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Animal-mediated terrestrial nutrient dynamics : investigating wastes, trophic transfer, and isotopic patterns

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Animal-mediated terrestrial nutrient dynamics: investigating wastes, trophic transfer, and isotopic patterns

by

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PhD thesis in Organism biology

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Animal-mediated terrestrial nutrient dynamics: investigating wastes, trophic transfer, and isotopic patterns

Abstract

Certain chemical elements are particularly important for organisms. Carbon (C), the skeleton of biomolecules, nitrogen (N) from proteins essential to all functions, and phosphorus (P), at the heart of the chemical energy of ATP, are so important that the structure of terrestrial ecosystems depends in part on the flow of these elements, but also on the relative proportion, or stoichiometry, of these elements in the soil. Heterotrophs, particularly animals, feed and produce waste in the form of faeces and urine containing these elements (C, N, P), the fate of which highly depends on the quantity and quality of this waste. Quantity and quality vary between species depending on physiological and dietary parameters, but this relationship is poorly documented. Body mass, which determines an individual's metabolic rate, as well as diet (herbivore, carnivore, omnivore, detritivore), resource quantity and quality are all factors likely to influence the quality and quantity of waste produced by animals, as well as the chemical homeostasis of their own body.

To study the factors determining the chemical composition of faeces and the chemical homeostasis of the animal on a broad phylogenetic scale, we assembled bibliographical data on a large number of terrestrial animal species and carried out new measurements. The analysis of this dataset shows that diet and resource quality are the main factors affecting waste composition. We also conducted an experiment to determine the effect of resource quantity on the chemical homeostasis, retention time and chemical properties of faeces in *Spodoptera littoralis*, both for the elements (C, N, P) and for certain isotopes of carbon and nitrogen. The reduction in the quantity of resources induces major physiological changes, including an increase in the efficiency of elemental absorption and of heavy isotopes, and conversely a reduction in the excretion

of nutrients (including N and P). This leads to an increase in the retention time of nutrients in the biomass and a reduction in the quality and quantity of waste products. In short, recycling slows down when resources become scarce. These results show that animals are biogeochemical nodes capable of adaptations to resource availability that should influence nutrient cycles and the properties of trophic chains.

Dynamique terrestres des nutriments médiée par les animaux: étude des déchets, du transfert trophique et des signatures isotopiques

Résumé

Certains éléments chimiques sont particulièrement importants pour les organismes. Le carbone (C), le squelette des biomolécules, l'azote (N) des protéines essentielles à toute fonction, et le phosphore (P), au cœur de l'énergie chimique de l'ATP sont si importants que la structure des écosystèmes terrestres, dépend en partie des flux de ces éléments, ainsi que de leur proportion relative, ou stœchiométrie, dans le sol. Or, les animaux se nourrissent et produisent des déchets sous forme de fèces et d'urine contenant ces mêmes éléments (C, N, P), dont le devenir dépend fortement de la quantité et de la qualité de ces déchets. Cependant, la quantité et la qualité des déchets varient entre espèces, a priori en fonction de paramètres physiologiques et alimentaires, mais cette relation est peu documentée. En particulier, la masse corporelle, qui détermine le taux métabolique de l'individu, et le régime alimentaire (herbivore, carnivore, omnivore, détritivore), la richesse nutritionnelle ou la quantité disponible de la ressource sont tous des facteurs susceptibles d'influencer la qualité et la quantité des déchets produits par les animaux, mais aussi leur homéostasie chimique.

Afin d'étudier les facteurs déterminants la composition chimique des fèces et l'homéostasie chimique de l'animal à une large échelle phylogénétique, nous avons assemblé des données bibliographiques sur un grand nombre d'espèces animales terrestres. Pour compléter la gamme d'espèces, nous avons par ailleurs effectué de nouvelles mesures. L'analyse montre que le régime alimentaire et la qualité de la ressource sont les facteurs principaux affectant la composition des déchets. La taille corporelle, quant à elle, a peu d'effets. Nous avons également mené une expérience au niveau intraspécifique pour déterminer l'effet de la quantité de ressource sur l'homéostasie chimique, le temps de rétention et les propriétés chimiques des fèces chez *Spodoptera littoralis*, et ce tant sur les éléments (C, N, P) que sur certains isotopes du carbone et

de l'azote. La réduction de la quantité de ressource induit des changements physiologiques importants, dont l'augmentation de l'efficacité d'absorption élémentaire et des isotopes lourds, et réciproquement une réduction de l'excrétion des nutriments (dont N et P). Cela provoque une augmentation du temps de rétention des nutriments dans la biomasse ainsi qu'une diminution de la qualité et de la quantité des déchets. En somme, le recyclage est ralenti lorsque la ressource devient rare. L'ensemble de ces résultats montrent que les animaux sont des nœuds biogéochimiques capables d'adaptations à la disponibilité de la ressource, qui à leur tour interagissent avec le cycle des nutriments et les propriétés des chaînes trophiques.

