explore those questions, trait-based approach has recently been favoured because traits inform organismal biological functioning. This approach is able to better explain underlying assembly mechanisms than taxonomy per se (Decaëns et al., 2008; McGill et al., 2006; Pey et al., 2014).

Detritivore communities are of particular importance as they have a major role in decomposition processes and associated ecosystem flux (David, 2014; García-Palacios et al., 2013). They also are at the basis of brown trophic food chains (Gessner et al., 2010). Moreover, most detritivores have limited dispersion capacities (Gongalsky and Persson, 2013). Individuals then must cope with their local litter resources. Litter improves the physical properties of detritivore habitats by improving water storage and offering a complex structure that isolates them from predators and abiotic parameter fluctuations (such as temperature) (David, 2014). Yet, this resource is nutritionally particularly poor compared to other plant resources (Li et al., 2021). Litter has notably low macroelement content which can critically impact decomposition and consumption by detritivores. Consequently, it may affect detritivore development and fitness (David and Gillon, 2009; Zimmer and Topp, 1997). From this point of view, nitrogen (N) and phosphorus (P) have been particularly investigated (Evans-White and Halvorson, 2017; Hättenschwiler et al., 2005). Leaf litter macroelement content first depends on tree species (Li et al., 2021), but also on physical and microbial agents during decomposition. Physical and microbial agents generally decrease chemical deterrents and increase macroelement concentration over time (Hättenschwiler et al., 2005). A high

macroelement content is generally associated to a high quality and a high decomposition and consumption rate (Evans-White and Halvorson, 2017; Hättenschwiler et al., 2005).

A gap between the elemental composition of a consumer and its resource may lead to body growth constraints (Sterner and Elser, 2017). When confronted to a gap between the elemental content of its resource and its own, a detritivore individual can adopt different strategies. It could adopt behavioral strategies such as compensation by increasing its feeding or assimilation rate (Jochum et al., 2017). It could also compensate its main food resource with another more nutrient-rich one (Crenier et al., 2017). It could also potentially adopt physiological strategies such as flexible homeostasis (i.e. a change in body chemical composition) (Cross et al., 2005; Small and Pringle, 2010; Tagliaferro et al., 2021). Yet, this latter strategy would deviate from the mainstream hypothesis of strict homeostasis which postulates that the chemical composition of an individual does not depend on its resource or its environment and does not change over time (Sterner and Elser, 2017). Detritivores could also reduce their growth and reproduction to compensate for limited macroelements (Rushton and Hassall, 1983; Zimmer and Topp, 1997).

A gap between the elemental content of resources and detritivores could also impact detritivores at higher organization levels (species, community). For a given species, population abundances and biomass can vary depending on how well the individuals survive, grow and reproduce on a given litter (Ott et al., 2014). At the community level, other types of mechanisms operate. First, detritivore species could interact, leading to competition for the highest-quality resource, or to facilitation mechanisms (Coulis et al., 2015; Hedde et al., 2010). It could result in a bottom-up control of the whole soil food web and impact other trophic levels such as predators (Marjakangas et al., 2022). All the above-mentioned mechanisms could lead to spatial segregation of detritivore species, with some species being unable to survive on a poor local resource (David et al., 2023; Ott et al., 2014).

Detritivore communities are known to depend on the local leaf litter resource. For example, macrodetritivore species richness increases with litter diversity (David et al., 2023). Detritivore biomass can also be influenced by litter chemistry (Ott et al., 2014). Yet, it remains to be known if detritivore communities chemically match their local litter chemistry. To our

knowledge, detritivore macroelement composition is rarely investigated (Zhang et al., 2022). When investigated, detritivore macroelement composition is not confronted with litter chemical quality. Furthermore, litter elements other than C, N, and P are rarely investigated even though huge differences in other elements (e.g. Ca, Mg) can occur between detritivore taxa (Zhang et al., 2022) and litter types (García-Palacios et al., 2016).

Here, we investigated whether macrodetritivore community chemistry depends on litter chemical quality (i.e., on litter macroelement contents). Detritivore community chemistry can be conceptually defined as the sum of each species' chemistry, pondered by their abundance and body mass:

$$\text{Community chemistry} = \sum_{sp} \text{Abundance}_{sp} * \text{MeanBodyMass}_{sp} * \text{Chemistry}_{sp} \quad (1)$$

Changes in community chemistry can be due to a change in one or more of these parameters. To answer this question, we selected pairs of forest sites differing by their litter chemical quality. On each site, we characterized the detritivore community by focusing on "litter transformers" (Diplopoda and Isopoda) (Lavelle and Spain, 2001; Wardle, 2002). We focused on these taxon because they constitute a homogeneous group among soil fauna whose diet quasi-exclusively relies on litter material (David, 2014). We quantitatively sampled these detritivores to estimate the abundance of each morphospecies. We also analyzed their main macroelement content for carbon (C), nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) (Zhang et al., 2022). Finally, we assessed morphospecies mean individual body mass.

First, we tested if litter chemical quality influenced detritivore community abundance, biomass, taxonomy, and chemistry (H1). We expected the presence of some morphospecies to change with litter chemical quality (e.g., morphospecies with high elemental needs may be found only on litter with high chemical quality). If some morphospecies depends on litter chemical quality, we expect to find much more morphospecies (investigated with morphospecies number) with potentially different abundance distributions (investigated with Shannon-Wiener index) on sites with high litter chemical quality. Furthermore, if low-quality litter excludes some morphospecies, we expect the range of morphospecies with contrasted chemical needs to be higher on sites with high-quality litter, associated with potentially different abundance and biomass distributions (investigated with Community Weighted

Means: CWMs, FDis and RaoQ indexes. FRic was not tested because of limited numbers of species per site).

If H1 were to be totally or partially validated, we aimed to investigate the underlying patterns explaining changes in community chemistry. For this, we tried to explain, as far as the data allow us to test for it, which parameters of the equation (1) explained this change and at which level of organization (Order or morphospecies levels). We then investigated if litter quality influenced the abundance, biomass, and chemistry of different detritivore taxa at the Order and morphospecies levels (H2). If morphospecies better perform on high-quality litter, the abundance, mean individual body mass, and total biomass may be higher on sites with high-quality litter. Yet, we expect morphospecies mean body mass not to change with litter quality if it depends more on the morphospecies identity than on the available resource. Finally, under the homeostasis hypothesis, morphospecies chemistry should not change with litter quality. Under the assumption that detritivore elemental composition reflects elemental needs, we tested if differences in morphospecies abundance with litter quality are influenced by detritivore chemistry.

All the upper assumptions were proposed assuming that competition for the resource is limited and does not exclude less competitive species.

Material and Method

Sites

To assess the effect of litter chemistry only and to limit the effects of other environmental filters acting on the community (such as biogeographical and pedo-climatic contexts), we chose to study 12 pairs of forest sites. Each pair comprised two sites close to each other (< 1km) with highly contrasted leaf litter (low vs high *a priori* quality) in the same pedo-climatic context. We selected sites having a uniform or dominant leaf litter species with a homogenous topography. We selected at least two pairs of sites in each of five different French regions (Pyrenean piedmont, Montagne Noire, Luberon, Vosges, Normandie) to be representative of a diversity of pedo-climatic contexts (Appendix, [Table S.IV.1](#)). By strongly limiting the effects of pedoclimatic context on community assemblage, even a weak difference between sites should be meaningful. Plus, using multiple pairs of sites across a diversity of pedoclimatic contexts allows us to observe general patterns.

Soil and litter sampling and analyses

We sampled soil and litter in the fall. On each site, we pooled 5 samples of soil collected with a corer. Soils were then air-dried, aggregates were gently broken by hand and sieved to 2 mm. Granulometry, pH, organic matter, nitrogen, phosphorus, and Cation Exchange Capacity (CEC) were analyzed by the SADEF laboratory (Aspach-Le-Bas, 68700, FRANCE). We collected freshly-fallen dead leaves and air-dried them. Leaves belonged to 9 species from 3 different families: *Alnus glutinosa*, *Betula pendula*, *Carpinus betulus*, *Corylus avellana* (Betulaceae), *Fagus sylvatica*, *Quercus ilex*, *Quercus petraea*, *Quercus pubescens* (Fagaceae), *Fraxinus excelsior* (Oleaceae). Only *Q. ilex* had a different phenology because abscission happens in spring. For pairs of sites with *Q. ilex* (Luberon sites), litter was then collected in spring, at the same time as fauna sampling.

Fauna

On each site, we sampled detritivores in spring by hand-sorting all macrodetritivore individuals from 5 soil blocs of 25 x 25 x 25 cm³ including litter. On the sites in Les Vosges, we extracted only 3 soil blocs because the sites were smaller. To have spatially independent samplings, soil blocs were at least 10 m away from each other. To avoid border effects, soil blocs were at least 10 m away from the boundaries of the site. Individuals were assigned to coarse morphospecies and counted for total abundance assessment (Appendix, [Table S.IV.4](#)). The abundance and taxonomy indexes were computed with only quantitative bloc sampling data. Additional detritivore individuals were sight-hunted on the whole site to ensure sufficient material for chemical analysis. Mean body mass and chemical composition were computed by also taking into account sight-hunted individuals. We focused on detritivore morphospecies belonging to 4 different orders and 2 different Classes: Glomerida, Julida, Polydesmida (Diplopoda), and Isopoda (Malacostraca). Detritivores were kept alive in cool plastic boxes and brought back to the laboratory. There, detritivores were sorted by morphospecies, placed in plastic boxes without litter, and kept for the night to purge to avoid intestinal contamination of chemical analyses. Individuals were placed in a freezer until being defrosted for chemical analyses.

Chemical analyses

We cleaned detritivores with milliQ water, dried them at 45°C for 4 days, weighed them to the nearest 0.1 mg, and pooled them into samples for chemical analyses. Each sample contained more than 20 mg of cumulated dry body mass and more than 2 individuals. For each morphospecies on each site, if we had sufficient analysis material, we performed two samples to have two analysis replicates. We ground samples into powder with a bead mill (FastPrep-24™ Classic Instrument). We quantified carbon (C) and nitrogen (N) content from a subsample of powder, using a Total nitrogen and Organic Carbon analyzer (TOC L, Shimadzu). We quantified phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) content in a subsample of powder, with an Induced Coupled Plasma – Mass Spectrometer (ICP-MS). For ICP-MS analyses, about 5 mg of dry powder was digested with 0.5 mL of 63-67 % nitric acid during one night at 95°C. The next morning, 10 (if the initial sample mass was below 4 mg) or 15 mL of milliQ water was added. Digestion was performed in a white room with over-pressurization, to avoid contamination. We also performed control (without powder) samples and used reference materials (Dogfish liver DOLT-3 and river prawn PRON-1) to control for data quality. Litter chemistry was analyzed following a similar procedure, with 4 analysis replicates of the litter of each site. We used apple leaf (NIST 1515), peach leaf (NIST 1547), and lichen (IAEA 336) as reference materials. All powder weightings were performed to the nearest 0.001 mg.

Statistical analyses

To rigorously compare results between sites of each pair, we computed delta indexes as follows:

$$\Delta = \frac{Index_{HighQualityLitter} - Index_{LowQualityLitter}}{Index_{HighQualityLitter} + Index_{LowQualityLitter}}. \Delta \text{ can take values between } -1 \text{ (} Index_{HighQualityLitter} =$$

0) and 1 (Index_{LowQualityLitter} = 0). $\Delta = 0$ when $Index_{HighQualityLitter} = Index_{LowQualityLitter}$. We then tested if Δ significantly differed from zero with a t-test. When multiple Δ indexes were tested, we applied the Benjamini & Hochberg (1995) correction to t-tests. When Δ values differed from normality distribution, we also used a non-parametric Wilcoxon test. All analyses were performed with R version 4.0.3.

To test if litter parameters differed between sites of each pair, we computed Δ indexes for litter C, N, P, K, Ca, and Mg content (Figure IV.1). To test if soil parameters differed between sites of each pair, we computed Δ indexes for soil sand, silt, loam, pH, CEC, Organic matter, P, and N content.

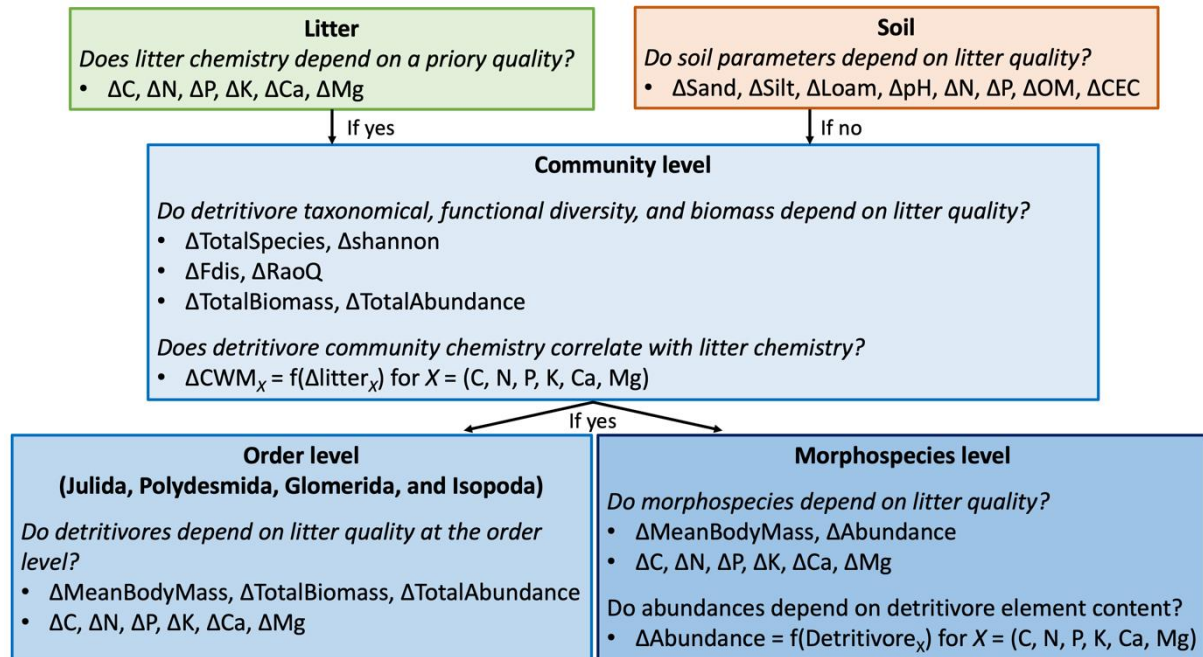


Figure IV.1: Articulation of the different questions investigated, and the variables tested for each question. Detritivore taxonomy and abundance indexes were computed with quantitative blocs sampling. Detritivore mean body mass and chemistry were computed by also taking into account sight-hunted individuals. Differences in litter chemistry validate the choice of litter species and their attribution to “high quality” and “low quality” litter (Figure IV.2B). The homogeneity of soil parameters supports the design trying to minimize pedo-climatic influences on detritivores (Appendix, Figure S.IV.2).

To investigate the amount of variability in detritivore chemistry that is explained by different factors, we applied the variance analysis method described by Messier et al. (2010). For each X element (C, N, P, K, Ca, and Mg), we performed a linear mixed model explaining the element content in all Sp morphospecies on each site, with *Region*, *Pair of sites*, *LitterQuality*, *Detritivore Order*, and *Morphospecies* as imbricated random factors (*lme* function from the *nlme* package: $X_{sp} \sim 1$, random = ~ 1 | *Region* / *PaireSite* / *LitterQuality* /

DetritivoreOrder / Sp). The variability explained by each imbricated random factor was then extracted with the *varcomp* function from the *ape* package.

To investigate the elements that could be the most limiting, we computed the elemental ratio between each detritivore morphospecies content on each site and its corresponding litter content, for each C, N, P, K, Ca, and Mg element. An element with a high ratio indicates that this element may be limiting.

To test if litter quality influenced detritivore community taxonomic indices, we computed the number of morphospecies, and the Shannon-Wiener index on each site. To test if litter quality influenced detritivore functional diversity based on chemistry, we computed the FDis and RaoQ indexes, community total biomass, and community total abundance on each site. For detritivore functional diversity, we computed the FDis and RaoQ indexes (with the *FD* package on the R software) with C, N, P, K, Ca, and Mg traits, pondered by abundance multiplied by mean body mass for each site. To study detritivore community biomass and to disentangle effects between biomass and abundance, we computed total abundance and total detritivore biomass ($\text{TotalBiomass} = \sum_{sp} \text{Abundance}_{sp} * \text{MeanBodyMass}_{sp}$) on each site. Mean body mass was computed as the mean individual body mass value for each morphospecies on each site, also taking into account sight-hunted individuals. For each index, we computed Δ values as above.

To test if litter chemistry matched detritivore community chemistry, we computed Community Weighted Means (CWM) indexes as follows:

$$\text{CWM}_X = \frac{\sum_{sp} \text{Abundance}_{sp} * \text{BodyMass}_{sp} * X_{sp}}{\sum_{sp} \text{Abundance}_{sp} * \text{BodyMass}_{sp}}$$
 for the content of X element in each sp morphospecies

on each site. For each C, N, P, K, Ca, and Mg element, we tested for a linear correlation between the Δ CWM index and the Δ index of litter content of the corresponding element.

To test if different detritivore orders were differently impacted by litter quality, we investigated differences in Julida, Glomerida, Polydesmida, and Isopoda taxa between the sites of each pair. For each taxon, we computed Δ indexes for total abundance, total biomass, and mean body mass. For each taxon, we also tested if Δ indexes of mean C, N, P, K, Ca, and Mg content (taking into account detritivores with abundance = 0 if their chemistry had been analyzed) significantly differed from zero.

To test for detritivore homeostasis, we computed Δ indexes of detritivore chemistry (for C, N, P, K, Ca, and Mg elements) for each morphospecies that was found on both sites of each pair and for which chemistry was analyzed. To test if the abundance and the mean body mass of morphospecies depended on litter quality, we computed Δ indexes of detritivore abundance and mean body mass for each morphospecies on both sites of each pair. To test if Δ Abundance depends on detritivore chemistry (i.e., if the abundance of morphospecies with high macroelement content is more impacted by litter quality), we tested the linear correlation between Δ Abundance and mean elemental content of each detritivore morphospecies on both sites (for C, N, P, K, Ca, and Mg elements).

Results

Soil and litter parameters

Mean litter composition was (mean \pm se) 46.36 ± 0.27 % C, 1.28 ± 0.08 % Ca, 1.22 ± 0.06 % N, 0.47 ± 0.04 % K, 0.18 ± 0.01 % Mg, and 0.09 ± 0.01 % P (See also Appendix, [Table S.IV.3](#)). Litter chemical composition significantly differed between the sites of each pair, with C content being lower, and N, P, and Mg contents being higher in the *a priori* high-quality litter ([Figure IV.2B](#), Appendix [Figure S.IV.1](#)). Soil parameters did not differ between sites of each pair ($\text{abs}(t) < 1.35$, $\text{df} = 11$, $p > 0.204$), except for P content which was slightly higher in sites with a high-quality litter ($t = 2.77$, $\text{df} = 11$, $p = 0.018$, $p.\text{corrected} = 0.145$) (Appendix, [Figure S.IV.2](#)).

Detritivore communities

Over the 5 pedo-climatic regions and the 12 pairs of sites, we collected 553 detritivore individuals in soil blocs. Detritivore communities ranged from 0 individual (3 sites in the Pyrenean piemond) to 134 individuals belonging to 4 orders and 9 species (in a site in Luberon with *Q. pubescens* litter) (Appendix, [Table S.IV.4](#)). Luberon sites exhibited especially high abundances, all taxa combined. To characterize detritivores, we performed 160 CN analyses, 153 ICP analyses, and measured the body mass of 1281 individuals. Mean detritivore composition was (mean \pm se) 33.56 ± 0.47 % C, 9.46 ± 0.34 % Ca, 5.97 ± 0.15 % N, 1.56 ± 0.04 % P, 0.55 ± 0.02 % K, and 0.30 ± 0.01 % Mg (Appendix, [Table S.IV.2](#)).

According to linear mixed models, detritivore composition was mostly due to the Order to which they belong (mean \pm se for C, N, P, K, Ca, and Mg elements combined: 46.8 ± 10.4 % of variability), then to morphospecies identity (39.6 ± 7.9 %), region (8.1 ± 3.0 %), pair of sites (4.2 ± 2.7 %), and litter quality (0.5 ± 0.5 %). Residuals accounted for 0.8 ± 0.8 % of the variability. The Order level was the first parameter explaining element content (See also Appendix, [Figure S.IV.3](#) and [Table S.IV.2](#)), except for C and Ca elements for which morphospecies was the first parameter (71.3 and 49.5 % of variability explained, respectively). For these two elements, Order level was only the second factor explaining variability (18.0 and 18.9 % of variability explained, respectively).

In most cases (78 out of 90), P was the element with the highest ratio between detritivore morphospecies and the corresponding litter. Over the entire dataset, the mean P ratio was 23.9 ± 1.2 , meaning that P content was on average 23.9 times higher in detritivores than in the corresponding litter. The Mean Ca ratio was 10.9 ± 0.6 , and only displayed the highest ratio on 11 occasions, always on sites in the Vosges region. Mean N, Mg, K, and C ratios were 4.8 ± 0.2 , 2.1 ± 0.1 , 1.9 ± 0.2 , and 0.7 ± 0.0 , respectively.

Communities' taxonomic diversity did not differ with litter quality for the total number of species. The Shannon-Wiener index only slightly differed with litter quality (Figure 2A). Both indexes exhibited generally higher values in sites with high-quality litter. Communities' total biomass and abundance did not significantly differ with litter quality. Yet, both indexes were generally higher in sites with high-quality litter. Chemical diversity at the community level significantly differed with litter quality. If sites with high-quality litter support a higher diversity of species, we expect FDis and RaoQ indexes to be higher on high-quality litter sites, compared to low-quality litter sites. Both FDis and RaoQ indexes were indeed significantly higher in sites with high-quality litter.

To investigate whether chemistry matched detritivore community chemistry, we tested for each X element if ΔCWM_X correlated with ΔLitter_X . The correlation was significant for Mg element (Table 1) and slightly significant for P. In both correlations, ΔCWM increased with ΔLitter .

Table IV.1: Linear correlations between Δ CWM and Δ Litter content for each element.

Element	F_{1,7}	Slope	R²	p-value	p-corrected
C	0.00	-0.06 ± 1.18	0.00	0.959	0.959
N	0.55	-0.09 ± 0.11	0.07	0.481	0.577
P	7.80	0.59 ± 0.21	0.53	0.027	0.081
K	1.49	0.27 ± 0.22	0.18	0.262	0.393
Ca	3.83	0.27 ± 0.14	0.35	0.091	0.182
Mg	28.38	0.75 ± 0.14	0.80	0.001	0.006

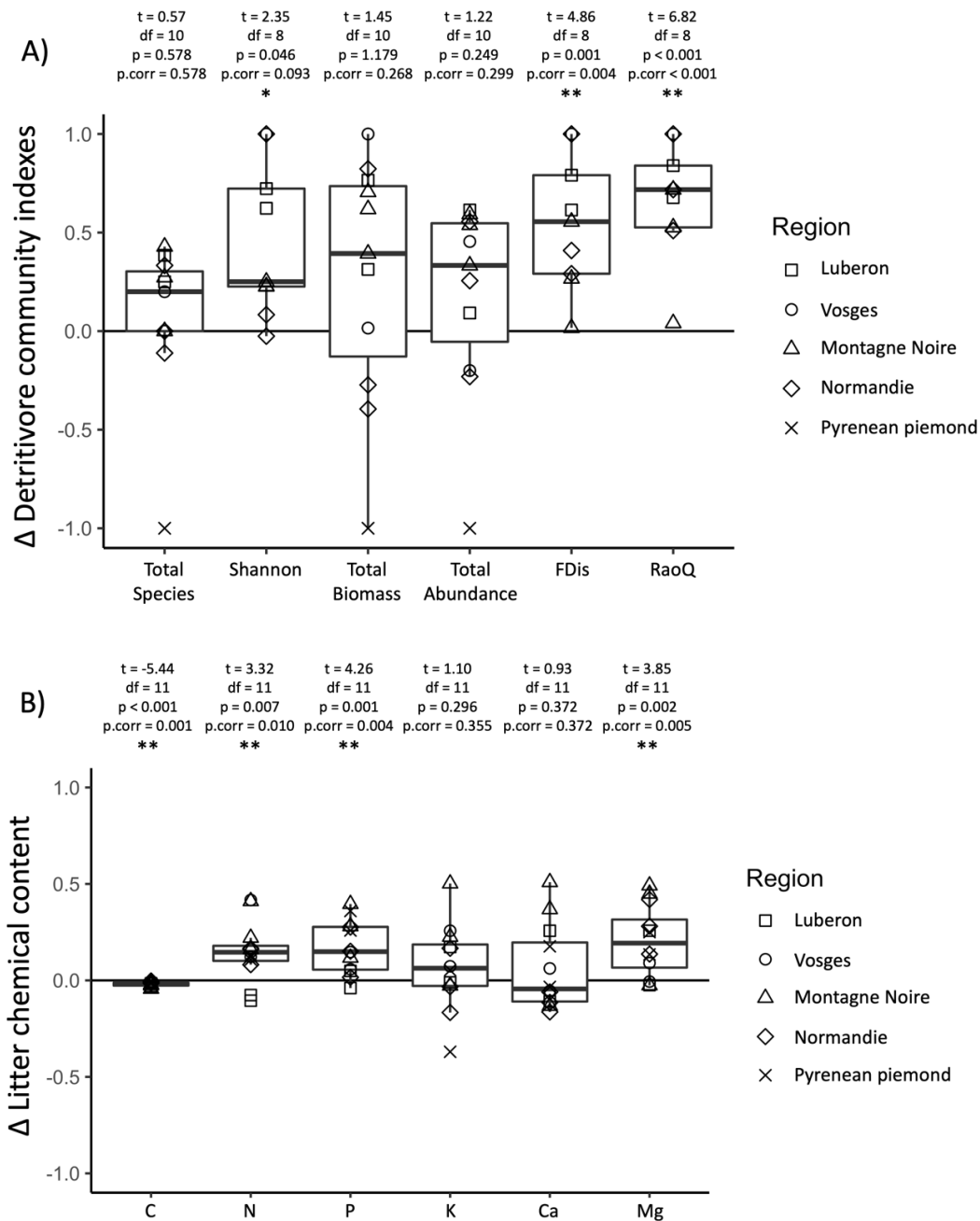


Figure IV.2: Δ indexes (differences between both sites of each pair) for (A) detritivore community metrics, and (B) Litter chemical composition. For each index, a t-test was performed to test if Δ values significantly differed from zero. A Δ value above zero indicates that the corresponding metric has a higher value on the site with a high-quality litter than on the corresponding site of the same pair with a low-quality litter. T-value (t), degree of freedom (df), p-value (p), and corrected p-value (p.corr) are indicated. One asterisk (*) indicates that the non-corrected p-value is < 0.05 and that the corresponding corrected p-value is ≤ 0.05 . Two asterisks (**) indicate that both p-values are < 0.05 . Each pedo-climatic region is indicated by a symbol.

Detritivore orders and morphospecies

To test if different detritivore orders were differently impacted by litter quality, we investigated Δ MeanBodyMass, Δ TotalBiomass, and Δ Abundance. Δ MeanBodyMass never significantly differed from zero. All orders exhibited higher TotalBiomass and Abundances in sites with high-quality litter, but this trend was slightly significant only for Glomerida (i.e., the non-corrected p-value was below 0.05 and the corrected p-value was above this threshold). As Glomerida Δ TotalBiomass and Δ Abundance distribution did not meet the normality assumption because of the low number of individuals, we also performed Wilcoxon tests. Neither of these parameters was significant with this non-parametric test ($V \leq 31$, $p \geq 0.060$). Similarly, for Polydesmida, no parameter was significant with Wilcoxon tests ($p \geq 0.299$).

To test if the chemistry of detritivores orders was differently impacted by litter quality, we tested Δ C, Δ N, Δ P, Δ K, Δ Ca, and Δ Mg for each detritivore order (See also Appendix, [Figure S.IV.4](#)). No Δ index was significantly different from zero for Isopoda ($\text{abs}(t) \leq 1.13$, $\text{df} = 8$, $p \geq 0.290$), Julida ($\text{abs}(t) \leq 1.15$, $\text{df} = 8$, $p \geq 0.285$), and Glomerida ($\text{abs}(t) \leq 1.53$, $\text{df} = 7$, $p \geq 0.169$). For Polydesmida, only Δ N was slightly significantly different from zero ($t = -3.55$, $\text{df} = 3$, $p\text{-value} = 0.038$; $p\text{-corrected} = 0.228$; $p_{\text{Wilcoxon}} = 0.125$). Other Δ indexes for Polydesmida were not significantly different from zero ($\text{abs}(t) \leq 2.23$, $\text{df} = 3$, $p \geq 0.112$).

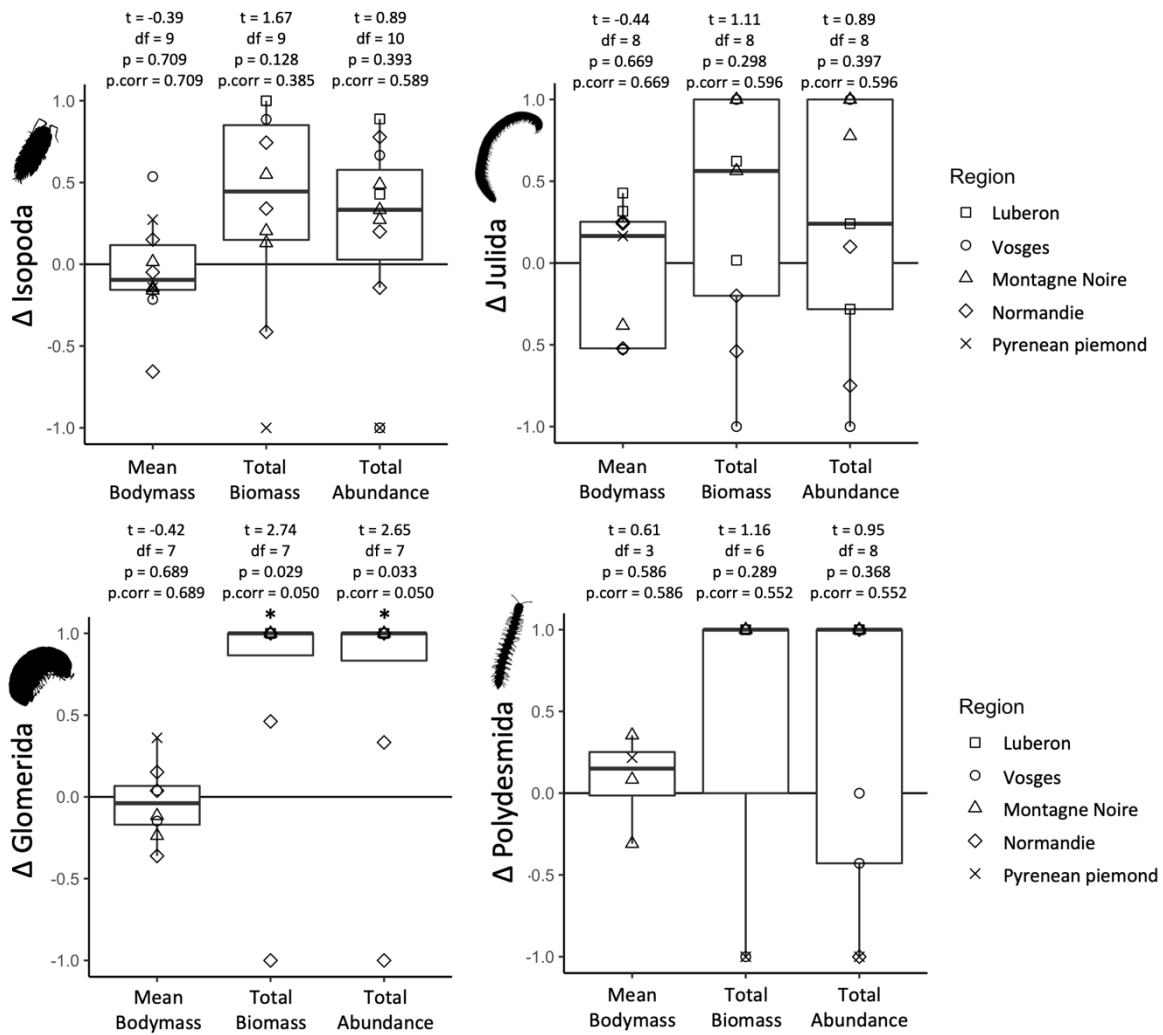


Figure IV.3: Δ indexes (differences between both sites of each pair) for Isopoda, Julida, Glomerida, and Polydesmida taxa. For each index, a t-test was performed to test if Δ values significantly differed from zero. A Δ value above zero indicates that the corresponding metric has a higher value on the site with a high-quality litter than on the corresponding site of the same pair with a low-quality litter. T-value (t), degree of freedom (df), p-value (p), and corrected p-value (p.corr) are indicated. One asterisk (*) indicates that the non-corrected p-value is < 0.05 and that the corresponding corrected p-value is ≤ 0.05 . Each pedo-climatic region is indicated by a symbol.

Overall, Δ indexes for detritivore morphospecies chemistry were not significantly different from zero for ΔC , ΔN ($\text{abs}(t) \leq 1.59$, $\text{df} = 35$, $p \geq 0.121$), nor for ΔP , ΔK , ΔCa , and ΔMg ($\text{abs}(t) \leq 1.42$, $\text{df} = 34$, $p \geq 0.166$) (Figure 4). Similarly, detritivore morphospecies exhibited no difference in mean body mass with litter quality ($t = 0.08$, $\text{df} = 34$, $p = 0.939$). Lastly,

Δ Abundance for all morphospecies found on both sites of each pair was not significantly different from zero ($t = 1.85$, $df = 24$, $p = 0.076$) even though abundance showed a trend for higher values on sites with high-quality litter. To test if Δ Abundance depended on detritivore chemistry, we tested the linear correlation between Δ Abundance and the mean elemental content of each detritivore morphospecies on both sites. Δ Abundance correlated with no detritivore element content ($F_{1,31} \leq 1.12$, $R^2 \leq 0.03$, $p \geq 0.297$).

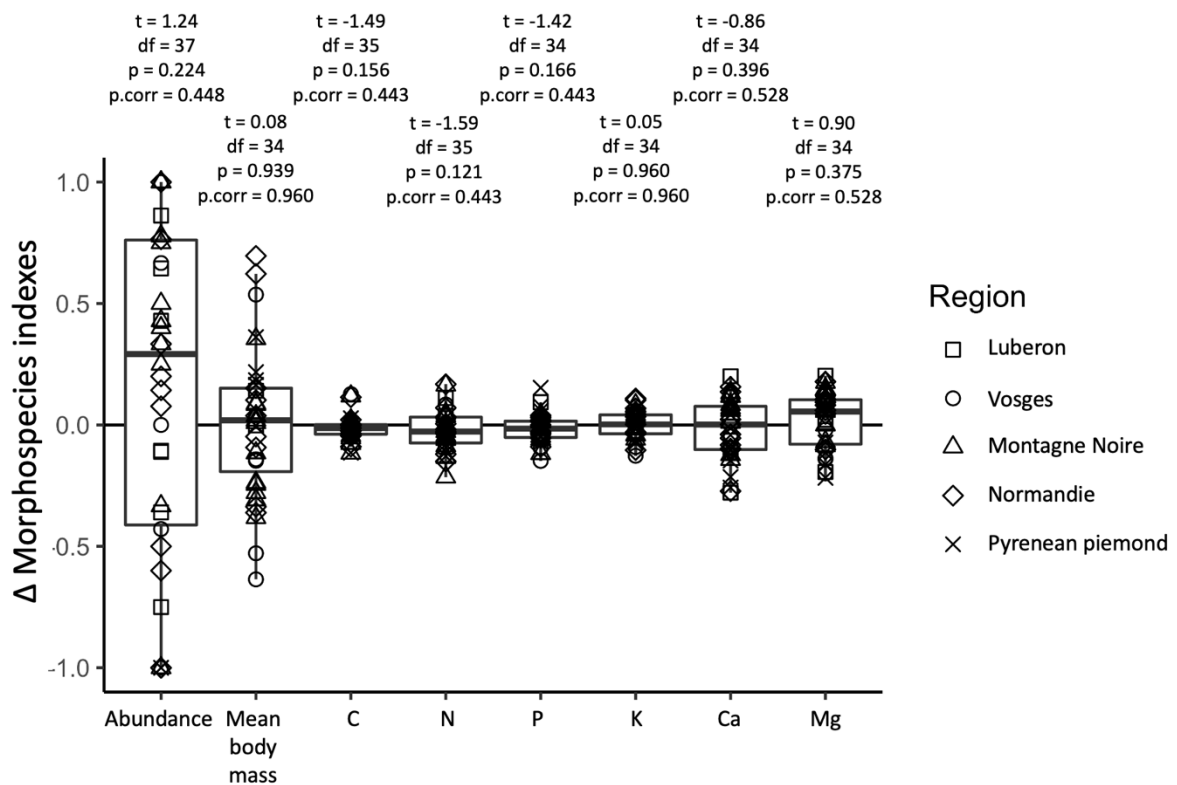


Figure IV.4: Δ of metrics at the morphospecies level. Here, metrics compare morphospecies that were found on both sites of each pair. Body mass and element content was also measured with additional sight-hunted individuals, which explains the lowest number of data points for “Abundance”. For each index, a t-test was performed to test if Deltas values significantly differed from zero. A Δ value above zero indicates that the corresponding metric has a higher value on the site with a high-quality litter than on the corresponding site of the same pair with a low-quality litter. T-value (t), degree of freedom (df), p-value (p), and corrected p-value ($p.corr$) are indicated. Each pedo-climatic region is indicated by a symbol.

Discussion

In this study, we showed that detritivore communities are slightly influenced by litter chemical quality. At the community level, we found that detritivore chemical diversity is higher on sites with high-quality litter. The difference of P and Mg Community Weighted Mean (CWM) content between sites of each pair increased with the difference of litter P and Mg content, respectively. At the Order level, we found little influence of litter quality on abundance, biomass, and body mass. At the morphospecies level, we found no significant influence of litter quality on abundance, body mass, and body chemistry. At all levels, abundance and total biomass showed the same consistent trend with higher values on sites with high-quality litter. As mean individual body mass was not influenced by litter quality, abundance seems to be the main driver of community chemical change. Differences in communities' chemical diversity may be due to the sum of non-significant or slightly significant differences in species abundances and species turnover.