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Introduction

In 1842, Professor John Stevens Henslow unearthed a transformative discovery in the quiet corners of Suffolk. His ingenious patent, born from a meticulous study of mineral deposits, unlocked a treasure trove of valuable phosphates, setting in motion an era of extensive mining, centred primarily in the fertile landscapes of Cambridgeshire and the Isle of Ely. Ipswich, a bustling town by the river, became the crucible for refining these newfound riches, courtesy of the Fison Company. Though the industry later faded into the annals of history during the 1880s, a brief renaissance occurred during World War I, and the mining of these rocks extended its reach westward into the heartlands of Buckinghamshire, as far as the tranquil Woburn Sands. These rocks were fossilised faeces: coprolites.

Shortly after the terrestrialisation of plants, animals started to roam the land, some 500 Ma ago (Kenrick et al., 2012). Arthropods were the first terrestrial animals, followed by vertebrates 100 Ma behind (Coates and Clack, 1995). Complete food webs, including plants, herbivores and carnivores of diverse clades, quickly emerged (van Straalen, 2021). These animals have since composed complex species assemblages, and today, the terrestrial animal community comprises a remarkable diversity of arthropods, molluscs, nematodes, plathelminths, annelids, birds, mammals and reptiles (Hutchinson, 1959). The members of the Animalia kingdom are characterised by several synapomorphies, including muscles, neurons, synapses, collagen, a differentiated digestive cavity, and the production of digestive enzymes by endodermic cells. They are heterotrophic, *i.e.* they get both their energy and nutrients from other organisms they consume, which can be remarkably diverse, from plants to other animals (Schoener, 1971), and most are capable of locomotion to search for resources. As a result, they are able to feed somewhere and defecate somewhere else. Testimony of their early impact on biogeochemistry has been unveiled through the discovery of a ubiquitous presence of coprolites, both in

marine and terrestrial systems (Edwards et al., 1995; Hagström and Mehlqvist, 2012; Seilacher et al., 2001).

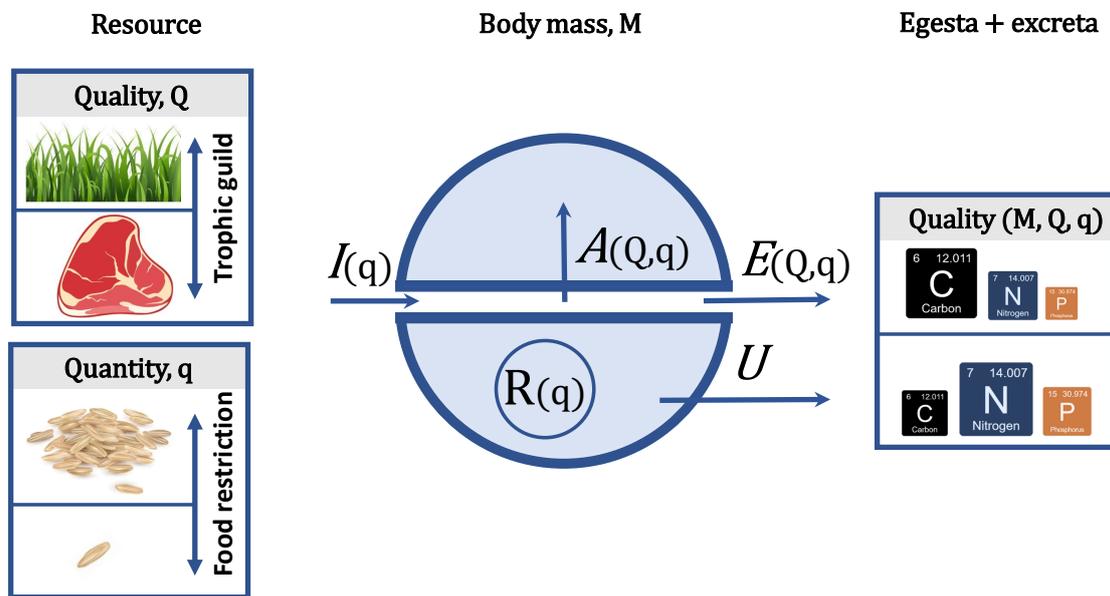


Figure 1: Overview of the hypotheses tested in the dissertation. I stands for ingestion, A for absorption, E for egestion, U for excretion, and R for reserves. Letters in parentheses represent the test of the effect of quantity (q), quality (Q) or body mass (M) on these processes. The effect of the trophic guild on egestion and excretion nutrient content is investigated under the hypotheses of ecological stoichiometry (Sterner et al., 2002a) in Chapters 1 and 2. The effect of body mass on egestion and excretion nutrient content is examined using both ecological stoichiometry (Sterner et al., 2002a) and the metabolic theory of ecology (Vanni and McIntyre, 2016) in Chapters 1 and 2. The effect of quality on absorption is also assessed after Richard et al. (2017) in Chapter 2. The effects of quantity on the process of absorption are assessed based on the hypothesis exposed in Burian et al. (2020) in Chapter 3. The effect of quantity on a qualitative estimation of reserves is explored in Chapter 4.