Our experiment was designed to minimize the influence of pedo-climatic variables on detritivores community assemblages, to isolate as much as possible the effect of litter chemistry. Litter chemistry was significantly different between *a priori* high-quality and low-quality litter (Figure IV.2B, Appendix Figure S.IV.1) which is a prerequisite to test for its effects on detritivore chemistry. Yet, differences in tree vegetation between pairwise sites could result from different long-term forest management and such differences could also impact detritivore communities, for example by modifying microhabitats such as woody debris (Topp et al., 2006). Detritivore communities might also be indirectly influenced by some soil parameters we did not consider such as soil humidity (David and Handa, 2010). Nevertheless, as a whole, the soil parameters we measured were not significantly different between the two sites of each pair (Appendix, Figure S.IV.2). Only soil P content was slightly different (the non-corrected p-value was below 0.05 while the corrected p-value was above this threshold). This trend for soil P content might be linked to litter P content (Capellesso et al., 2016). Plants growing on P-rich soil may have P-rich senescent leaves (Hofmann et al., 2016). Finally, direct or indirect biotic interactions between detritivores and other biological actors (predators, competitors, pathogens...) could also influence detritivore communities (Baker, 1985; Wu et al., 2014; Zimmer et al., 2005). However, we assume that differences in biotic interactions

between sites were limited as sites were in a similar pedoclimatic and topographical context. Furthermore, such differences in biotic interactions could be partly due to resource-driven processes, i.e., to changes in litter chemical quality (Marjakangas et al., 2022).

We are then confident that using pairs of sites allowed us to isolate the effect of litter chemical quality. By strongly limiting the effects of pedoclimatic context on community assemblages, even the weak differences observed between sites should be meaningful. Furthermore, using multiple pairs of sites across a diversity of pedoclimatic contexts indicate that the patterns we observed are generic.

At the community level, litter quality influenced detritivore chemical diversity (Figure IV.2A). Taxonomic diversity was only slightly influenced. Detritivore total biomass and abundance were not significantly influenced by litter quality, even though both parameters showed a trend for higher values on high-quality litter sites. The total number of morphospecies was not significantly influenced even though it showed a trend for higher values on sites with high-quality litter. Yet, Shannon diversity was slightly but significantly higher, indicating a higher unpredictability of sampled species (i.e., a more homogeneous repartition of abundances between species), on sites with a high-quality litter (Graça et al., 2005). The difference in significance levels between the total number of species and the Shannon-Wiener index may be due to differences in the abundance of each species. Alternatively, it can also be due to slight changes in species composition. About functional diversity, FDis and RaoQ indexes were significantly higher on sites with high-quality litter. Changes in FDis indicate changes in the abundance-weighted mean distance to the abundance-weighted mean trait values of the community (Laliberté and Legendre, 2010). Changes in the RaoQ index indicate changes in the abundance-weighted sum of pairwise functional distances between species (Mouchet et al., 2010). FDis and RaoQ indexes are often closely correlated (Laliberté and Legendre, 2010). The higher they get, the higher the chemical diversity (Mouillot et al., 2013). Here, they indicate that detritivore communities are chemically more diverse on sites with high-quality litter. This can be due to (1) the presence of different species with different chemical compositions between sites, (2) different abundances of each species, (3) different chemical composition of species that are present on both sites, (4) different body mass values of species that are present on both sites. These four hypotheses are not mutually exclusive, but our results support the first and second

hypotheses (trends for higher taxonomic diversity and abundances on sites with a high-quality litter) and tend to exclude the third and fourth ones (no difference in morphospecies body chemical composition and body mass with litter quality). The index for functional richness (FRic) would have been informative here. Comparisons between FRic values (abundance not included) with FDis or RaoQ would have indicated if the difference in functional chemical diversity at the community level can be explained by changes in detritivore species abundances or by changes in species functional identity (i.e., changes in species chemical composition) (Mouillot et al., 2013). Yet, we could not use this index because it could not be computed on several sites because of low numbers of different morphospecies (3 species required, Appendix [Table S.IV.4](#)).

Differences in CWM of P and Mg content increased with differences in litter P and Mg content between sites of each pair, respectively (

[Table IV.1](#)). The influence of P litter content on detritivore P content was expected as P is an element that is often limiting for consumers relying on plant resources, especially detritivores (Evans-White and Halvorson, 2017) and as P was the element with the highest ratio between detritivore and litter contents. Under the hypothesis that detritivore communities are influenced by litter chemistry, a large difference in litter P content between close sites is expected to lead to a high difference in P content in the detritivore community. Higher litter P content may allow a larger range of detritivores to live there, whatever their needs in the P element (Kaspari and Yanoviak, 2009; McGlynn et al., 2007; Ott et al., 2014). The correlation for the Mg element was surprising. This element is not particularly known to be limiting for detritivores, and the Mg ratio between detritivore and litter content is low. Two mechanisms might explain this correlation. First, this effect could be due to a non-strict homeostasis for Mg content. Yet, analyses at the morphospecies level do not support this hypothesis as ΔMg did not differ from zero. Second, Mg and Ca are chemically close (they are both alkaline earth metals and have a similar size) and Mg and Ca content are closely correlated in detritivores ($R^2 = 0.63$, $F_{1,87} = 148.9$, $p < 0.001$) but not in litter ($R^2 < 0.01$, $F_{1,22} < 0.1$, $p = 0.944$). Detritivores might then rely more on the Mg element if the Ca element is scarce in the resource, and inversely. It can also explain why we found no correlation for the Ca element even though Ca was the second element with the highest ratio and as it is of major importance for detritivore teguments (Kaspari and Yanoviak, 2009). An innovative study

identified the key importance of litter Ca and Mg content in driving detritivore–litter interaction in streams (Santonja et al., 2020). To our knowledge, no study investigated this question for soil detritivores. The absence of correlation for the N element was also surprising as N is considered to be a major element for detritivores (García-Palacios et al., 2013). Yet, the N ratio was low and might not be so limiting for detritivores as their N-needs may be lower than P- or Ca-needs (Kaspari and Yanoviak, 2009; Ott et al., 2014).

A variance analysis revealed that detritivore chemistry was mostly influenced by the Order level (Appendix, [Figure S.IV.3](#)). Studying detritivores at the Order level then allows to have chemically homogeneous taxa. This level of grouping that is higher than morphospecies also allows to have a higher number of data points on each site than when considering morphospecies. No detritivore Order was particularly affected by litter quality ([Figure IV.3](#) and Appendix [Figure S.IV.4](#)). Glomerida total abundance and biomass were slightly significantly higher on sites with high-quality litter. This is surprising because Glomerida are not particularly rich in macroelements (Appendix, [Table S.IV.2](#)). This suggests that Glomerida is not the Order with the highest elemental needs and that it should not be the most sensitive one to litter chemical quality. We found no influence of litter quality on detritivore mean chemical composition, except for Polydesmida N content. Yet, this slightly significant result should be considered with caution as they are supported by a low number of points with non-normal distributions. These effects were not significant according to non-parametric tests that are not biased by data distribution but also less powerful, which underlies the need for more data collection to conclude on this point. Overall, no detritivore Order mean body mass and chemical composition is particularly affected by litter quality. For all four detritivore orders, total abundance and biomass show the same trend with higher values on sites with high-quality litter. These findings support the hypothesis that litter quality influences detritivore communities through changes in detritivore abundances across taxonomical levels. They do not support the hypothesis that detritivore chemical composition and body mass change with litter quality. Unfortunately, we could not investigate taxonomic and functional diversity at the Order level because of a too low number of data points to compute the relevant metrics (Shannon, CWM, FDis, RaoQ) for these questions. It underlies the need for more data collection to conclude on this point.

At the morphospecies level, we found no influence of litter quality on any parameter (Figure IV.4). Our results then support the mainstream hypothesis that detritivores are homeostatic (Jochum et al., 2017). It also suggests that mean individual body mass is not influenced by litter quality. Lastly, detritivore abundance showed a trend for higher values on sites with high-quality litter, but this trend was not significant. The difference in abundance with litter quality did not correlate with any detritivore element content. This last result does not support the hypothesis that species with higher elemental needs are more sensitive to litter quality. Using more precise estimates for elemental needs such as Threshold Elemental Ratios (TER) (Sterner and Elser, 2017) might give more information about this putative mechanism.

To conclude, our study reveals that litter chemical quality influences the chemical footprint of detritivore communities, especially through P and Mg changes. This effect is limited and may be due to an increase in species abundance. We found no evidence that species chemistry and body mass are impacted by litter quality. This supports the strict homeostasis hypothesis, indicating no physiological adaptations. We also found very few differences in species richness. Differences in species presence with different functional identities might contribute to this effect, but this was not the main mechanism. Abundance changes might be also linked to other mechanisms such as competition, facilitation, predation, and parasitism.

Authors contributions

TM and BP initiated the study. TM, MC, EF, FMD, MS, MD, and BP imagined the design of the experiment and conducted fieldwork. TM, BP, DB, FC, SH, FJ, and GLR imagined the protocol for chemical analyses and conducted chemical analyses. TM analyzed the results with the help of CL and BP. TM wrote the first draft of the manuscript with the help of BP. TM and BP reviewed the final version. The final version included in this manuscript was not reviewed by co-authors. They cannot be accountable for any mistake in this version.

Data archiving

Data will be archived on the Dryad depository at the time the paper is accepted for publication.

Conflict of interest

The authors declare that they have no known competing interests.

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Epilogue (EN)

In this chapter, our study reveals that litter chemical quality influences the chemical footprint of detritivore communities, especially through P and Mg changes. Detritivore community chemistry slightly matched with litter chemistry (Figure 6). In line with our expectations from chapter II, detritivore community phosphorus content was influenced by litter phosphorus content, but this effect was weak. Differences in detritivore communities with litter quality were mainly due to differences in detritivore abundances. Our results support the mainstream hypothesis that detritivores are homeostatic, indicating no physiological adaptations. Detritivore mean body mass was also not influenced by litter quality. Contrarily to a strong niche differentiation hypothesis (Figure 7, hypothesis H3), detritivore communities were not specifically linked to litter properties. This final chapter rather confirms the weak influence of trait-matching for detritivore–litter interactions (Figure 7, hypothesis H2).

Épilogue (FR)

Dans ce chapitre, notre étude révèle que la qualité chimique de la litière influence l'empreinte chimique des communautés de détritivores, notamment par le biais des changements de P et de Mg. La composition chimique des communautés de détritivores concorde légèrement avec celle de la litière (Figure 6). Conformément à nos attentes du chapitre II, la teneur en phosphore des communautés de détritivores était influencée par la teneur en phosphore de la litière, mais cet effet était faible. Les différences au sein des communautés de détritivores, liées à la qualité de la litière, étaient principalement dues à des différences d'abondances de détritivores. Nos résultats soutiennent l'hypothèse classique selon laquelle les détritivores sont homéostatiques, ce qui indique l'absence d'adaptations physiologiques. La masse corporelle moyenne des détritivores n'était pas non plus influencée par la qualité de la litière. Contrairement à l'hypothèse de forte différenciation des niches (Figure 7, hypothèse H3), les communautés de détritivores n'étaient pas spécifiquement liées aux propriétés de la litière. Ce dernier chapitre confirme plutôt la faible influence de la concordance des traits dans les interactions entre les détritivores et la litière (Figure 7, hypothèse H2).

GENERAL DISCUSSION

What constrains litter consumption by detritivores?

The results of this thesis underline the importance of biomechanical constraints to explain litter consumption by detritivores. The influence of body mass was weak in Chapter II. We interpret this as the effect of weak metabolic constraints. Mechanical constraints were the first constraints applying in Chapter II, and the second ones behind metabolic constraints in Chapter III. In both chapters, mechanical constraints were best represented by litter toughness (or litter softness). This parameter was of crucial importance in both chapters. In Chapter II, results pointed to a non-linear effect of litter toughness. Litter toughness decreased consumption rates until a given threshold (around 400 kPa). Above this threshold, consumption was minimal. In Chapter III, we used taxon-specific sigmoid models to best describe the influence of litter toughness (softness) on consumption rates. These models allowed us to identify litter toughness thresholds between 150 and 350 kPa depending on the detritivore taxon. Detritivore traits, and especially the proxy for biting force, had a surprisingly low effect. The index we used, and especially head width, correlated quite well with the maximum biting force capacity of insects (Rühr et al., 2022; Wheeler and Evans, 1989). Yet, other traits may have been considered to complete the computation of the force index. Estimating incisor sharpness or wear could have proven useful (Clissold, 2007). Alternatively, more complex mechanic models take into account the angle muscles make with mandibles or the mandible section area (Blanke, 2019; Le Provost et al., 2017). However, these parameters are more challenging to measure. A direct measurement of maximal biting force would be very informative but the procedure is tedious and does not apply yet to aquatic individuals (Rühr and Blanke, 2022). The over importance of mechanical constraints is consistent with predictions of Chapter I: if detritivores are to ingest litter, they first have to cut it, break it, and physically process it. Mechanical constraints stand as a very early filter on the way to consumption and the outcome of these constraints drives consumption.

Elemental constraints had a lower importance than mechanical constraints in Chapters II and III. In Chapter II, elemental constraints are best represented by constraints in P content. The importance of P constraints is in line with expectations from Detritivore / Litter ratios in each element, P being the element with the highest ratio (P ratio = 28 in Chapter II and 24 in Chapter IV). This indicates that P is likely to be the most limiting element for detritivore

metabolism. This importance of P element is also visible in Chapter IV as Community Weighted Mean (CWM) for P content was influenced by litter P content between sites of each pair. P constraints may then have consequences at the community level by partially filtering species but not affecting species' homeostasis. The weak effect of N-content (Chapters II and III) is surprising. Litter N-content is known in the literature to be a major trait reflecting litter palatability (Frouz et al., 2015; García-Palacios et al., 2013; Zhang et al., 2015). Yet, as litter P and N content are correlated (Li et al., 2021), and as N is more systematically investigated than P, a study bias might have given litter N-content too much emphasis. The weak effect of Ca-content (Chapter II) is also surprising. Ca content was much higher in detritivores with highly-sclerotized teguments (Diplopoda and Crustaceans) than in litter. The opposite was true for insect larvae. We then expected to see different reactions between these two groups, regarding Ca constraints. This was not the case, which can be due to the bimodal distribution of detritivore Ca content. It can also be interpreted as the fact that other constraints predominate. Elemental constraints seem to have limited effects at the community level. Chapter IV reveals that the detritivore community is chemically impacted by litter (FDIs and RaoQ indexes are higher on sites with a higher quality litter). In sites with higher quality litter, detritivore abundances, total biomass, and taxonomic diversity tended to be higher, but the difference was rarely significant. Analyses revealed that detritivore species were homeostatic. Surprisingly, we found no significant correlation between the difference in abundance between sites and the chemistry of detritivores. Some strategies such as complementation or compensation might explain this observation (Crenier et al., 2017; Jochum et al., 2017). Significant differences at the community level may then be due to the combination of slight differences at the population level. Yet, as explained in Chapter I, using element content as a proxy of elemental constraints is limited. It does not consider that the assimilation rate by a given detritivore can vary between elements and that it depends on food type (Halvorson et al., 2016). For each element, the assimilation rate depends on the litter molecules in which each element is found (e.g. C element will be more easily assimilated if it is part of a soluble carbohydrate than a lignin (Cragg et al., 2015)). It also depends on digestive and assimilation capacities of the detritivore and its endosymbionts (Bärlocher and Porter, 1986; Zimmer, 2002). Element content also does not consider the losses of each element by each detritivore taxon. Estimations of element contents in feces could help to better estimate real element needs (Halvorson et al., 2018), but this requires large amounts of feces (Fenoy et al., 2021).

Threshold Elemental Ratios (TER, i.e. the ratios at which the nutrient limitation of consumers growth switches from one element to another; (Frost et al., 2006)) can also help to have more realistic estimations of elemental needs (Frost et al., 2006; Fuller et al., 2015).

In Chapters II and III, the weak effect of detritivore body mass was surprising. The log-log correlation between consumption rate (excluding consumption rate values close to zero) and detritivore body mass was weak, and the estimated coefficient significantly deviated from the $\frac{3}{4}$ value that is expected under the metabolic theory ($R^2 = 0.02$, $F_{1,482} = 7.8$, $p = 0.006$, Coefficient = 0.12 ± 0.04 for Chapter II; $R^2 = 0.19$, $F_{1,243} = 56.3$, $p < 0.001$, Coefficient = 0.44 ± 0.06 for Chapter III). This deviation from metabolic theory predictions is expected if other constraints such as mechanical constraints arise. The identified effect of litter toughness can explain consumption rate values below expectations. Other elemental constraints may explain deviations from expectations. Lastly, metabolic content may differ between different litter. One gram of one litter may then differentially fill detritivore energetical needs. Direct or indirect (lipids, carbohydrates, proteins) caloric measurements of litter could help answer this question (Li et al., 2021; Mathews and Kowalczewski, 1969). Measuring both litter energetical content and detritivores' energy reserves (e.g. glycogen or lipids, (Fenoy et al., 2021)) could allow to test for a real energetical match between detritivores and litter. Other constraints such as digestive constraints presented in Chapter I could complete the full characterization of constraints. Yet, digestive constraints present a high methodological challenge as assimilation is highly influenced by microorganisms that are present both on litter and in detritivores' digestive tract (Bredon et al., 2020; Zimmer, 2002; Zimmer and Bartholmé, 2003). Studying digestive constraints could be the topic of an entire Ph.D. thesis. Lastly, as the first constraints presented in Chapter I as spatial constraints are probably mainly acting at the population level and hence depend on a different context, with different questions and hypotheses than the ones we investigated. Also, as spatial constraints are the easiest ones to control, we always tried to suppress or minimize their influence (by studying only bipartite interactions in Chapters II and III, and by using a design with pairs of monospecific-litter sites in Chapter IV). Yet, laboratory tests such as choice consumption tests could have helped identifying key traits in food search, detection, and selection (Graça and Cressa, 2010; Tuck and Hassall, 2004).

What is the importance of trait-matching?

Overall, trait-matching only poorly applied in our studies. The interaction between detritivore species and litter was low (11 and 15 % of mass-independent consumption rate variability for Chapter II and III, respectively). This indicates that trait-matching can only explain a modest portion of the variability in the data. We could not identify trait-matching for mechanical constraints in Chapter II or in Chapter III. The match for P in Chapter II was in line with predictions of the ecological stoichiometric theory, but it explained a very low amount of variability (1.4 %). The weak pieces of evidence for a match between litter quality and chemistry and detritivore communities in Chapter IV reinforces the conclusion that trait-matching only poorly influences detritivore–litter interactions. This finding is very interesting as trait-matching was never formally tested for detritivore–litter interactions apart from scarce field correlations studies (Brousseau et al., 2019; Raymond-Léonard et al., 2018). About the statistical tools we used to identify trait-matching, we did not use the classical RLQ and fourthcorner approaches because they only poorly applied to our designs. For instance, in Chapters II and III, litter were different for aquatic and terrestrial detritivores, which prevented using common RLQ and fourthcorner analyses. The approaches we used ((X-Y)² matching term (Brousseau et al., 2018; Rohr et al., 2016), sigmoid model based on Holling's equations (Holling, 1959; Ott et al., 2012)) are more appropriate to our design and to the mechanisms we wanted to investigate than RLQ and fourthcorner. For Chapter II, as toughness seems to act with a threshold effect, we also could have used log(X/Y) matching term which better accounts for threshold match (Neu et al., 2023; Rohr et al., 2010). Yet, these models performed badly as they tended to fit extreme data points, resulting in overfitting. For these reasons, we did not use them in Chapter II. We may then have missed a matching rule, especially between biting force and litter toughness traits. But this match would not have explained more than ~10% of consumption rate variability.

A potentially concerning limitation of these studies is the natural correlation between traits. For example, there was a correlation between litter toughness and litter N-content ($R^2 = 0.28$, $F_{1,22} = 8.5$, $p = 0.008$ in Chapter II; $R^2 = 0.57$, $F_{1,14} = 18.8$, $p < 0.001$ for Chapter III). There was also a log-log correlation between detritivore biting force index and body mass at the taxon level ($R^2 = 0.79$, $F_{1,7} = 16.0$, $p = 0.005$ for Chapter II; $R^2 = 0.54$, $F_{1,6} = 6.9$, $p = 0.039$ for

Chapter III). There were also correlations between element concentrations, both for detritivores and litter. It is extremely challenging to experimentally modify one trait without affecting others (Danger et al., 2013; Jackrel et al., 2016). Confronting models as in Chapter II, and dissociating the effect of each trait independently and of each matching term seems like an appropriate method to discriminate the effects of different traits. We are then confident that the constraints and traits we identified as ruling the interaction are indeed functionally important.

Are they key differences between aquatic and terrestrial ecosystems?

Overall, as expected from Chapter I, we observed almost no systematic difference between aquatic and terrestrial detritivore-litter interactions. The identity of the ecosystem explained 0 and 7% of mass-independent consumption rate variability in Chapter II and III, respectively. This result is in line with the few other studies that compared litter consumption for both aquatic and terrestrial detritivores (Dray et al., 2014; Rota et al., 2022). It validates the relevance of trait-based approach which allows to identify consistent rules about species interactions across ecosystems. One surprise, however, came from the Trichoptera larvae (caddisfly) we studied. This taxon always exhibited surprisingly high consumption rate values, whether absolute or body mass-corrected, both for Chapters II and III. Quasi-null consumption rate values were very rare for caddisfly larvae. As Trichoptera are the only taxon belonging to Holometabola, this high consumption rates might be explained as an adaptation to the energetical costs of complete metamorphosis. In other laboratory consumption tests with several detritivore taxa, Trichoptera regularly displays the highest consumption rates (Fenoy et al., 2021; Graça et al., 2001; Rota et al., 2022). Yet, other studies do not systematically show high consumption rate values for Trichoptera compared to other taxa (Dray et al., 2014; Ohta et al., 2016). Another explanation could come from the fact that the Trichoptera species we studied cut discs through leaves to build their case. They might have particularly strong or sharp mandibles which would remove most of mechanical constraints. This explanation is in line with the very high threshold value for litter toughness identified in Chapter III (357 kPa for Trichoptera vs 263 kPa for Gammarus which was the second-highest significant threshold).

How can we go from bipartite interactions to decomposition processes?

Concerning potential applications to improve models of decomposition at the field scale, our results point to the major importance of key litter traits (toughness). Both Chapters II and III point to a higher importance of litter than detritivore identity in explaining consumption rates. In Chapter II, 22 and 33 % of variability in mass-independent consumption rate was explained by the conditioning treatment and leaf species, respectively. Detritivore taxon accounted for 12 % of the variability. In Chapter III, 0 and 36 % of the variability in mass-independent consumption rate was explained by litter species and litter sampling time, respectively. Detritivore taxon accounted for 14 % of the variability. Detritivore taxon then explains less than one-quarter of variability in mass-independent consumption rate, while litter identity explains one-third to half of the variability. Overall, the residual variability in mass-independent consumption rate that cannot be explained by our experimental setup reached 32 % for Chapter II and 42 % for Chapter III. This variability can be interpreted as intra-specific variability. In a similar experiment, intra-specific variability also explained 36 % of mass-specific consumption rates (Rota et al., 2022). The study of interactions at the individual level allows to explain a significant part of consumption variability (Rota et al., 2022, 2018). However, applying individual trait effects at a larger scale is challenging. Studies at the individual level are generally limited to a few species and characterizing the whole population trait distribution of each species remains challenging. Studying the performance of consumption rates of different litter by different detritivore species and linking it to traits then appears as an important step to explain detritivore-litter interactions at the community level, without characterizing all possible interactions.

Several points of major importance must be considered before our results on litter consumption by detritivores can be used to help modeling decomposition at higher (regional or global) scales. First, ingestion is not the whole part of detritivore–litter interaction. Litter direct mineralization by detritivores seems to be modest (Marks, 2019). They transform an important part of litter into feces. Feces then undergo their own decomposition process which is indirectly influenced by detritivores (Coq et al., 2022; Joly et al., 2020; Špaldoňová and Frouz, 2019). Eventually, detritivores themselves die and may decompose (Seastedt and Tate,

1981). Second, as a first step, this thesis can be seen as mostly focusing on the fundamental niche of detritivores (Chapters II and III) rather than on the realized one. The realized niche of detritivore depends on complex interactions with other biotic (facilitators e.g., microorganisms, competitors e.g., other detritivores, predators) and abiotic (e.g., temperature) agents. These interactions may impact the rules we identified (Lagrue et al., 2015). For example, food complementation or biotic and abiotic filtering could explain the differences between the expected P match and the weak impact of litter quality on the detritivore community chemistry we observed in Chapter IV. Another interesting example of how realized niche can differ from fundamental one is given by Ganault et al. (2022). In a laboratory experiment with entire leaves, they showed that detritivore species tend to prefer *a priori* unpalatable litter because of its tubular shape which makes it an attractive microhabitat. Understanding the functional network of decomposition gathering all influencing species and abiotic parameters is a major challenge (Gravel et al., 2016). Identifying bipartite rules may contribute to inferring interactions at the network level. Our studies can then be considered as a first step to answer this challenge.

Conclusion: What are detritivores? (EN)

I would like to conclude about what this thesis tells us about what detritivores are. The interaction between detritivores and litter is singular because litter is dead organic matter. The qualification of interaction itself is questionable as litter does not react to consumption as living organisms do. Litter has no defense mechanisms apart from residual chemical compounds or structural apparatus (Dudgeon et al., 1990; Nakamura et al., 2022). The nature of this relationship is expected to have consequences on the evolutive interaction between detritivores and plants from which litter comes. We can expect some detritivores to have a specialized trophic niche in focusing on a given litter species or litter at a given decomposition point (Figure 7, hypothesis H3). Competition for quality litter could drive such specialization patterns. As plant growth may indirectly depend on the decomposition of its own litter to obtain nutrients back (Sayer, 2005) we can even predict direct or indirect co-evolutionary patterns between specific plants and specialized detritivores (Whitham et al., 2006). Yet, as litter does not directly react to consumption, it seems that this kind of specialized interaction at evolutionary time scales would be unlikely, unstable, and rare. Our studies confirmed the

mainstream hypothesis that detritivores are mainly generalists and opportunistic consumers (Crenier et al., 2017; Rubio-Ríos et al., 2023). We identified different taxon-specific reactions to litter characteristics (Chapter III), but these differences are modest and do not argue for clear and distinct trophic niches. Our results support the hypothesis that interactions are mainly limited by litter attributes, with a limited effect of detritivore functional identity (Figure 7, hypothesis H2). The weak importance of trait-matching in our data supports the idea that detritivores have a limited diet specialization. Trait-matching is likely to be more important when both interacting species have a closer and stronger interaction, whether they are mutualistic or antagonistic (Neu et al., 2023). The idea that trait-matching should be stronger for strong and specific interactions was hypothesized (Bartomeus et al., 2016) but still lacks evidence. We also only studied macrodetritivores, limiting ourselves to arthropod taxa. Other organisms such as meso- or micro-detritivores might exhibit clear trophic niche specialization associated with trait-matching. The results of this thesis tell us that arthropod macrodetritivores are generalist consumers with a trend to specialization. Different macrodetritivores species differently react to litter constraints, but they also show remarkable convergent reactions to the large plant litter diversity, even though they come from very different phylogenetic groups and live in very different ecosystems.

Conclusion : Qu'est-ce qu'un détritivore ? (FR)

Je voudrais conclure sur ce que cette thèse nous apprend sur les détritivores. L'interaction entre les détritivores et la litière est singulière car la litière est une matière organique morte. La qualification même d'interaction est discutable puisque contrairement aux organismes vivants, la litière ne réagit pas à la consommation. Elle ne possède pas de mécanismes de défense en dehors des composés chimiques résiduels ou de propriétés structurales (Dudgeon et al., 1990; Nakamura et al., 2022). La nature de cette relation pourrait avoir des conséquences sur l'interaction évolutive entre les détritivores et les plantes dont provient la litière. On peut s'attendre à ce que certains détritivores aient une niche trophique spécialisée et qu'ils se concentrent sur une espèce de litière donnée ou sur une litière à un point donné de décomposition (Figure 7, hypothèse H3). La compétition pour une litière de qualité pourrait conduire à de tels schémas de spécialisation. Comme la croissance des plantes peut dépendre indirectement de la décomposition de leur propre litière pour récupérer les

nutriments (Sayer, 2005), nous pouvons même prédire des schémas co-évolutifs directs ou indirects entre des plantes spécifiques et des détritivores spécialisés (Whitham et al., 2006). Cependant, comme la litière ne réagit pas directement à la consommation, il semble que ce type d'interaction spécialisée à l'échelle évolutive serait peu probable, instable et rare. Nos études ont confirmé l'hypothèse générale selon laquelle les détritivores sont principalement des consommateurs généralistes et opportunistes (Crenier et al., 2017; Rubio-Ríos et al., 2023). Nous avons identifié différentes réactions aux caractéristiques de la litière qui sont spécifiques à certains taxons (chapitre III), mais ces différences sont modestes et ne plaident pas en faveur de niches trophiques claires et distinctes. Nos résultats soutiennent l'hypothèse selon laquelle les interactions sont principalement limitées par les caractéristiques de la litière, avec un effet limité de l'identité fonctionnelle des détritivores (Figure 7, hypothèse H2). L'importance faible de la concordance de traits dans nos données soutient l'idée que les détritivores ont une spécialisation alimentaire limitée. La concordance de traits est susceptible d'être plus importante lorsque les deux espèces en interaction ont une interaction plus étroite et plus forte, qu'elle soit mutualiste ou antagoniste (Neu et al., 2023). L'idée selon laquelle la concordance de traits devrait être plus forte pour des interactions fortes et spécifiques a été formulée (Bartomeus et al., 2016), mais manque encore de preuves. De plus, nous n'avons étudié que les macrodétritivores, en nous limitant aux arthropodes. D'autres organismes tels que les méso- ou microdétritivores pourraient présenter des spécialisations de niches trophiques claires associées à de la concordance de traits. Les résultats de cette thèse nous montrent que les macrodétritivores arthropodes sont des consommateurs généralistes avec une tendance à la spécialisation. Différentes espèces de macrodétritivores réagissent différemment aux contraintes de la litière, mais elles montrent également des réactions remarquablement convergentes face à la grande diversité de la litière végétale, alors même qu'elles proviennent de groupes phylogénétiques variés et vivent dans des écosystèmes différents.

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GLOSSARY

Breakdown: Disaggregation of detritus into leachate, fine particulate organic matter (0.5 μm – 1 mm), and inorganic matter. Synonym: decomposition (Marks, 2019).

Conditioning: From a detritivore perspective, it is the physical and microbial transformations of litter that make it more palatable.

Decomposers *sensu lato*: Every organism trophically relying on dead organic matter. We rely on this definition in the manuscript.

Decomposers *sensu stricto*: Microorganisms (bacteria, fungi) consuming dead organic matter.

Decomposition *sensu lato*: Decomposition processes including inorganic chemical oxidation, leaching, microbial decomposition, and decomposition and disintegration by soil animals (Petersen and Luxton, 1982). We rely on this definition in the manuscript.

Decomposition *sensu stricto*: All biological processes contributing to organic matter mass loss and transformation, not including physical losses caused by abrasion, fragmentation, or leaching (Gessner et al., 2010).

Detritivores: Animals (metazoa) eating or grazing on detritus and/or eating microorganisms on detritus. This definition excludes protists (polyphyletic unicellular eukaryotes feeding on bacteria) that are sometimes considered detritivores even though they are not metazoans.

Detritus: Coarse (> 1 mm) dead organic matter.

Trophic interaction: Action of a consumer organism taking at least part of its organic matter resource from the organic matter of another organism, whether dead or alive.

Leachate: The suite of organic compounds that dissolve when a leaf is immersed in water (Marks, 2019).

Litter: Detritus of vegetal origin.

Litter species: Identity of the plant species from which the litter item is originating.

Metabolism: From an ecology point of view, it is the total amount of energy consumed by an organism.

Mineralization: The biological process of converting organic matter to mineral forms; mineralization generates carbon dioxide (CO_2), ammonium (NH_4^+), phosphate (PO_4^{3-}), sulfate (SO_4^{2-}), and other molecules (Marks, 2019).

Ecological network: a network in which different types of organisms (e.g., plants and animals) are linked by biotic (trophic or nontrophic) interactions, which can be mutually beneficial (as for pollination and seed dispersal) or antagonistic (as for herbivory) (Schleuning et al., 2020).

Saprophagous: Organism that consume dead organic matter.

Traits: Individual and measurable characteristics (morphological, physiological, chemical) that can explain the effect or the response of the individual on/to its biotic and abiotic environment.

Trait-matching: Interaction between traits of two organisms, that drive the interaction between these organisms. Incompatible matching traits between species may impair the interaction.

APPENDIX CHAPTER II

Supplementary Material for:

Litter consumption by macrodetritivores depends more on mechanical than on elemental constraints

Théo Marchand¹, Lola Estabes¹, Benjamin Pey¹

¹ Laboratoire Écologie Fonctionnelle et Environnement, Université de Toulouse, CNRS, Toulouse, France

Table S.II.1: Water characteristics of the stream (determined four times during March – April 2022 with a WTW™ Multi 3420 SET C) where aquatic detritivores were collected (mean ± standard deviation).

pH	Total dissolved solid (g.L ⁻¹)	O ₂ (mg.L ⁻¹)	T (°C)
7.5 ± 0.2	67 ± 1	11.2 ± 0.5	9.8 ± 2.2

Table S.II.2: Soil characteristics (measured by pooling four samples) where terrestrial detritivores were collected.

Texture			pH	Carbonates (g/kg)	Organic matter (g/kg)	Cation Exchange Capacity (Metson) (mol/kg)
Sand (%)	Silt (%)	Clay (%)				
57.3	24.7	18.0	5.2	< 5	72.9	214

Table S.II.3: Temporal identity of all 4 consumption tests' replicates for each detritivore – litter treatment pair. Consumption tests happened over 11 weeks from February to May.

Litter treatment	Detritivore species								
	<i>Nemoura sp.</i>	<i>Gammarus fossarum</i>	<i>Potamophylax cingulatus</i>	<i>Tipula sp.</i>	<i>Polydesmus inconstans</i>	<i>Philoscia affinis</i>	<i>Porcellio monticola</i>	<i>Glomeris marginata</i>	<i>Cylindroiulus londinensis</i>
<i>Ailanthus altissima</i>	1, 2, 4, 5	1, 2, 4, 5	1, 2, 4, 5	1, 4, 4, 5	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10
<i>Ailanthus altissima</i> (T)					7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10
<i>Ailanthus altissima</i> (A)	2, 3, 4, 5	2, 3, 4, 5	2, 3, 4, 5	3, 3, 4, 5					
<i>Robinia pseudoacacia</i>	1, 2, 4, 5	1, 2, 4, 5	1, 2, 4, 5	1, 4, 4, 5	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10
<i>Robinia pseudoacacia</i> (T)					7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10
<i>Robinia pseudoacacia</i> (A)	2, 3, 5, 5	2, 3, 5, 5	2, 3, 4, 5	3, 3, 4, 5					
<i>Juglans regia</i>	1, 2, 4, 5	1, 2, 4, 5	1, 2, 4, 5	1, 2, 4, 6	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10
<i>Juglans regia</i> (T)					7, 8, 9, 11	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10
<i>Juglans regia</i> (A)	2, 3, 4, 5	2, 3, 4, 5	2, 3, 4, 5	3, 3, 4, 5					
<i>Carpinus betulus</i>	1, 4, 5, 6	1, 2, 4, 5	1, 2, 4, 5	1, 4, 4, 5	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10
<i>Carpinus betulus</i> (T)					7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10
<i>Carpinus betulus</i> (A)	2, 3, 4, 5	2, 3, 4, 5	2, 3, 4, 5	3, 3, 4, 5					
<i>Acer platanoides</i>	2, 4, 4, 5	1, 2, 4, 5	1, 2, 4, 5	1, 2, 4, 5	7, 8, 9, 10	7, 8, 10, 10	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10
<i>Acer platanoides</i> (T)					7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10
<i>Acer platanoides</i> (A)	2, 3, 4, 6	2, 3, 4, 5	2, 3, 4, 5	3, 3, 4, 5					
<i>Prunus avium</i>	1, 2, 4, 5	1, 2, 4, 5	1, 2, 4, 5	1, 4, 4, 5	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10
<i>Prunus avium</i> (T)					7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10
<i>Prunus avium</i> (A)	2, 3, 4, 5	2, 3, 4, 5	2, 3, 4, 5	3, 4, 4, 5					
<i>Quercus petrea</i>	1, 2, 4, 5	1, 2, 4, 5	1, 2, 4, 5	1, 2, 4, 5	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10
<i>Quercus petrea</i> (T)					7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10
<i>Quercus petrea</i> (A)	2, 3, 4, 5	2, 3, 4, 5	2, 3, 4, 5	3, 4, 5, 6					
<i>Platanus xhispanica</i>	2, 4, 4, 5	1, 2, 4, 5	1, 2, 4, 5	1, 4, 4, 5	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 10
<i>Platanus xhispanica</i> (T)					7, 8, 9, 10	7, 8, 9, 10	7, 8, 9, 11	7, 8, 9, 10	7, 8, 9, 10
<i>Platanus xhispanica</i> (A)	2, 3, 4, 5	2, 3, 4, 5	2, 3, 4, 5	3, 3, 4, 5					

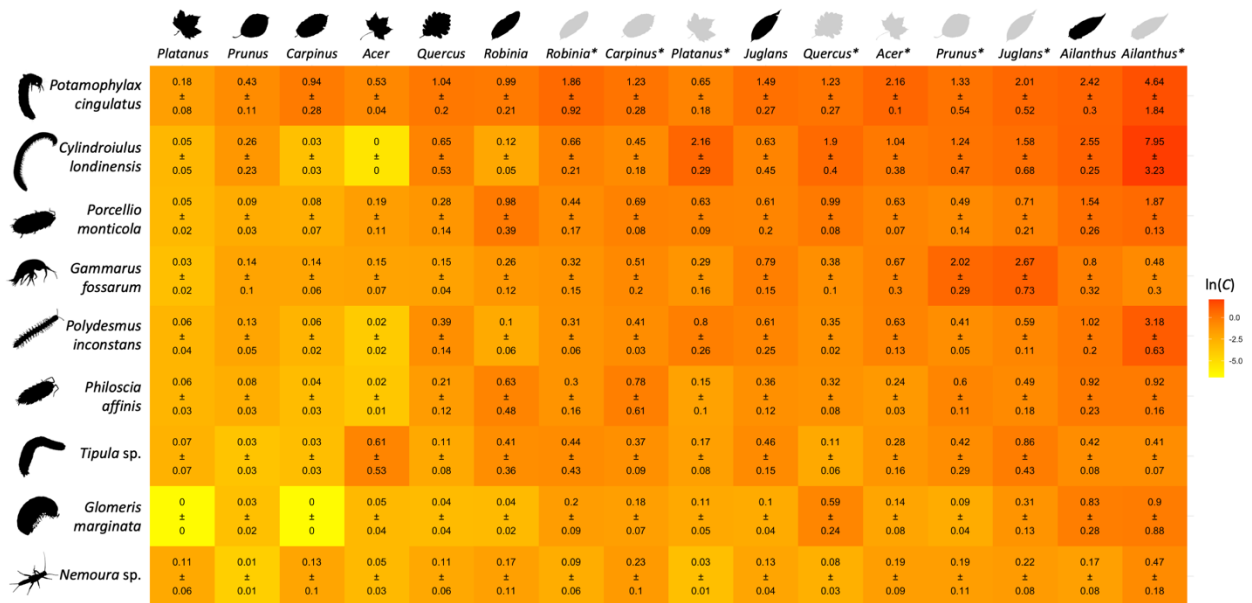


Figure S.II.1: Individual consumption rate (C , $\text{mg}\cdot\text{d}^{-1}$, mean \pm se). Species are ordered by increasing (for litters) or decreasing (for detritivores) mean value (\pm se) of consumption rates. For litter treatments, black color indicates leached litters, and grey color with an asterisk (*) indicates leached and conditioned litters (aquatic and terrestrial). Color follows a logarithmic scale based on consumption rate.