Terrestrial life differs markedly in its dynamics from the older marine systems (Sardans et al., 2012). Particularly, terrestrial systems contain more producer biomass like plants than consumer biomass like animals (Ayal, 2011), while the inverse is true in marine ecosystems (Bar-On et al., 2018). In aquatic ecosystems where nutrients are homogeneously distributed in the medium and where access to light requires avoiding sinking in the water column, small-size planktonic autotrophs with an efficient surface-to-volume ratio are favoured. In contrast, in terrestrial ecosystems, the need to overtop neighbours to access light and to have extensive root systems to acquire nutrients have favoured large, slow-growing plants. Because of this slow growth and their recalcitrant chemical composition, terrestrial plants can sustain less consumer biomass than the fast-growing phytoplankton does in marine systems (Shurin et al., 2006). But despite their lower standing biomass, terrestrial consumers sig-

nificantly contribute to the functioning of their ecosystems (Doughty, 2017; Metcalfe et al., 2014; Schmitz et al., 2014; Daufresne, 2021), and they can have various impacts on, for instance, nutrient recycling, as we shall see in this dissertation (Elser and Urabe, 1999; Daufresne, 2021).

Indeed, animals affect the various compartments of terrestrial ecosystems and the fluxes between them. Their effects are generally described as either direct or indirect, following the classification given in (Bardgett and Wardle, 2010). Direct effects, on the one hand, include the consumption of plants, which reduces plant biomass (Schmitz, 2008) and favours the maintenance of grassland ecosystems (Waldram et al., 2008), soil trampling, which can change soil microbial diversity (Schrama et al., 2013), but also waste deposition (faeces, urine, etc. Frost and Hunter 2008; Sitters and Olde Venterink 2018). Indirect effects include animal interference between plants and soil biota (Bardgett and Wardle, 2003; Wardle et al., 2004). For instance, herbivory can induce changes in plant tissue allocation (Fornara and Du Toit, 2008) and root exudation (Bardgett and Wardle, 2003), which can favour or limit soil micro-organisms. Over the long term, litter quantity and quality can shift due to these animals' effects on primary productivity and plant species composition (Ritchie et al., 1998; Côté et al., 2004; Ripple and Beschta, 2012). Early studies on the effect of herbivores in the Serengeti showed that the direct effects regulate primary productivity and nutrient recycling balance (McNaughton, 1979; McNaughton et al., 1988). In Yellowstone National Park, N fluxes through animal egesta and excreta have been shown to be larger than N fluxes through litterfall (Frank et al., 1994), indicating a very important role of this nutrient return pathway. Secondary consumers also impact plants through trophic cascade (Schmitz et al., 2000), but their direct effects through wastes have been relatively poorly explored (Schmitz et al., 2010). Some studies, however, suggest that important belowground processes like soil nutrient content, can not be explained without considering animal waste production (Mikola et al., 2009). In this dissertation, we will focus on the return of nutrients to soil through excretion and egestion, and to the factors that control it, and how it can affect ecosystem functioning, specifically in the terrestrial realm.

To power all energy-requiring processes and to build new biomass during growth or reproduction, animals consume food. However, not all food is entirely digested, which results in the production of faeces (egestas), while nutrients absorbed can later result in excretion. Incomplete digestion occurs

because the time needed for degradation into single monomer units is too long, but this partial digestion is still energetically favourable for the animal, which during digestion and absorption harvests more energy than invested (Schneider et al., 1975; Weiss and Tebbe, 2018). Egestion, the release of these undigested remains, is performed to ensure proper transit of newly ingested food (Stevens and Hume, 2004). Nutrients found in egestions are "repackaged" compared to ingested material due to digestive processes (Clissold et al., 2010). Indeed, egestion contains what has not been absorbed, but also bacteria (Stephen and Cummings, 1980; Watson et al., 2019) dead epithelial cells (Phillipson, 1971; Shah et al., 1982) and intestinal secretions (Tamminga et al., 1995). After being absorbed and used in the various metabolic pathways, wastes are generated, and excreted in the form of urine or other secretions (e.g., sweat, Montain et al. 2007). Excretion is performed to release into the environment molecules that are not energetically useful to the animal, which are toxic (Schmidt-Nielsen, 1997), or for thermo-hydroregulation (Rozen-Rechels et al., 2019; Clarke and Rothery, 2008; Mitchell et al., 2018). The anatomy of most terrestrial animals (arthropods, reptiles, birds) leads to the simultaneous release of egesta and excreta through the cloaca (Lecointre et al., 2001). Only mammals produce separate excreta and egesta, with different chemical properties (Sitters and Olde Venterink, 2021). Thus, animals remove nutrients from their environment, immobilise some in their biomass, and release some back into the environment through egesta and excreta, making them biogeochemical nodes in ecosystems (Milchunas and Lauenroth, 1993; Hobbs, 1996; Bardgett and Wardle, 2003). Moreover, animals transport nutrients from the site of ingestion to the site of defecation/excretion, which influences the spatial distribution of ecosystem fertility (Enquist et al., 2020; Wolf et al., 2013). The recognition of how animals significantly influence nutrient cycles in space and time marked the birth of the field of zoogeochemistry (Schmitz et al., 2018).