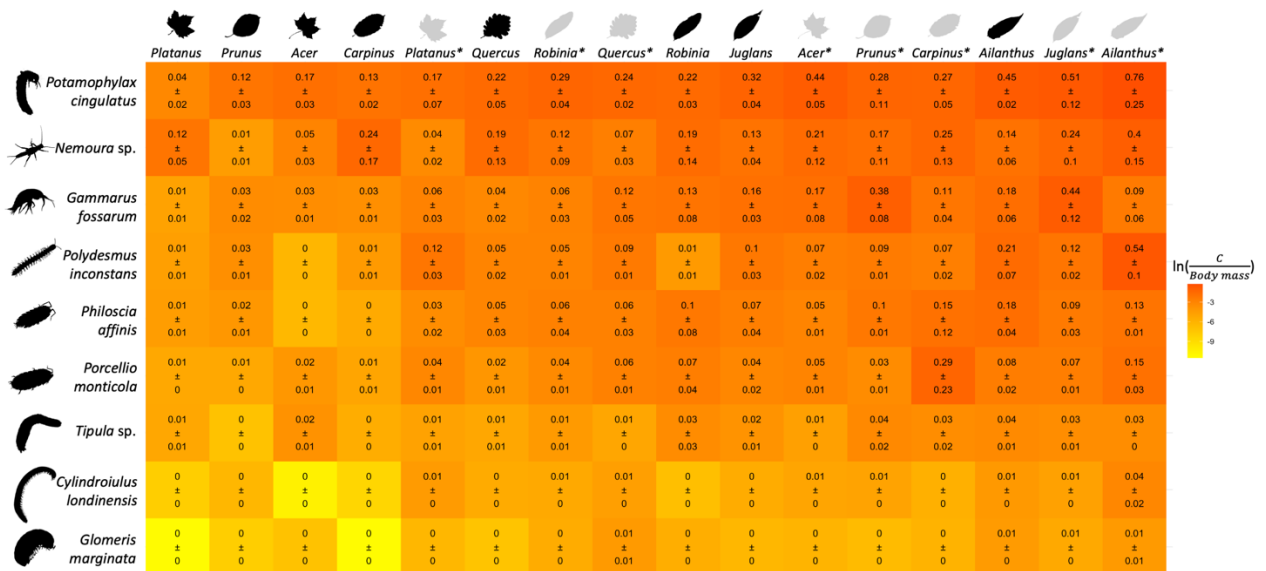


Figure S.II.2: Consumption rate divided by body mass ($\text{mg}\cdot\text{mg}^{-1}\cdot\text{d}^{-1}$, mean \pm se). Species are ordered by increasing (for litters) or decreasing (for detritivores) mean value (\pm se) of consumption rates divided by body mass. For litter treatments, black color indicates leached litters, and grey color with an asterisk (*) indicates leached and conditioned litters (aquatic and terrestrial). Color follows a logarithmic scale based on consumption rate.

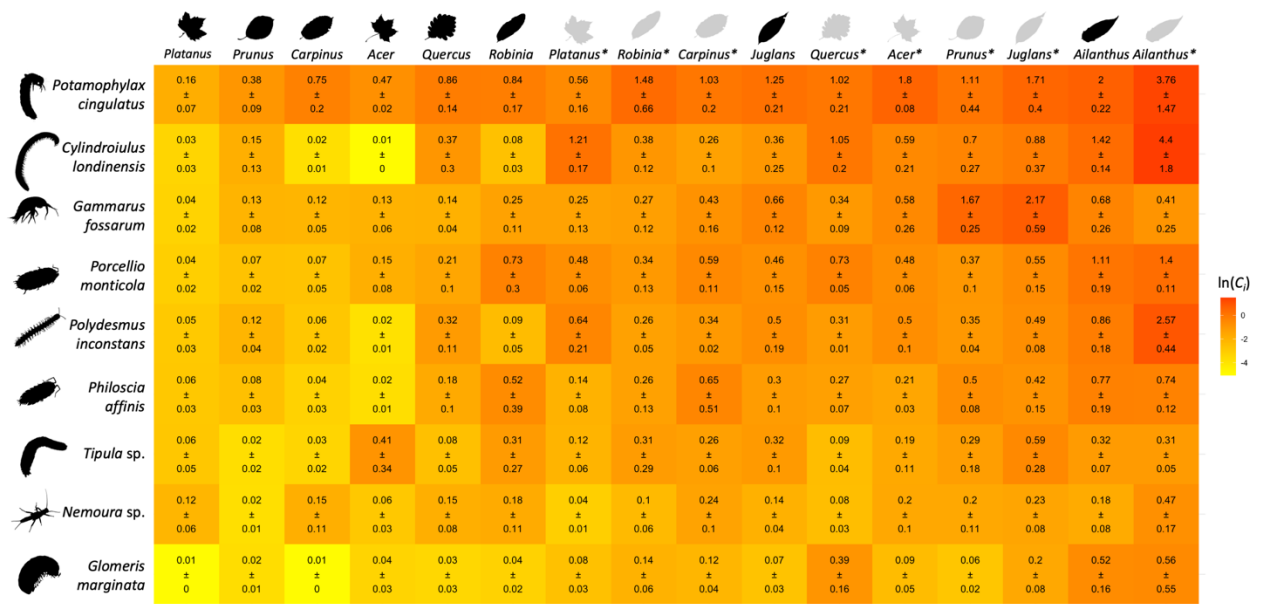


Figure S.II.3: Mass-independent consumption rate (C_i , $\text{mg} \cdot \text{mg}^{-0.11} \cdot \text{d}^{-1}$, mean \pm se). Species are ordered by increasing (for litters) or decreasing (for detritivores) mean value (\pm se) of mass-independent consumption rates. For litter treatments, black color indicates leached litters, and grey color with an asterisk (*) indicates leached and conditioned litters (aquatic and terrestrial). Color follows a logarithmic scale based on consumption rate.

Table S.II.4 Litter consumption rates and traits values. Litter species are order according to a gradient based on the first axis of the PCA (Figure II.1), with unconditioned litter first, then with terrestrial (T) and aquatic (A) conditioning treatments. C, N, P, K, and Ca are in % of dry mass.

Litter treatment	Conditioning duration (d)	Consumption rate (C, mg.d ⁻¹)		Consumption rate divided by bodymass (mg.mg ⁻¹ .d ⁻¹)		Toughness (kPa)	Thickness (mm)	C (%)	N (%)	P (%)	K (%)	Ca (%)
		mean ± se	[0.1 – 0.9] quantiles	mean ± se	[0.1 – 0.9] quantiles							
<i>Ailanthus altissima</i>		1.19 ± 0.15	[0.18 - 2.40]	0.15 ± 0.02	[0.01 - 0.39]	72 ± 6	0.06 ± 0.00	45.04 ± 0.46	1.84 ± 0.13	0.09 ± 0.01	0.10 ± 0.00	2.83 ± 0.12
<i>Ailanthus altissima</i> (T)	7	2.96 ± 0.86	[0.03 - 5.35]	0.18 ± 0.05	[0.00 - 0.48]	44 ± 3	0.05 ± 0.01	44.45 ± 0.46	2.16 ± 0.10	0.11 ± 0.01	0.20 ± 0.01	2.86 ± 0.03
<i>Ailanthus altissima</i> (A)	4	1.50 ± 0.63	[0.13 - 4.17]	0.32 ± 0.10	[0.02 - 0.82]	38 ± 2	0.04 ± 0.00	47.56 ± 0.79	2.86 ± 0.04	0.10 ± 0.00	0.18 ± 0.00	2.18 ± 0.12
<i>Robinia pseudoacacia</i>		0.41 ± 0.10	[0.00 - 1.28]	0.09 ± 0.02	[0.00 - 0.26]	247 ± 14	0.09 ± 0.00	47.51 ± 1.30	2.21 ± 0.27	0.04 ± 0.01	0.08 ± 0.00	3.09 ± 0.19
<i>Robinia pseudoacacia</i> (T)	17	0.38 ± 0.07	[0.03 - 0.85]	0.03 ± 0.01	[0.00 - 0.07]	164 ± 25	0.08 ± 0.01	45.89 ± 0.45	2.07 ± 0.04	0.06 ± 0.01	0.12 ± 0.01	3.50 ± 0.15
<i>Robinia pseudoacacia</i> (A)	10	0.68 ± 0.29	[0.00 - 1.36]	0.12 ± 0.03	[0.00 - 0.34]	225 ± 35	0.07 ± 0.00	46.69 ± 0.19	2.29 ± 0.04	0.04 ± 0.00	0.13 ± 0.00	2.82 ± 0.07
<i>Juglans regia</i>		0.58 ± 0.09	[0.11 - 1.44]	0.09 ± 0.02	[0.00 - 0.22]	181 ± 20	0.07 ± 0.00	38.63 ± 0.61	0.68 ± 0.01	0.05 ± 0.00	0.81 ± 0.18	6.19 ± 0.05
<i>Juglans regia</i> (T)	14	0.74 ± 0.17	[0.15 - 1.24]	0.06 ± 0.01	[0.00 - 0.14]	96 ± 12	0.07 ± 0.01	38.89 ± 0.26	0.85 ± 0.03	0.05 ± 0.00	0.24 ± 0.01	8.44 ± 0.41
<i>Juglans regia</i> (A)	9	1.44 ± 0.33	[0.08 - 3.34]	0.31 ± 0.07	[0.03 - 0.62]	67 ± 7	0.06 ± 0.00	38.81 ± 0.25	1.25 ± 0.02	0.05 ± 0.00	0.21 ± 0.02	7.98 ± 0.38
<i>Carpinus betulus</i>		0.16 ± 0.06	[0.00 - 0.45]	0.05 ± 0.02	[0.00 - 0.13]	322 ± 20	0.11 ± 0.01	46.43 ± 0.17	0.89 ± 0.02	0.04 ± 0.00	0.14 ± 0.01	1.69 ± 0.07
<i>Carpinus betulus</i> (T)	23	0.50 ± 0.13	[0.10 - 0.85]	0.10 ± 0.05	[0.00 - 0.16]	175 ± 43	0.08 ± 0.00	45.79 ± 0.26	1.25 ± 0.05	0.06 ± 0.00	0.14 ± 0.01	2.29 ± 0.19
<i>Carpinus betulus</i> (A)	11	0.58 ± 0.13	[0.18 - 1.19]	0.17 ± 0.04	[0.01 - 0.35]	229 ± 26	0.08 ± 0.00	44.05 ± 0.99	1.07 ± 0.21	0.05 ± 0.01	0.14 ± 0.03	1.77 ± 0.39
<i>Acer platanoides</i>		0.18 ± 0.07	[0.00 - 0.50]	0.03 ± 0.01	[0.00 - 0.11]	443 ± 27	0.12 ± 0.00	44.26 ± 0.36	0.81 ± 0.01	0.04 ± 0.00	0.10 ± 0.01	3.75 ± 0.12
<i>Acer platanoides</i> (T)	24	0.53 ± 0.10	[0.10 - 1.03]	0.04 ± 0.01	[0.00 - 0.07]	227 ± 23	0.09 ± 0.01	44.24 ± 0.22	0.95 ± 0.03	0.06 ± 0.00	0.15 ± 0.01	4.16 ± 0.26
<i>Acer platanoides</i> (A)	14	0.82 ± 0.22	[0.06 - 2.15]	0.21 ± 0.05	[0.00 - 0.52]	303 ± 18	0.12 ± 0.00	44.49 ± 0.62	1.12 ± 0.01	0.06 ± 0.00	0.12 ± 0.00	4.22 ± 0.11
<i>Prunus avium</i>		0.13 ± 0.03	[0.00 - 0.35]	0.02 ± 0.01	[0.00 - 0.07]	329 ± 22	0.10 ± 0.00	42.52 ± 0.51	0.68 ± 0.01	0.03 ± 0.00	0.09 ± 0.04	2.83 ± 0.32
<i>Prunus avium</i> (T)	17	0.57 ± 0.12	[0.11 - 1.06]	0.05 ± 0.01	[0.00 - 0.11]	167 ± 15	0.12 ± 0.01	43.60 ± 0.35	0.90 ± 0.01	0.04 ± 0.00	0.12 ± 0.01	3.69 ± 0.36
<i>Prunus avium</i> (A)	10	0.99 ± 0.24	[0.01 - 2.48]	0.22 ± 0.05	[0.01 - 0.51]	113 ± 10	0.10 ± 0.00	43.32 ± 0.76	1.01 ± 0.02	0.03 ± 0.00	0.08 ± 0.00	2.98 ± 0.03
<i>Quercus petraea</i>		0.33 ± 0.08	[0.00 - 0.79]	0.06 ± 0.02	[0.00 - 0.16]	649 ± 34	0.16 ± 0.01	45.47 ± 1.48	0.82 ± 0.07	0.05 ± 0.00	0.12 ± 0.01	1.82 ± 0.03
<i>Quercus petraea</i> (T)	31	0.83 ± 0.16	[0.23 - 1.82]	0.05 ± 0.01	[0.01 - 0.11]	317 ± 32	0.16 ± 0.00	46.13 ± 0.51	1.31 ± 0.04	0.07 ± 0.01	0.14 ± 0.01	2.55 ± 0.09
<i>Quercus petraea</i> (A)	15	0.45 ± 0.14	[0.01 - 1.38]	0.11 ± 0.03	[0.00 - 0.26]	322 ± 29	0.15 ± 0.00	46.56 ± 0.27	1.40 ± 0.01	0.06 ± 0.00	0.13 ± 0.00	2.16 ± 0.02
<i>Platanus xhispanica</i>		0.07 ± 0.02	[0.00 - 0.21]	0.02 ± 0.01	[0.00 - 0.07]	563 ± 26	0.15 ± 0.01	48.27 ± 0.11	0.57 ± 0.01	0.03 ± 0.00	0.05 ± 0.00	1.84 ± 0.31
<i>Platanus xhispanica</i> (T)	32	0.77 ± 0.19	[0.00 - 2.35]	0.04 ± 0.01	[0.00 - 0.13]	352 ± 43	0.13 ± 0.00	47.82 ± 0.24	0.78 ± 0.12	0.05 ± 0.01	0.07 ± 0.00	2.03 ± 0.10
<i>Platanus xhispanica</i> (A)	18	0.29 ± 0.08	[0.03 - 0.69]	0.07 ± 0.02	[0.00 - 0.17]	489 ± 37	0.17 ± 0.01	48.83 ± 0.19	0.89 ± 0.02	0.04 ± 0.00	0.09 ± 0.00	1.78 ± 0.12

Table S.II.5: Detritivore species consumption rates and traits values. Detritivore species are ordered by increasing body mass, with aquatic species first. C, N, P, K, and Ca are in % of dry body mass.

Detritivore species (Order)	Dry body mass (mg)		Consumption rate (C, mg.d ⁻¹)		Consumption rate divided by body mass (mg.mg ⁻¹ .d ⁻¹)		Biting force (F index)	Mandible gape (mm)	C (%)	N (%)	P (%)	K (%)	Ca (%)
	mean ± se	[0.1 – 0.9] quantiles	mean ± se	[0.1 – 0.9] quantiles	mean ± se	[0.1 – 0.9] quantiles	mean ± se	mean ± se	mean ± se	mean ± se	mean ± se	mean ± se	mean ± se
<i>Nemoura sp.</i> (Plecoptera)	1.00 ± 0.03	[0.62 - 1.30]	0.15 ± 0.02	[0.00 - 0.43]	0.16 ± 0.02	[0.00 - 0.49]	0.50 ± 0.01	0.41 ± 0.02	43.57 ± 0.72	10.80 ± 0.09	0.86 ± 0.04	0.77 ± 0.01	0.21 ± 0.01
<i>Gammarus fossarum</i> (Amphipoda)	4.90 ± 0.17	[3.44 - 6.45]	0.61 ± 0.10	[0.01 - 1.49]	0.13 ± 0.02	[0.00 - 0.34]	0.55 ± 0.02	0.49 ± 0.02	35.09 ± 0.74	7.43 ± 0.13	0.82 ± 0.03	0.64 ± 0.03	9.70 ± 0.67
<i>Potamophylax cingulatus</i> (Trichoptera)	5.05 ± 0.30	[2.44 - 7.81]	1.44 ± 0.18	[0.34 - 2.57]	0.29 ± 0.03	[0.08 - 0.49]	0.82 ± 0.05	0.71 ± 0.09	46.20 ± 0.28	9.34 ± 0.18	1.18 ± 0.07	2.14 ± 0.23	0.25 ± 0.03
<i>Tipula sp.</i> (Diptera)	29.40 ± 4.18	[5.98 - 55.90]	0.33 ± 0.06	[0.00 - 0.74]	0.02 ± 0.00	[0.00 - 0.05]	0.73 ± 0.04	0.47 ± 0.02	46.45 ± 0.92	9.67 ± 0.28	0.87 ± 0.11	1.69 ± 0.17	0.32 ± 0.05
<i>Polydesmus inconstans</i> (Polydesmida)	6.03 ± 0.27	[3.57 - 9.18]	0.57 ± 0.10	[0.02 - 1.21]	0.10 ± 0.02	[0.00 - 0.18]	0.86 ± 0.04	0.33 ± 0.01	27.66 ± 0.41	5.49 ± 0.16	2.10 ± 0.16	0.61 ± 0.04	17.78 ± 0.93
<i>Philoscia affinis</i> (Isopoda)	6.35 ± 0.36	[4.07 - 10.48]	0.38 ± 0.06	[0.00 - 0.87]	0.07 ± 0.01	[0.00 - 0.16]	0.81 ± 0.04	0.79 ± 0.08	38.42 ± 0.49	7.76 ± 0.09	1.40 ± 0.10	0.93 ± 0.09	8.74 ± 0.84
<i>Porcellio monticola</i> (Isopoda)	14.66 ± 0.68	[9.23 - 22.01]	0.64 ± 0.07	[0.02 - 1.50]	0.06 ± 0.02	[0.00 - 0.09]	0.98 ± 0.02	1.00 ± 0.02	33.15 ± 0.68	5.78 ± 0.03	1.23 ± 0.05	0.60 ± 0.02	13.46 ± 0.08
<i>Glomeris marginata</i> (Glomerida)	56.59 ± 1.97	[40.28 - 78.74]	0.22 ± 0.06	[0.00 - 0.43]	0.00 ± 0.00	[0.00 - 0.01]	2.63 ± 0.04	1.13 ± 0.06	30.69 ± 0.61	4.87 ± 0.14	1.88 ± 0.07	0.31 ± 0.01	15.25 ± 0.66
<i>Cylindroiulus londinensis</i> (Julida)	156.70 ± 5.16	[107.32 - 203.12]	1.33 ± 0.30	[0.00 - 2.50]	0.01 ± 0.00	[0.00 - 0.02]	1.62 ± 0.25	1.06 ± 0.05	27.38 ± 0.66	4.32 ± 0.14	1.56 ± 0.09	0.28 ± 0.02	13.90 ± 1.37

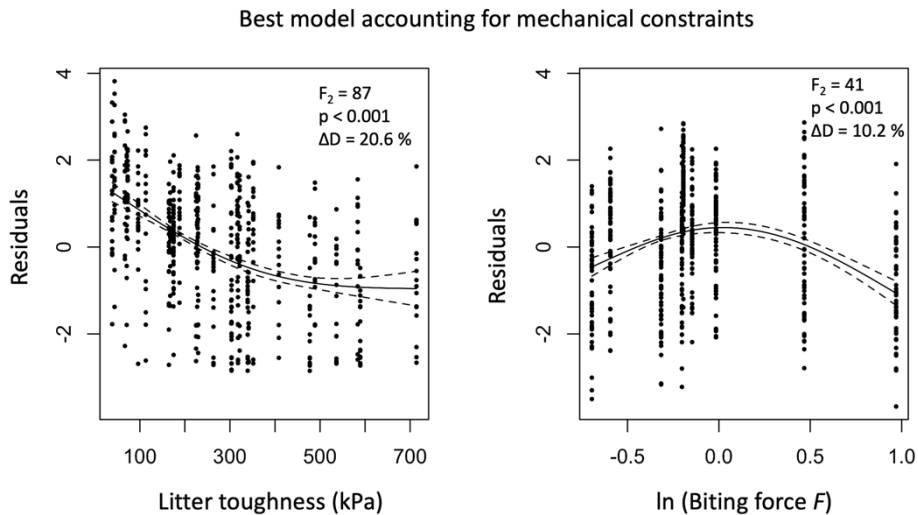


Figure S.II.4: Best model accounting for mechanical constraints. Each window shows the effect of a parameter on residuals. ΔD is the difference in deviance explained by the model when the parameter is added. Parameters are ordered by decreasing ΔD . Total model explained 30.8 % of deviance.