Understanding the effect of animal wastes on nutrient cycles requires an estimation of both the quantity and quality of the waste biomass since both influence recycling rates (Mitra and Flynn, 2007; Hessen, 2008; Kagata and Ohgushi, 2011a), but also of the biomass consumed (Atkinson et al., 2017). If large-scale fluxes are well described by quantities of nutrients being transferred from compartments to compartments, differences in nutrient content of wastes have been shown to influence the release rate into soils. As a general rule, more concentrated sources of nutrients are more easily decomposed and remineralized than diluted ones (Arenberg and Arai, 2019; Wang et al.,

2018a; Fielding et al., 2012; Schrama et al., 2013; Lovett and Ruesink, 1995). As opposed to concentrated sources, diluted ones favour the utilization of nutrients by micro-organisms, a process termed immobilization (Arenberg and Arai, 2019; Joly et al., 2018). In the following paragraphs, we define how we will use the concepts of quality and quantity in this dissertation to study the effect of animals wastes on nutrient recycling.

Plants and animals do not grow on the same sources of nutrients (C, N, P), mostly inorganic for the first and organic, more complex biomass for the second. Yet examining processes which include both plants and animals with a common metric of quality is practical due to potential feedback. A possibility is to choose the simplest possible scale. The elemental approach, *i.e.* analysing quality and quantities in terms of content in carbon (C), nitrogen (N), phosphorus (P), and more broadly in terms of periodic table elements, gives the advantage of being universal and well-defined and has thus been used in the study of nutrient cycling for decades (see Cherif 2012 for a complete review), both in terrestrial and aquatic settings (Sterner and Elser, 2002; Loladze et al., 2000; Schiettekatte et al., 2020; Sperfeld et al., 2016; Sardans et al., 2012). This elemental approach is at the heart of ecological stoichiometry, the study of “*how the availability of multiple elements, including C, N, and P, constrain ecological interactions*” (Sterner and Elser, 2002; Atkinson et al., 2022). We can define quality as the chemical composition of resources that enables optimal functioning of the organism, regarding growth maintenance, and reproduction. Specifically, high-quality resources for animal consumers are often defined based on similarity to the animal body stoichiometry in terms of carbon, nitrogen and phosphorus.

While animals’ requirements can not be solely defined by elements, since it lacks the details about some essential nutrients, like essential amino acids or vitamins, it generally succeeds at probing the general quality of the diet (Sperfeld et al., 2016, 2017). Similarly, elemental contents can’t describe the amount of indigestible material like cellulose, or plant defence molecules inside diets, like tannins. However, N content is used to estimate protein content, C content can be linked to carbohydrates or lipids, and important minerals are absorbed in their almost-elemental, inorganic forms. Therefore, macronutrients, proteins, lipids and carbohydrates, which are the natural currencies of animal nutrition, can, in part, be described by elemental content. Similarly, the growth of micro-organisms feeding on waste depends on nutrient content

(Frost and Hunter, 2007; Aarons et al., 2004; Frost and Hunter, 2008). For plants, elements, apart from C, represent well the availability of nitrates, ammonia, and phosphates which are the form of uptake. In summary, the elemental approach, based on content in carbon (C), nitrogen (N), and phosphorus (P), provides a universal and well-defined metric for examining both plant and animal processes, making it a valuable tool in nutrient cycling studies.

However, focusing on a single currency, for instance C, N and P separately, sometimes prevent processes from being understood thoroughly. Early studies of animal nutritional ecology in terrestrial ecosystems have mostly focused on a single currency, e.g. energy or N (White, 1993; McNaughton et al., 1988), but it has proven fruitful to include several nutrients in the study of numerous ecological processes (Tilman, 1982; Sterner and Elser, 2002; Raubenheimer and Simpson, 2004; Simpson et al., 2006; Raubenheimer et al., 2009; Simpson et al., 2010). Indeed, nutrients interact with each other in biological processes. In particular, quality is sometimes defined in terms of limiting nutrients. When a process (e.g. growth, respiration) requires two or more elements in specific relative amounts, the lack of one, while the other is plentifully available, can impede the whole process. For example, a lack of P, which is crucial to ribosomal RNA needed for protein synthesis, can impede the growth of the entire organism despite N being abundant (a phenomenon studied within the growth rate hypothesis, see Elser et al. 2000; Isanta-Navarro et al. 2022). In this case, P is said to be the limiting nutrient for growth. We can also use the resource N/P ratio compared to the threshold elemental ratio, at which growth limitation switches from one element to another, to characterize resource quality (Frost et al., 2006).

In the context of nutrient cycling, the quality of animal wastes has often been probed using stoichiometric ratios (Sitters and Olde Venterink, 2018; Wang et al., 2018a). Studies on the decomposition of litter or animal waste indicate that stoichiometric ratios, particularly C/N, C/P and N/P, were a major driver of subsequent nutrient fate (Enríquez et al. 1993; Güsewell and Gessner 2009; Wang et al. 2018a; Sitters et al. 2014). Including both stoichiometric ratios and absolute concentrations is often advised to avoid some of the biases associated with one or another, including the non-normality of ratios (Isles, 2020; Le Gall and Behmer, 2014; Clissold et al., 2010, 2013; Lee et al., 2008). Throughout this work, we thus make use of both absolute nutrient content and stoichiometric ratios to probe the general concept of waste quality.