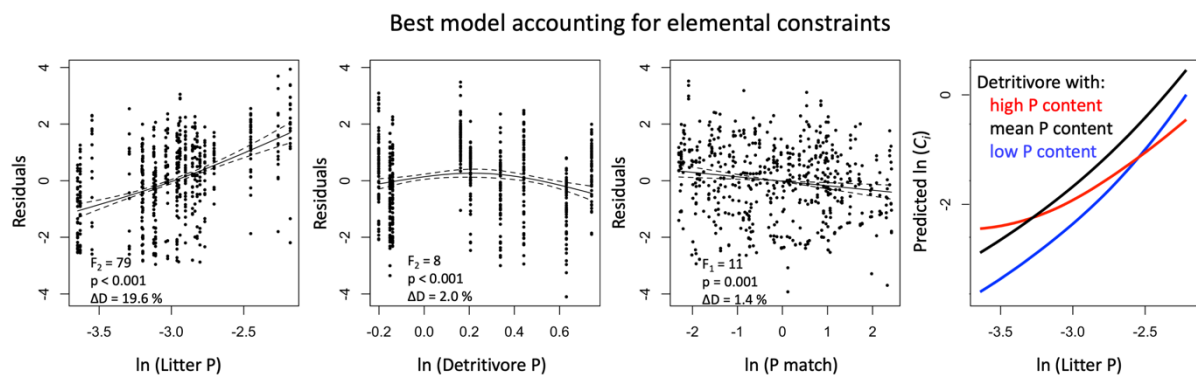


Figure S.II.5: Best model accounting for elemental constraints. The three first windows show the effect of a parameter on residuals. ΔD is the difference in deviance explained by the model when the parameter is added. Parameters are ordered by decreasing ΔD . Total model explained 24.9 % of deviance. The fourth panel of the right shows $\ln (C_i)$ predictions as a function of litter P, for detritivores with highest (red line) and lowest P content (blue line). The black line represents the predictions for a hypothetical detritivore species with a mean P value.

Best model accounting for both mechanical and elemental constraints

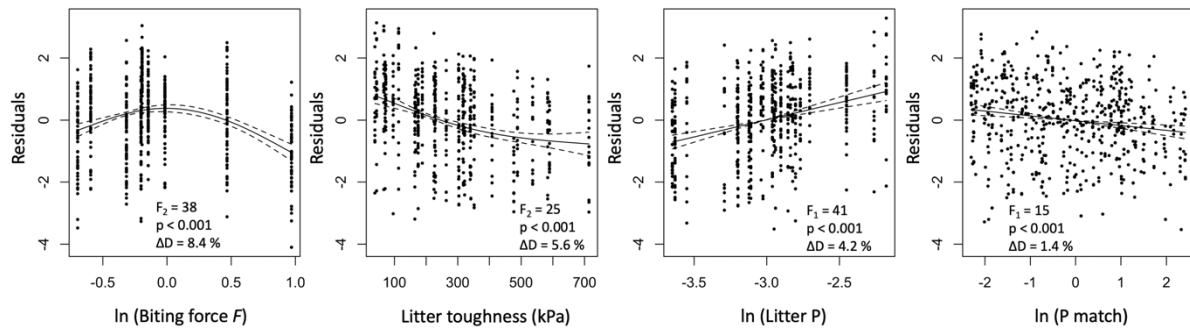


Figure S.II.6: Best model accounting for both mechanical and elemental constraints. Each window shows the effect of a parameter on residuals. ΔD is the difference in deviance explained by the model when the parameter is added. Parameters are ordered by decreasing ΔD . Total model explained 36.6 % of deviance.

APPENDIX CHAPTER III

Supplementary Material for:

Mechanical traits as drivers of trophic interaction between macrodetritivores and leaf litterThéo Marchand¹, Benjamin Pey¹, Corinne Pautot¹, Antoine Lecerf¹¹ Laboratoire Écologie Fonctionnelle et Environnement, Université de Toulouse, CNRS, Toulouse, France**Table S.III.1: Water characteristics of the two stream sites determined once (11th January 2021) with a WTWTM multi-parameter field meter (ref. Multi 3420 SET C).**

	pH	Conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$)	O ₂ (mg.L ⁻¹)	T (°C)
“Oak” stream	8.3	383	12.7	1.6
“Hornbeam” stream	8.4	569	13.2	1.5

Table S.III.2: Soil characteristics of the two terrestrial sites. Values for each site were determined based a composite sample made by mixing four spatial replicates.

	Texture			pH	Carbonates (g.kg ⁻¹)	Organic matter (g.kg ⁻¹)	Cation Exchange Capacity (Metson) (mol.kg ⁻¹)
	Sand (%)	Silt (%)	Clay (%)				
“Oak” site	23.0	47.7	29.3	4.6	< 5	33.1	106
“Hornbeam” site	22.8	56.9	20.3	5.0	< 5	28.8	67

Table S.III.3: Regional weather (Palminy station – 30km from field sites, Meteo-france.fr data of 2002-2020 period)

Mean annual temperature (°C)	Total annual precipitations (mm)
13.2	715

Table S.III.4: Weather conditions (mean \pm se values) one week before each detritivore sampling on the field. Loggers were left on the field during the whole experiment, recording one measurement each hour. Loggers in streams were Hobo® UA-002-64 attached in the water. Loggers in terrestrial sites were Hobo® MX2302A placed in a hole (5cm deep) in the soil.

Field site	Dates	Temperature (°C)	Relative Humidity (%)
"Oak" stream	t0: 01/12/2020	6.84 \pm 0.09	NA
	t1: 11/01/2021	3.72 \pm 0.08	
	t2: 25/02/2021	9.17 \pm 0.12	
"Hornbeam" stream	t0: 01/12/2020	7.15 \pm 0.09	
	t1: 11/01/2021	-0.20 \pm 0.11	
	t2: 25/02/2021	8.94 \pm 0.14	
"Oak" site	t0: 26/11/2020	9.30 \pm 0.07	46.7 \pm 2.2
	t1: 10/02/2021	8.52 \pm 0.06	47.1 \pm 2.0
	t2: 11/03/2021	9.31 \pm 0.06	48.5 \pm 2.3
	t3: 01/06/2021	13.68 \pm 0.10	52.4 \pm 2.3
	t4: 13/07/2021	16.61 \pm 0.06	47.9 \pm 2.4
	t5: 02/11/2021	12.81 \pm 0.06	50.4 \pm 2.3
"Hornbeam" site	t0: 26/11/2020	7.09 \pm 0.08	46.6 \pm 2.1
	t1: 10/02/2021	7.67 \pm 0.07	44.2 \pm 2.1
	t2: 11/03/2021	8.31 \pm 0.09	50.9 \pm 2.4
	t3: 19/04/2021	7.45 \pm 0.08	51.0 \pm 2.3
	t4: 13/07/2021	15.89 \pm 0.09	50.7 \pm 2.3

Table S.III.5: individual body mass, morphological traits used for the calculation of the biting force index, and frequency of feeding experiments for each macrodetritivore taxa. M_W is mandible width; M_L is mandible length. The ratio between M_W and M_L represents the mechanical advantage of the mandible (Brousseau et al., 2018; Wheeler and Evans, 1989). Taxa are presented by increasing mean body mass, with aquatic macrodetritivores first.

Taxa	Dry body mass (mg)		Head width (% of body length, mean \pm se)	M_W / M_L (mean \pm se)	Molar length (% of body length, mean \pm se)	Litter exposition in the field (t = days since the start number of replicates (n) for litter feeding experiments at each time point)	
	(mean \pm se)	[0.1 – 0.9] quantiles				Hornbeam	Oak
<i>Capnia</i>	0.87 \pm 0.08	[0.50 – 1.35]	16.3 \pm 1.5, n=5	0.52 \pm 0.01, n=5	1.34 \pm 0.20, n=5	t = 0, 54, 99 n = 4, 10, 5	
<i>Gammarus</i>	9.32 \pm 0.50	[5.45 – 13.51]	8.8 \pm 0.2, n=11	0.49 \pm 0.02, n=11	1.65 \pm 0.06, n=11	t = 0, 54, 99 n = 4, 9, 5	t = 0, 54, 99 n = 7, 10, 8
Limnephilinae	24.25 \pm 1.95	[8.63 – 41.82]	11.3 \pm 1.1, n=10	0.48 \pm 0.01, n=10	2.27 \pm 0.27, n=9	t = 0, 54, 99 n = 6, 9, 5	t = 0, 54, 99 n = 6, 10, 8
<i>Philoscia</i>	6.71 \pm 0.36	[3.46 – 9.76]	21.9 \pm 0.6, n=10	0.48 \pm 0.01, n=10	1.28 \pm 0.08, n=10	t = 82, 111, 152, 236 n = 3, 7, 4, 5	t = 0, 82, 111, 195, 236, 349 n = 4, 3, 5, 5, 4, 5
<i>Porcellio</i>	13.25 \pm 1.06	[3.88 – 20.44]	21.6 \pm 0.6, n=10	0.53 \pm 0.02, n=10	1.49 \pm 0.06, n=10	t = 82, 111, 152, 236 n = 4, 7, 8, 9	t = 0, 82, 111, 195, 236, 349 n = 3, 4, 5, 3, 3, 1
<i>Leptoiulus</i>	14.16 \pm 1.30	[7.98 – 21.57]	4.8 \pm 0.1, n=11	0.62 \pm 0.03, n=11	0.75 \pm 0.02, n=11	t = 82, 111, 236 n = 7, 2, 4	t = 0, 82, 111, 195, 236, 349 n = 2, 3, 1, 2, 2, 3
<i>Glomeris</i>	87.10 \pm 8.45	[25.33 – 165.02]	23.9 \pm 0.6, n=10	0.79 \pm 0.02, n=10	3.27 \pm 0.08, n=10	t = 82, 111, 152, 236 n = 2, 4, 6, 3	t = 0, 82, 111, 195, 236, 349 n = 1, 5, 5, 4, 5, 7
<i>Cylindroiulus</i>	179.09 \pm 15.89	[98.19 – 296.88]	7.7 \pm 0.3, n=10	0.66 \pm 0.03, n=10	1.29 \pm 0.05, n=10	t = 82, 111, 152, 236 n = 1, 3, 6, 3	t = 82, 111, 195, 236, 349 n = 2, 1, 3, 3, 5

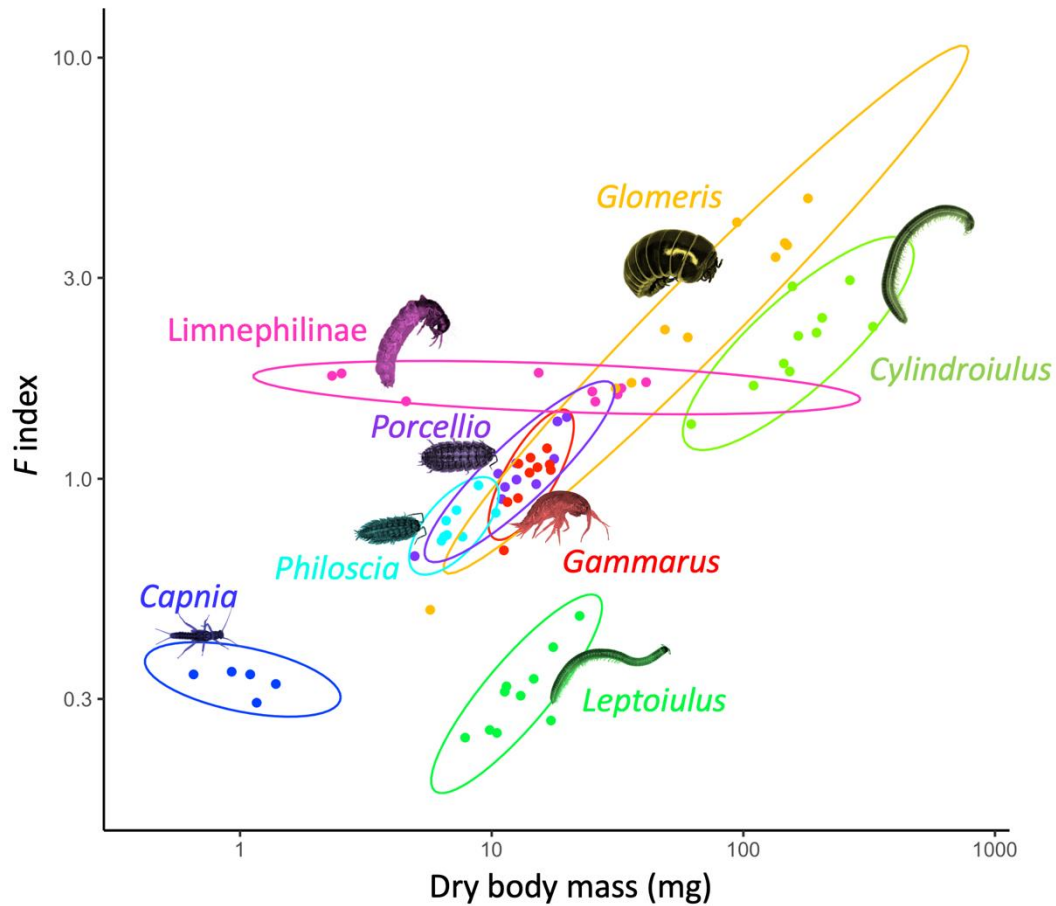


Figure S.III.1: Representation of macrodetritivore taxa in a 2-D plane based on morphological traits. Each point is a dissected individual. Dry body mass is in mg. The F index is the biting force index, a proxy for mandibular strength. It is the head width multiplied by the lever arm of the mandible (Mandible width / Mandible length). X and Y are log scales. For all macrodetritivore taxa, ellipses depict 95% confidence intervals.

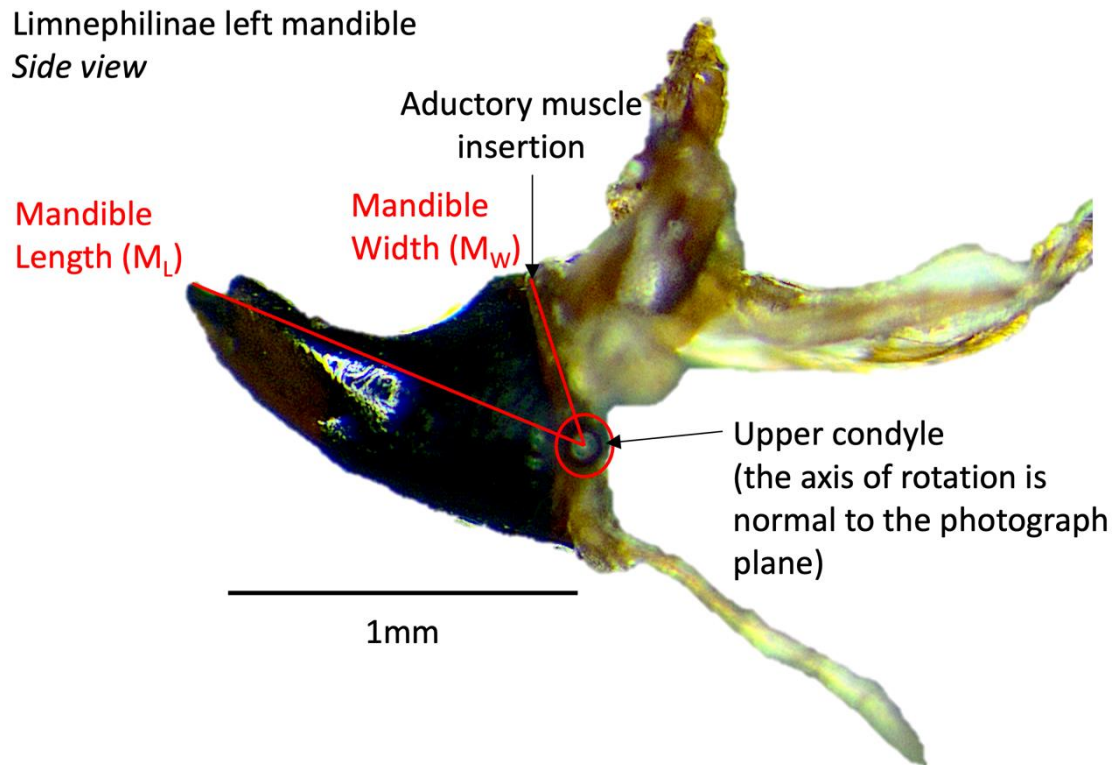


Figure S.III.2: Left mandible of a *Limnephilinae*. The mandible was dissected under an Olympus SZX10 for precise measurements of mandible length (M_L) and width (M_W).