It is also essential to define quantities in waste fluxes. The processes of feeding, digestion, egestion, etc., being dynamic, it makes sense to include time in the definition of quantities produced. Hence, fluxes ($\text{mass} \times \text{time}^{-1}$), rates ($\text{mass} \times \text{time}^{-1} \times \text{mass}^{-1}$) and efficiencies ($\text{rate} \times \text{rate}^{-1}$) are chosen to probe the quantities involved in ecological or physiological processes. At the individual level, metabolic rate, excretion rate and intake rate are routinely used to conduct mass-balance studies, and particularly in the context of nutrient cycling (Vanni et al., 2002). These rates can be expressed in their mass-specific version, which enables the comparison of organisms of contrasted body masses (Clauss, 2019; Vanni and McIntyre, 2016) and species and fluxes on a standardised basis (Schmitz and Leroux, 2020). For example, in the context of animal-driven nutrient recycling, waste fluxes have been compared to litterfall, showing that N egested or excreted by animals can represent larger fluxes in some ecosystems than senescent plants (Frank et al., 1994). These standardised estimates are also helpful for change-of-scale extrapolations and modelling, which assume standard individuals and populations (Malhi et al., 2022). For instance, nutrient release rates by animals can be associated with population densities and homeranges to estimate ecosystem-scale fluxes (Doughty et al., 2013; Berzaghi et al., 2018) or spatial redistribution of nutrients by animals (Dangal et al., 2017; Doughty, 2017; Otero et al., 2018; Wolf et al., 2013).

On the grounds of ecological stoichiometry, an important body of knowledge on the effects of animals on nutrient cycles both in aquatic and terrestrial systems has emerged. The important paper from Elser and Urabe in 1999 predicted that the stoichiometry of nutrient release by animals could affect the primary producer's nutrient limitation. If an animal feeds on a primary producer with a higher N:P ratio than itself, it will preferentially absorb P, and release wastes with an even higher N:P than the primary producer to maintain its stoichiometric homeostasis (like in fig. 2). This could theoretically lead the limitation of the autotroph population to shift from N to P (Sternner, 1990). However, in the aquatic realm, inverted pyramids of biomass resulting from high autotroph productivity suggest high nutrient cycling rates with a large contribution of animals to the dissolved nutrient pool through grazing and waste (see Cyr and Pace 1993; Cebrian and Lartigue 2004), whereas it might be less true in the terrestrial realm, where autotrophs dominate biomass standing stocks (but see Frank et al. 1994). Since the 1980s, the classic theory

of consumer-driven nutrient recycling in terrestrial systems developed and proposed different mechanisms to explain several situations where the effect of animals on recycling varies (for a complete review, see [Bardgett and Wardle 2010](#); [DeAngelis 1992](#)). Importantly, according to this theory, animals can optimize primary production through grazing in certain conditions of differences between the N/P ratio provided and used in the ecosystem ([de Mazancourt et al., 1998](#); [Daufresne and Loreau, 2001b](#); [Kagata and Ohgushi, 2011b](#)). We will see in the following paragraphs that an important distinction is made based on the fertility of the system.

In nutrient-rich systems, consumers divert some of the primary production as growth but supply the soil with labile (nutrient-rich) substances through wastes, which stimulates soil decomposer activity ([Wang et al., 2018b,a](#); [Sitters et al., 2014](#); [Aarons et al., 2004](#)). The accelerating effect of animals in these nutrient-rich systems lies in the fact that animal wastes contain nutrients in forms that are more easily decomposed than plant litterfall, which speeds up remineralization, resulting in an increase in nutrient availability to plants ([Bardgett and Wardle, 2003](#)). The positive effects of animals on the rate of nutrient cycling have been highlighted in tundra ([Van Der Wal et al., 2004](#)), temperate grasslands ([Bardgett et al., 2001](#)), dry grasslands ([Frank and McNaughton, 1992](#)), savannas ([Sitters et al., 2014](#)), and forests ([Frost and Hunter, 2007](#)).

In contrast, in nutrient-poor systems, animals divert a proportionally larger fraction of primary production for their growth. Moreover, they selectively feed on the richest parts of plants, often new shoots, which would have otherwise been the easiest decomposed litterfall, leaving only poor litter, which is decomposed slower ([Bardgett and Wardle, 2003](#)). Selective feeding can also favour the growth of the avoided defended plants that produce low-quality litter ([Ritchie et al., 1998](#)). This negative effect of herbivory can override the positive effects of returning nutrients to the soil through wastes in nutrient-poor systems ([Bardgett and Wardle, 2010](#)). Such negative effects of animals on nutrient cycling have been unveiled in savannas ([Ritchie et al., 1998](#)), boreal forests ([Pastor et al., 1993](#)), salt marsh ([van Wijnen et al., 1999](#)), taiga ([Kieland and Bryant, 1998](#)) and regenerating forests ([Harrison and Bardgett, 2004](#)).

If the net effects of animals have been assessed in various terrestrial contexts, a particular difficulty is to isolate partial effects from each other. Studies

often compare the presence of herbivores to their absence to quantify the net effect herbivore communities on soil nutrient availability (Carline et al., 2005; Frank, 2008; Zhang et al., 2011; Nitschke et al., 2015; Sitters et al., 2017b). But more rarely have the isolated effects of waste been assessed in natural settings. Two studies, however, test the effect of the addition of faeces on soil nutrient availability (Barthelemy et al., 2015). One, done in a grassland ecosystem, tested the effect of increasing the density of *Rangifer tarandus* (reindeer) faeces whilst still letting the reindeer graze. The authors concluded that standing plant biomass increased in faeces-denser plots despite grazing, along with microbial C and N stocks (Barthelemy et al., 2015; Kagata and Ohgushi, 2011b). Another study using frass of the lepidopteran *Mamestra brassicae* larvae concluded that N-rich frass increased soil N availability, but N-poor frass reduced both soil N availability and plant growth. This last study suggests that the isolated effect of waste addition on soil nutrient availability is not always positive and, crucially, that the chemical composition is key in predicting the outcome of waste effects on soils.

Overall, classical consumer-driven recycling theory states that whether the effects of animals on nutrient cycling are positive or negative depends on the overall nutrient pool of the system: positive when the nutrient pool is large, and negative when the nutrient pool is small (Sitters et al., 2020). But evidence accumulated since indicates that these broad principles are valid only within certain circumstances (Stark and Grellmann, 2002; Bakker et al., 2009; Cherif and Loreau, 2013; Schrama et al., 2013; Stark et al., 2015; Sitters et al., 2017a). Particularly, a later view on terrestrial nutrient cycling (Bardgett and Wardle, 2010) stresses that some aspects of nutrient cycles that would account for stoichiometric constraints have been overlooked.

In the 2010's, Cherif and Loreau developed a different framework integrating stoichiometric constraints. In situations where plant C/X are low (X stands for a generic nutrient), it is anticipated that herbivory can lead to a reduction in microbial activity. This reduction would result from herbivores consuming plant biomass, thereby decreasing the supply of C to the soil. It is expected that this reduction in microbial activity would have an adverse impact on N availability, due to a decrease in mineralization rates (Cherif and Loreau, 2013). At higher plant C/X ratio, a positive effect of herbivory on nutrient availability through a decrease in immobilization rates can be expected (Cherif and Loreau, 2013). This framework states that the effect of animals is generally

positive for resources that are very rich in nutrients, for the reasons classically invoked (recycling of labile, nutrient-rich waste). For intermediate values of nutrients in the resource, the positive effect of herbivores diminishes, even becoming negative, before increasing again for resources that are very poor in nutrients towards a weak but positive effect, due to the reduction in the input of very poor quality detritus to the soil. This has been, in part, confirmed experimentally in [Bakker et al. 2009](#), where the authors found a negative relationship between plant N concentration and soil N availability. These studies highlight the need to consider the decomposition process more thoroughly in a stoichiometric framework, especially the mineralization/immobilization pathways.

Recently, a model emphasizing the very low pool of nutrients contained in herbivore populations compared to the one contained in autotrophs also highlights other ways that herbivores can impact nutrient cycling ([Daufresne, 2021](#)). In particular, through trophic cascade, they can decrease the amount of autotrophs and soil organic matter but increase the nutrient mineral pool. This increase in the mineral fraction of nutrients in soil modifies the magnitude of nutrient loss from the ecosystem, resulting in different soil mineral N/P ratio.

The traditional theory of consumer-driven recycling suffers other limitations, such as the focus on explaining N dynamics over other nutrients. However, P has been shown to be limiting on a significant part of the globe ([Elser et al., 2007](#); [Du et al., 2020](#)), and it is also the case for potassium ([Fay et al., 2015](#)). In aquatic ecosystems, the recycling of N and P by consumers can vary due to differential absorption and release ([Elser and Urabe, 1999](#)). This process ultimately plays a role in determining which nutrient, either N or P, limits primary producers ([Elser et al., 1988](#)). Since the drivers of P availability in soils significantly depart from that of N ([Chapin et al., 2011](#)), the classical, single flux-based theory might not apply without integrating stoichiometric constraints, as well as for other nutrients which are key to ecosystem functioning. Differential cycling of, for instance, N and P, could be introduced by animals by the production of wastes that release N and P at different rates during decomposition. Just like nutrient release rate varies among litter of different types ([Enríquez et al., 1993](#); [Coûteaux et al., 1995](#); [Güsewell and Gessner, 2009](#); [Manzoni et al., 2010](#)), it is known that waste from different animals also releases nutrients at various temporal scales ([Anderson and Coe, 1974](#)). Nutrients can ultimately pour into the mineral or organic

compartments depending on climatic conditions, but also depending on its chemical composition, and especially on the stoichiometric ratios between C, N and P (hereon C:N:P, [Sitters et al. 2014](#)). In terrestrial ecosystems, the variation in faeces C:N:P has been documented and particularly highlighted in large African herbivores. For example, browsers have been shown to produce faeces with higher N content than grazers ([Codron et al., 2007](#)). [Sitters et al.](#) showed in 2014 that variation among 15 large African herbivores faeces C:N:P induced variable decomposition rates. However, the drivers of this variation remain poorly understood.