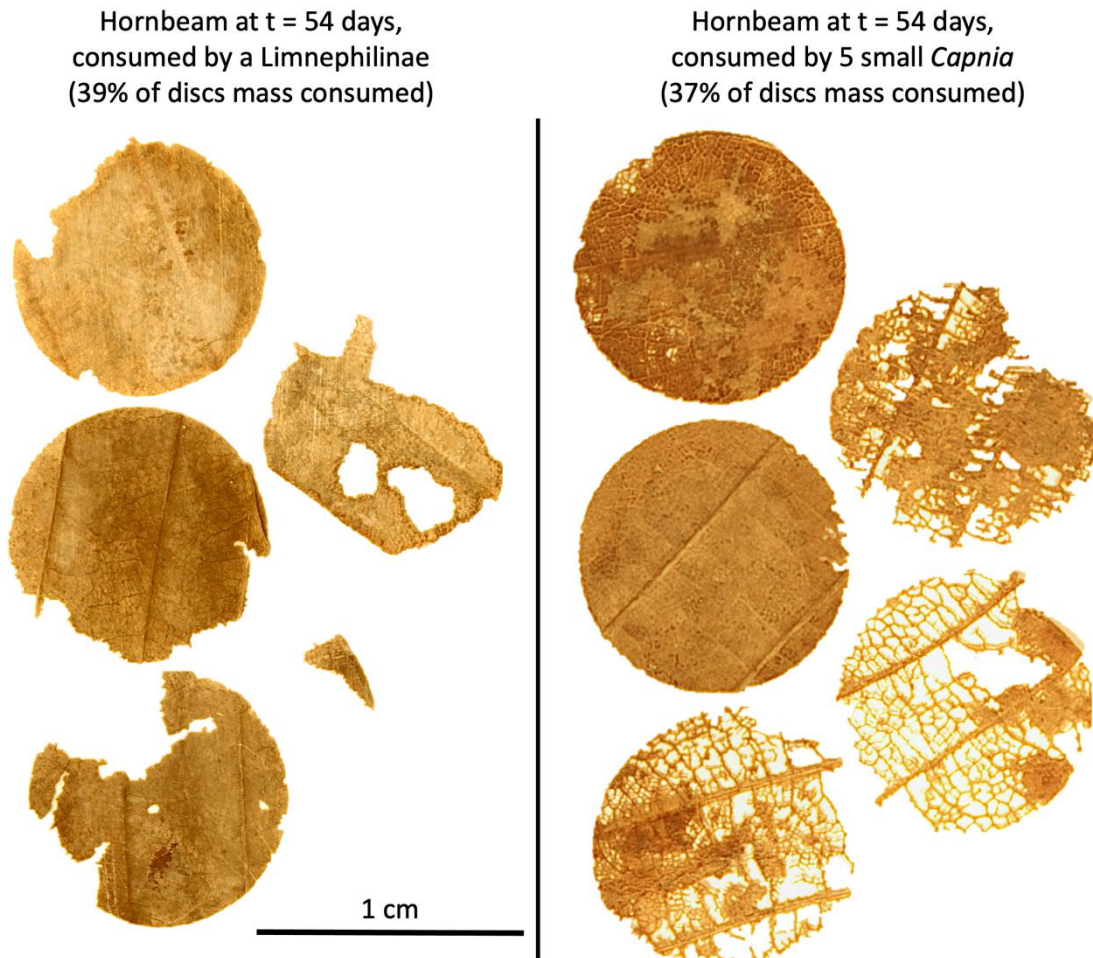


Figure S.III.3: Photographs of remaining litter of five hornbeam discs at the end of feeding experiments with a *Limnephilinae* individual (left) or five small *Capnia* (right). Those photographs suggest that *Limnephilinae* cut discs through the limb and consumed big chunks of leaves whereas *Capnia* scrap the surface (this is especially visible on the upper disc) and tear apart small fragments from the discs. Initial discs are all 1cm diameter. Photo credit: Valentina Soto.

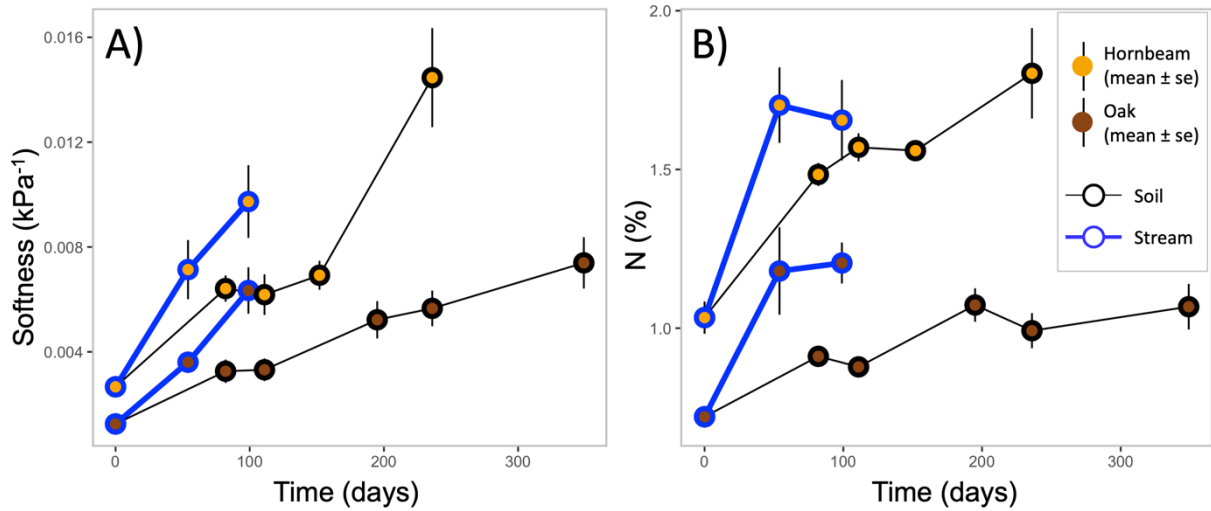


Figure S.III.4: Litter (A) softness and (B) N content over time. Data for hornbeam and oak are represented by yellow and brown circles, respectively. Values for litter exposed to microbial decomposition in streams and soils, are connected by thick blue and thin black traits, respectively. Dots show mean \pm se values.

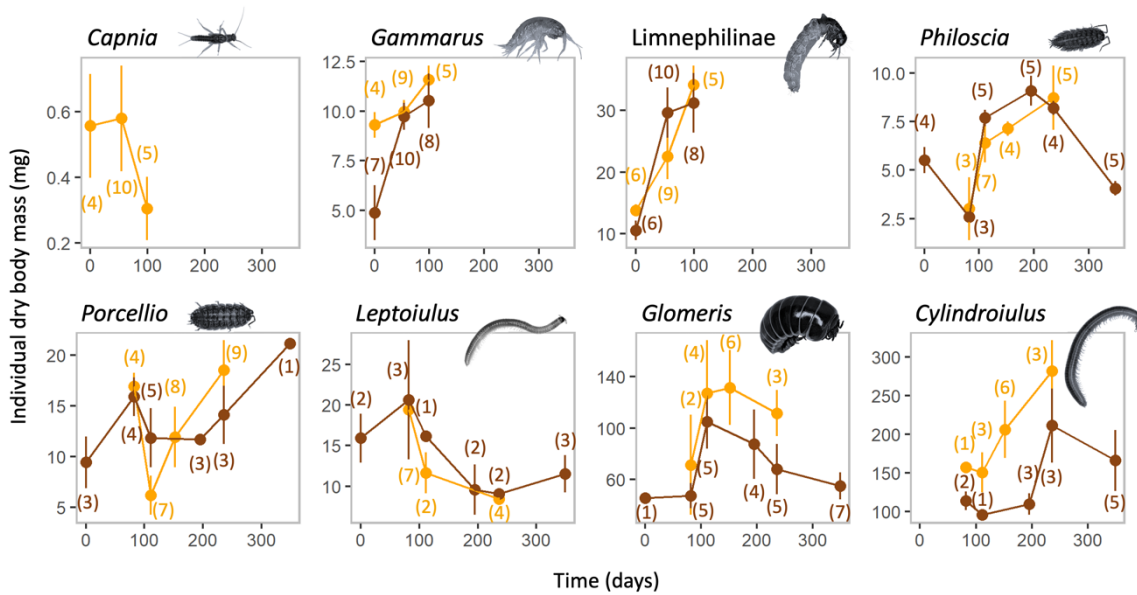


Figure S.III.5: Individual dry body mass over time for each macrodetritivore taxon. Oak and hornbeam litters are represented by brown and orange circles, respectively. Values are mean \pm se. Vertical scales are different for each macrodetritivore taxa. Numbers in parenthesis indicate the number of replicates (i.e., the number of separately tested individuals, except for *Capnia*, see material and methods section) that were used at each time point.

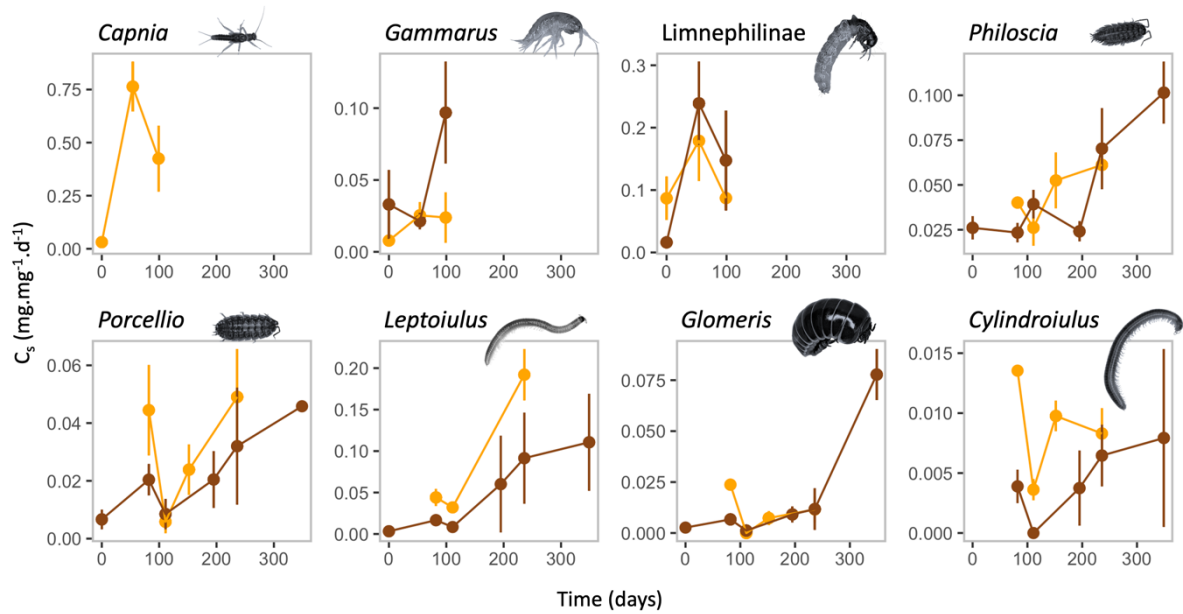


Figure S.III.6: Mass-specific rate of litter consumption (C_s) over time for each macrodetritivore taxa. Oak and hornbeam litters are represented by brown and orange circles, respectively. Values are means \pm se. Vertical scales are different for each macrodetritivore taxa.

APPENDIX CHAPTER IV

Supplementary Material for:

Leaf litter chemistry contributes to shape detritivore community's functionality

Théo Marchand¹, Matthieu Chauvat², Estelle Forey², Florence Maunoury-Danger³, Mathieu Santonja⁴, Mickaël Danger³, Philippe Usseglio-Polatera³, David Baqué¹, Frédéric Candaudap¹, Sophia Hansson¹, Frédéric Julien¹, Christophe Laplanche¹, Gaël Le Roux¹, Virginie Baldy⁴, Raphaël Gros⁴, Benjamin Pey¹

¹ Laboratoire Écologie Fonctionnelle et Environnement, Université Paul Sabatier, CNRS, Toulouse, France

² Ecodiv URA/EA-1293, Normandie Université, Université de Rouen, IRSTEA, SFR Scale 4116, UFR Sciences et Techniques, 76821 Mont Saint Aignan Cedex, France

³ Laboratoire interdisciplinaire des environnements continentaux, CNRS UMR 7360, Université de Lorraine, 8, rue du général Delestraint, 57070 Metz, France

⁴ Aix Marseille Université, Avignon Université, CNRS, IRD, IMBE, Marseille, France

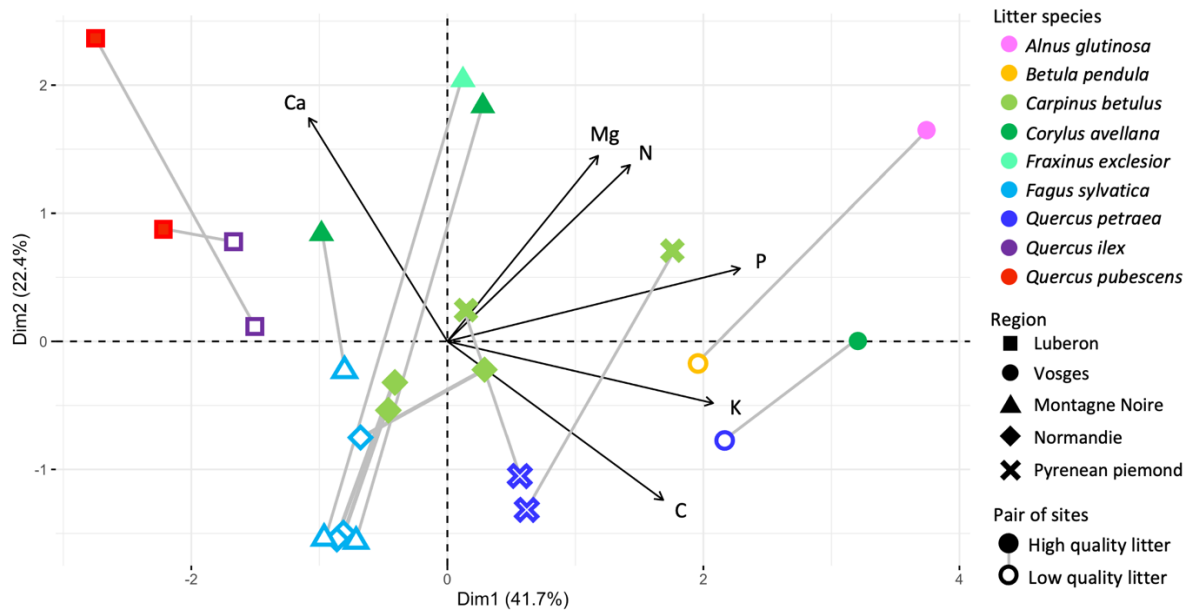


Figure S.IV.1: Litter chemical traits. Litter of a-priori higher quality is always higher in the graph than the litter of lower quality from the corresponding site of each pair. The first two axis represent 64.1% of variability.

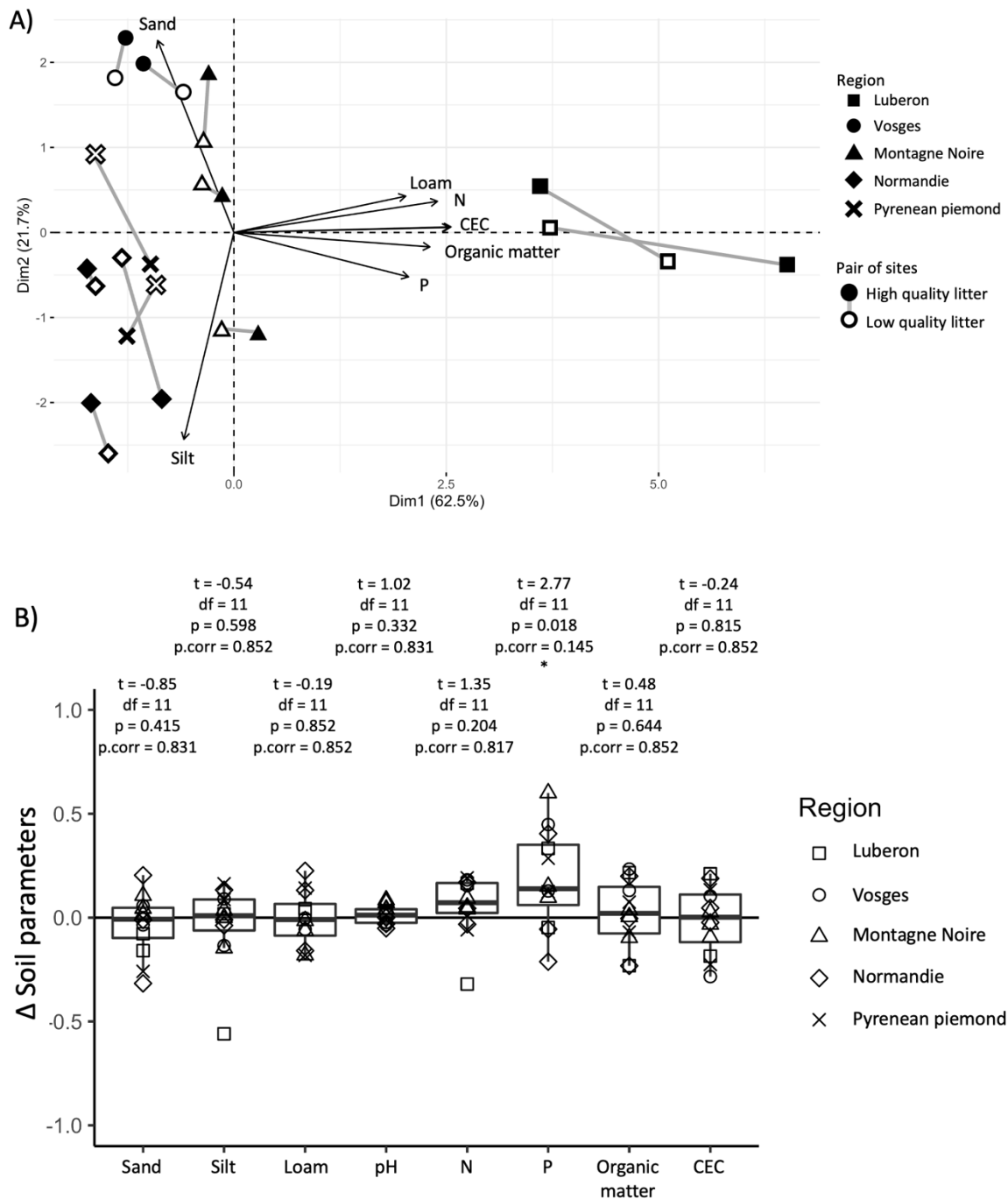


Figure S.IV.2: Soil parameters represented by (A) a PCA and (B) Δ indexes. (A) PCA of soil parameters. The first two axis represent 84.2 % of variability. Soils group by pedo-climatic region. (B) Δ indexes (differences between both sites of each pair) for soil parameters. For each index, a t-test was performed to test if Δ values significantly differed from zero. A Δ value above zero indicates that the corresponding metric has a higher value on the site with a higher quality litter than on the other site of the same pair. T-value (t), degree of freedom (df), p-value (p), and corrected p-value (p.corr) are indicated. One asterisk (*) indicates a non-corrected p-value

< 0.05 and a corrected p -value ≥ 0.05 while two asterisks (**) indicate that both p -values are < 0.05 . Each pedo-climatic region is indicated by a symbol.