In aquatic settings, it was shown that the ratio of N to P released in herbi-

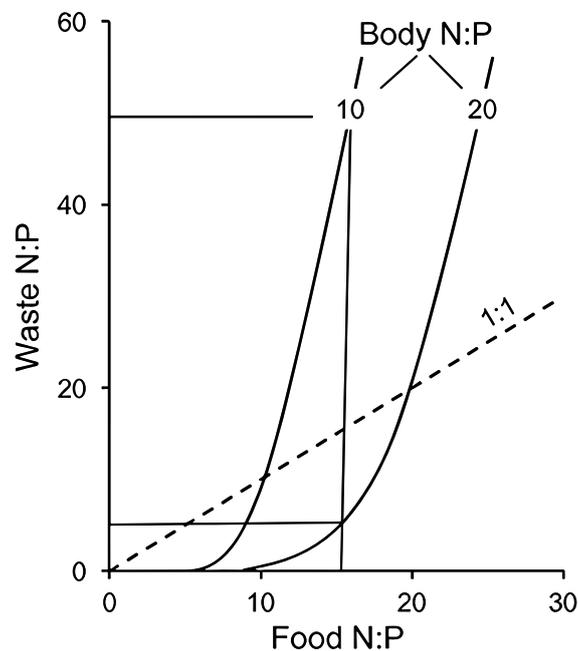


Figure 2: Predicted relationships for the N:P of the consumer’s waste products as a function of its food N:P and body N:P. Displayed are two curves depicting herbivores with body N:P values of 10 and 20. The anticipated correlation between waste N:P and food N:P is positive, and consumers, based on their individual body N:P ratios, will recycle nutrients at varying proportions when consuming the same food. For instance, if both herbivores feed on plants with an N:P ratio of 15, the herbivore with a lower N:P value (10) must retain a relatively higher amount of P. Consequently, it will excrete waste materials with a considerably higher N:P ratio compared to the herbivore with a higher body N:P. Redrawn from [Sternner and Elser 2002](#).

vore wastes partially depends on the chemical composition of food and on the herbivore requirements for these nutrients, at timescale under the lifetime of an individual ([Sternner, 1990](#); [Urabe et al., 1995](#); [Elser and Urabe, 1999](#)). These “rules” can in part apply to terrestrial ecosystems ([Sitters et al., 2017a](#)). Of foremost importance to our subject is the model first developed by Sternner

and Elser in 2002 in which waste N:P is predicted based on food N:P and body N:P (fig. 2). Assuming that the consumer is homeostatic in terms of stoichiometry, *i.e.* of constant body composition, the model states that food N:P and waste N:P are positively correlated for a given body stoichiometry, and that body N:P and waste N:P are negatively correlated at constant food N:P (see fig. 2). This is due to the differential retention depending on body requirements. Organisms richer in P would retain more P, thereby excreting less P. Still in aquatic ecosystems, tests of this model led to contrasted conclusions about the relative role of body and food stoichiometry, some showing effects of body stoichiometry (Vanni et al., 2002; Urabe, 1993) while other don't find such effects (McManamay et al., 2011; Torres and Vanni, 2007). Moreover, some indications that body size and temperature could play an even more critical role than body stoichiometry in nutrient recycling suggest that integration of metabolism in the model is needed to reliably predict the effects of animals on nutrient dynamics (Allgeier et al., 2015; Vanni and McIntyre, 2016). Predicting waste stoichiometry has therefore been shown to be most precise when including both body stoichiometry and body mass in aquatic systems (Vanni and McIntyre, 2016).

In the terrestrial realm, investigations on the joint variation of food, body and waste stoichiometry for the study of nutrient recycling are rarer and mostly focus on a single nutrient (Sitters et al., 2017a). According to Sitters et al. 2017a, only one study tested the predicted negative relationship between body N:P and waste N:P in the terrestrial realm and concluded that no such relationship was visible in their insect model (Zhang et al., 2014). Still in invertebrates, a large study covering 130 lepidopteran species uncovered a positive correlation between food C:N and waste C:N (Kagata and Ohgushi, 2012a). In other cases, a positive relationship was found between food P and waste P, but neither for N nor for N:P in a species of locust (Zhang et al., 2014). Maybe the fact that invertebrates tolerate only minimal variations of food N:P within one species prevents substantial variation of N:P from being observed in wastes, which might make the food - waste stoichiometric relationship only visible at the inter-specific scale. In vertebrates, the picture is a little more complex. Most studies on vertebrates focus on faeces from mammals (Gil-Jiménez et al., 2015; Osborn and Ginnett, 2001; Jhala, 1997; Wrench et al., 1997; Hobbs, 1996). However, the framework developed by Sterner and Elser was intended to model the N:P ratio of the "total waste" that invertebrates produce, which is the equivalent of faeces + urine in mammals. Nevertheless, Elser and Sterner's