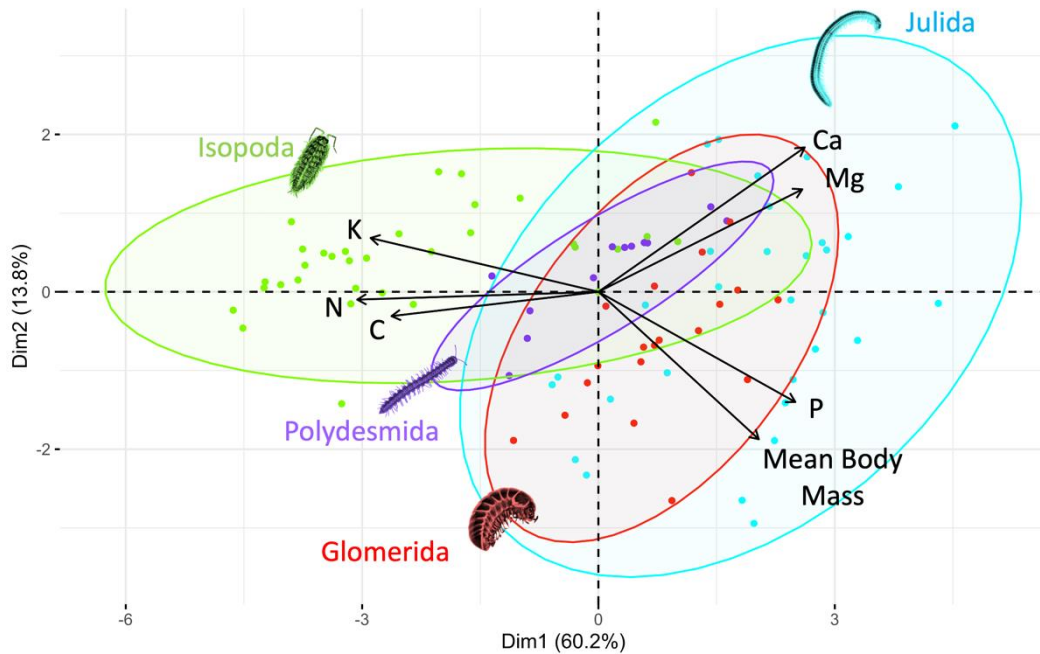


Figure S.IV.3: PCA of detritivore traits. Each point is a morphospecies belonging to one site. Detritivores are grouped by Orders (95% - confidence ellipses). The first two axis represent 74 % of variability.

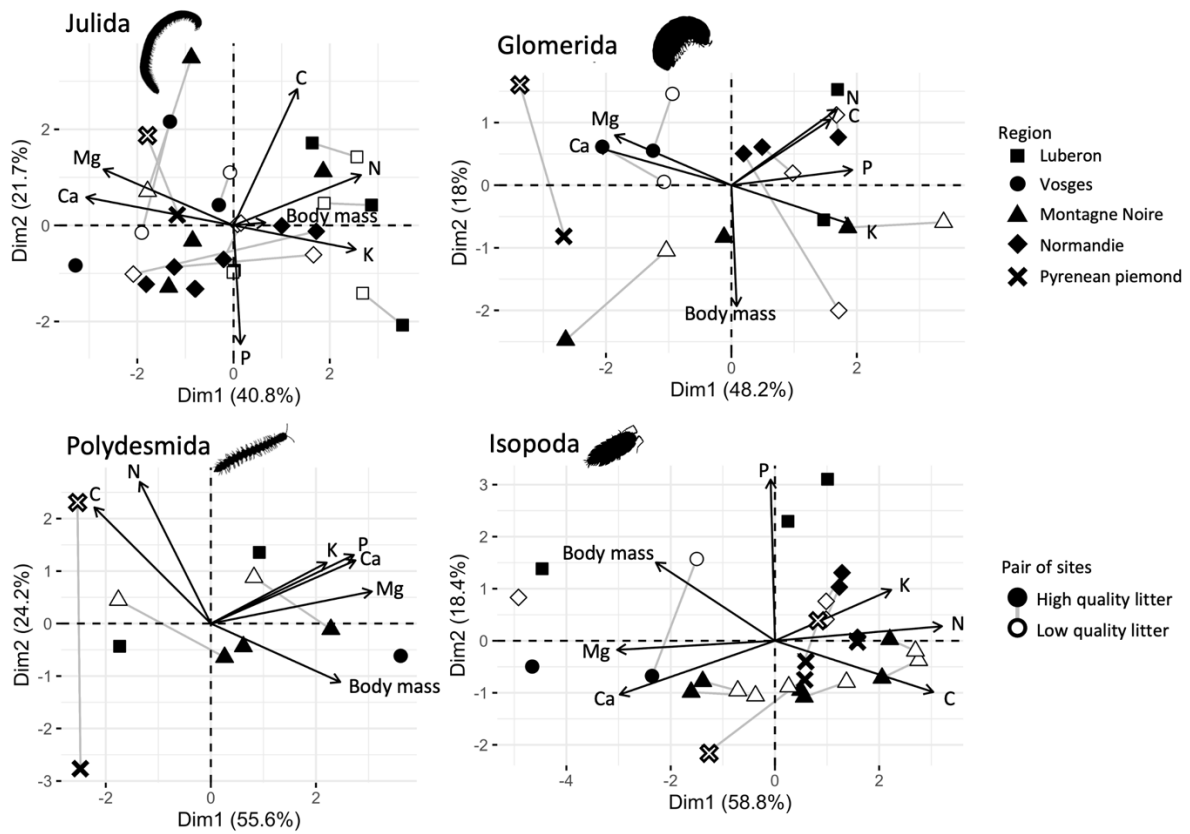


Figure S.IV.4: PCA of detritivore traits for each Order. Each point is a morphospecies belonging to one site. When a morphospecies was found on both sites of each pair, points are connected with a grey line. The first two axis represent at least 62.5 % of variability.

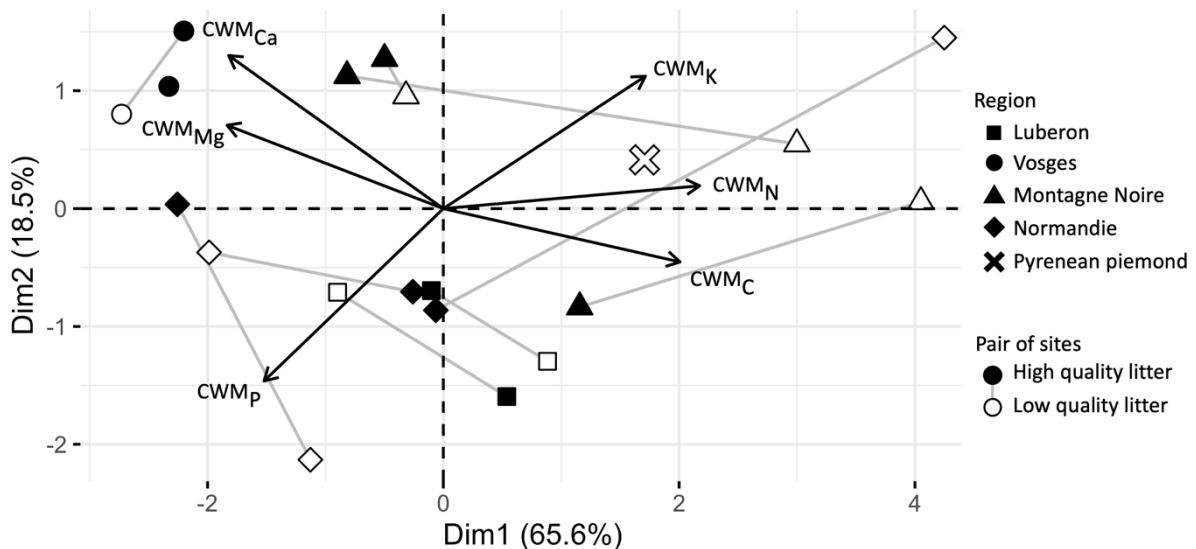


Figure S.IV.5: PCA of detritivore Community Weighted Means (CWM) for each of C, N, P, K, Ca, and Mg elements. Each point is a detritivore community. Paired sites are connected with a grey line. The first two axis represent 84.1 % of variability.

Table S.IV.1: Characteristics of each pair of sites.

Region	Soil	Main Litter of each site (Palatable litter – refractory litter)	Latitude	Longitude	Elevation (m)	Mean annual T(°C) (Météo-France, 1991 – 2020 data, closest station)	Mean annual precipitations (mm) (Météo-France, 1991 – 2020 data, closest station)
Pyrenean piemond	Calcosol	<i>Carpinus betulus</i> – <i>Quercus petraea</i>	43.30	0.85	350	13.2	715
	Calcosol	<i>Carpinus betulus</i> – <i>Quercus petraea</i>	43.24	0.84	375	(Palaminy (31))	(Palaminy (31))
Montagne Noire	Brunisol	<i>Fraxinus excelsior</i> – <i>Fagus sylvatica</i>	43.40	2.16	625	13.8	896
	Rankosol	<i>Corylus avellana</i> – <i>Fagus sylvatica</i>	43.44	2.10	650		
	Brunisol - Rankosol	<i>Corylus avellana</i> – <i>Fagus sylvatica</i>	43.45	2.20	725	(Dourgne (81))	(Dourgne (81))
Normandie	Brunisol	<i>Carpinus betulus</i> – <i>Fagus sylvatica</i>	49.44	0.70	50	10.9	848
	Brunisol	<i>Carpinus betulus</i> – <i>Fagus sylvatica</i>	49.43	0.74	25		
	Brunisol	<i>Carpinus betulus</i> – <i>Fagus sylvatica</i>	49.44	0.77	50	(Rouen-Boos (76))	(Rouen-Boos (76))
Luberon	Calcosol	<i>Quercus pubescens</i> – <i>Quercus ilex</i>	43.80	5.31	500	14	697
	Calcosol	<i>Quercus pubescens</i> – <i>Quercus ilex</i>	43.80	5.31	500	(Cabrieres d'Avignon (84))	(Cabrieres d'Avignon (84))
Vosges	Brunisol	<i>Alnus glutinosa</i> – <i>Betula pendula</i>	48.51	7.11	475	10.5	837
	Brunisol	<i>Corylus avellana</i> – <i>Quercus sp.</i>	48.51	7.11	475	(St Maurice (54))	(St Maurice (54))

Table S.IV.2: Detritivore traits for each Order

	Number of CN analyses	C (%)	N (%)	Number of ICP analyses	P (%)	K (%)	Ca (%)	Mg (%)	Number of weighted individuals	Individual dry body mass (mg)
Isopoda	54	34.63 ± 0.56	6.31 ± 0.14	50	1.24 ± 0.02	0.73 ± 0.02	9.10 ± 0.39	0.25 ± 0.01	499	13.66 ± 0.51
Julida	47	29.67 ± 0.64	4.53 ± 0.13	46	1.97 ± 0.04	0.40 ± 0.01	12.30 ± 0.49	0.47 ± 0.02	374	91.22 ± 5.25
Polydesmida	18	28.85 ± 0.65	5.39 ± 0.11	16	1.85 ± 0.06	0.55 ± 0.01	11.12 ± 0.67	0.32 ± 0.03	63	19.20 ± 1.88
Glomerida	41	30.95 ± 0.57	4.64 ± 0.13	40	1.87 ± 0.05	0.36 ± 0.01	11.16 ± 0.44	0.27 ± 0.01	365	60.76 ± 2.33

Table S.IV.3: Litter chemical traits for each site. For each pair, the first site is the site with the low-quality litter, and the second site is the site with the high-quality litter.

Region	Paire of site	Litter	C (%)	N (%)	P (%)	K (%)	Ca (%)	Mg (%)
Luberon	1	<i>Q. ilex</i>	46.50 ± 0.46	1.19 ± 0.07	0.06 ± 0.00	0.11 ± 0.01	2.13 ± 0.15	0.10 ± 0.00
		<i>Q. pubescens</i>	43.21 ± 0.47	0.97 ± 0.07	0.06 ± 0.00	0.16 ± 0.01	3.61 ± 0.26	0.17 ± 0.02
	2	<i>Q. ilex</i>	46.43 ± 0.54	1.05 ± 0.06	0.06 ± 0.01	0.18 ± 0.02	2.92 ± 0.48	0.13 ± 0.01
		<i>Q. pubescens</i>	43.80 ± 1.11	0.90 ± 0.04	0.06 ± 0.01	0.17 ± 0.01	2.35 ± 0.11	0.12 ± 0.00
Normandie	1	<i>F. sylvatica</i>	46.25 ± 0.21	0.89 ± 0.08	0.06 ± 0.01	0.46 ± 0.08	0.74 ± 0.05	0.07 ± 0.01
		<i>C. betulus</i>	45.48 ± 0.35	1.05 ± 0.09	0.06 ± 0.01	0.43 ± 0.02	0.59 ± 0.03	0.18 ± 0.02
	2	<i>F. sylvatica</i>	45.95 ± 0.82	0.96 ± 0.23	0.07 ± 0.02	0.35 ± 0.06	0.87 ± 0.13	0.14 ± 0.03
		<i>C. betulus</i>	45.71 ± 0.20	1.33 ± 0.13	0.10 ± 0.02	0.49 ± 0.08	0.62 ± 0.04	0.18 ± 0.00
	3	<i>F. sylvatica</i>	46.40 ± 0.46	0.84 ± 0.09	0.06 ± 0.01	0.44 ± 0.06	0.72 ± 0.08	0.08 ± 0.01
		<i>C. betulus</i>	45.10 ± 0.12	1.18 ± 0.09	0.10 ± 0.01	0.32 ± 0.01	0.64 ± 0.03	0.14 ± 0.01
Montagne Noire	1	<i>F. sylvatica</i>	47.52 ± 0.37	1.08 ± 0.10	0.04 ± 0.00	0.25 ± 0.02	0.52 ± 0.04	0.11 ± 0.01
		<i>C. avellana</i>	45.10 ± 0.40	1.50 ± 0.04	0.10 ± 0.01	0.39 ± 0.13	1.60 ± 0.13	0.32 ± 0.01
	2	<i>F. sylvatica</i>	47.81 ± 0.11	1.01 ± 0.06	0.05 ± 0.01	0.15 ± 0.02	0.82 ± 0.07	0.09 ± 0.01
		<i>F. excelsior</i>	45.87 ± 0.62	2.41 ± 0.04	0.08 ± 0.01	0.15 ± 0.01	1.79 ± 0.07	0.24 ± 0.01
	3	<i>F. sylvatica</i>	47.14 ± 2.90	0.84 ± 0.05	0.04 ± 0.00	0.14 ± 0.02	1.06 ± 0.05	0.26 ± 0.01
		<i>C. avellana</i>	43.20 ± 4.63	1.32 ± 0.14	0.04 ± 0.01	0.41 ± 0.12	0.81 ± 0.22	0.24 ± 0.07
Pyrenean piemond	1	<i>Q. petraea</i>	47.38 ± 0.06	0.70 ± 0.07	0.05 ± 0.00	1.01 ± 0.10	1.10 ± 0.09	0.21 ± 0.03
		<i>C. betulus</i>	46.01 ± 0.12	0.87 ± 0.05	0.09 ± 0.01	0.46 ± 0.11	1.03 ± 0.02	0.27 ± 0.03
	2	<i>Q. petraea</i>	47.80 ± 0.15	0.71 ± 0.10	0.07 ± 0.01	0.86 ± 0.13	0.94 ± 0.13	0.19 ± 0.04
		<i>C. betulus</i>	46.34 ± 0.28	0.92 ± 0.03	0.14 ± 0.02	0.95 ± 0.29	1.34 ± 0.28	0.31 ± 0.04
Vosges	1	<i>Q. sp</i>	48.68 ± 0.23	1.27 ± 0.10	0.18 ± 0.02	0.74 ± 0.05	0.97 ± 0.12	0.16 ± 0.01
		<i>C. avellana</i>	47.38 ± 0.25	1.62 ± 0.04	0.20 ± 0.01	1.25 ± 0.19	1.10 ± 0.03	0.19 ± 0.01
	2	<i>B. pendula</i>	49.13 ± 0.90	1.36 ± 0.03	0.14 ± 0.01	0.63 ± 0.11	1.19 ± 0.04	0.24 ± 0.00
		<i>A. glutinosa</i>	48.40 ± 1.42	3.31 ± 0.12	0.19 ± 0.01	0.73 ± 0.11	1.06 ± 0.08	0.24 ± 0.03

Table S.IV.4: Detritivore abundances on each site. For each pair, the first site is the site with the low-quality litter, and the second site is the site with the high-quality litter. Detected morphospecies number does not take into account sight-hunted individuals.

Region	Paire of sites	Litter	Isopoda		Julida		Polydesmida		Glomerida		Total	
			Abundance (Nb individuals / m2)	Morphospecies number	Abundance (Nb individuals / m2)	Morphospecies number	Abundance (Nb individuals / m2)	Morphospecies number	Abundance (Nb individuals / m2)	Morphospecies number	Abundance (Nb individuals / m2)	Morphospecies number
Luberon	1	<i>Q. ilex</i>	3.2	1	240	2	0	0	0	0	252.8	3
		<i>Q. pubescens</i>	32	1	134.4	2	19.2	1	118.4	1	304	5
	2	<i>Q. ilex</i>	6.4	1	89.6	3	0	0	0	0	102.4	4
		<i>Q. pubescens</i>	108.8	3	150.4	3	60.8	1	99.2	2	428.8	9
Normandie	1	<i>F. sylvatica</i>	6.4	1	22.4	2	3.2	1	12.8	1	51.2	5
		<i>C. betulus</i>	51.2	2	35.2	2	0	0	0	0	86.4	4
	2	<i>F. sylvatica</i>	22.4	2	22.4	2	0	0	3.2	1	51.2	5
		<i>C. betulus</i>	19.2	2	3.2	1	3.2	1	6.4	1	32	5
	3	<i>F. sylvatica</i>	6.4	1	0	0	0	0	0	0	6.4	1
		<i>C. betulus</i>	9.6	1	0	0	0	0	12.8	1	22.4	2
Montagne Noire	1	<i>F. sylvatica</i>	12.8	3	0	0	0	0	0	0	12.8	3
		<i>C. avellana</i>	22.4	2	3.2	1	0	0	0	0	25.6	3
	2	<i>F. sylvatica</i>	19.2	2	0	0	0	0	0	0	19.2	2
		<i>F. excelsior</i>	38.4	2	22.4	2	3.2	1	0	0	64	5
	3	<i>F. sylvatica</i>	32	3	3.2	1	0	0	0	0	38.4	4
		<i>C. avellana</i>	102.4	3	25.6	1	19.2	2	3.2	1	150.4	7
Pyrenean piemond	1	<i>Q. petraea</i>	0	0	0	0	0	0	0	0	0	0
		<i>C. betulus</i>	0	0	0	0	0	0	0	0	0	0
	2	<i>Q. petraea</i>	9.6	3	0	0	9.6	1	0	0	19.2	4
		<i>C. betulus</i>	0	0	0	0	0	0	0	0	0	0
Vosges	1	<i>Q. sp</i>	5.3	1	0	0	26.7	1	0	0	32	2
		<i>C. avellana</i>	0	0	5.3	1	10.7	1	5.3	1	21.3	3
	2	<i>B. pendula</i>	10.7	1	10.7	1	10.7	1	0	0	32	3
		<i>A. glutinosa</i>	53.3	1	0	0	10.7	1	21.3	1	85.3	3