theory is often mistakenly applied interchangeably for faeces or urine (Sitters et al., 2017a; le Roux et al., 2020a). In mammals, body N:P is rarely measured. In most studies on mammals, N, or P, but not both, are measured, indeed revealing a positive correlation between resource and waste nutrient content for N (Gil-Jiménez et al., 2015; Verheyden et al., 2011; Osborn and Ginnett, 2001; Jhala, 1997) and P (Wrench et al., 1997; Zhang B., 2016).

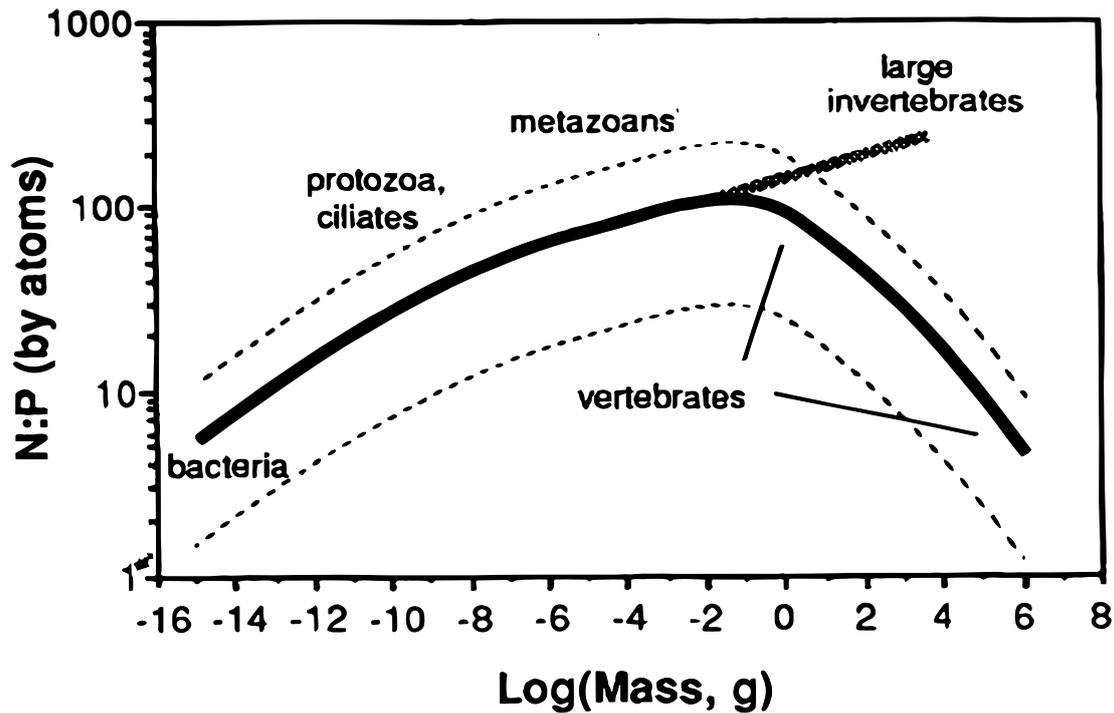


Figure 3: Predicted variation in organism body N:P ratio as a function of organism size. Re-drawn from Elser et al. 1996.

As suggested above, the effect of body stoichiometry on waste stoichiometry has also been proposed to be mediated by body mass. Body mass can be expected to have several effects on waste production and nutrient content. One can be understood as the effect of body mass on metabolism, and the other as its effect on growth rate. Mass-specific metabolic rate is lower at high body mass in homeotherms due to thermal inertia (Brown et al., 2004), which evolutionarily enables the intake of energetically poorer resources (Richard et al., 2017). At lower body mass, high energetical requirements might pose a constraint on the type of resource energetically suitable (Price and Hopkins, 2015; Pineda-Munoz et al., 2016). As a consequence, there might be various mass-specific nutritional requirements among animals of various body masses. This should translate into nutrient intake rate and, therefore, into nutrient

release. It is known that trophic guild and body mass are partially linked (Price and Hopkins, 2015; Pineda-Munoz et al., 2016). Notably, herbivores can in general reach higher body sizes than carnivores (Clauss et al., 2013). Therefore, the type of resources might in part control body mass. In the aquatic realm, rates of nutrient release have been associated with the effect of body mass on metabolic scaling (Vanni and McIntyre, 2016). No studies exist for terrestrial fauna on the effect of body mass on nutrient release rates, even though studies investigating scaling of body mass and intake exist (Clauss et al., 2007; Müller et al., 2013).

Body mass might also influence waste nutrient content through the correlation between body size, growth rate and body P content (fig. 3). Small animals are fast-growing, which should be accompanied by high P-rich ribosomal RNA content needed for growth machinery. On the contrary, large animals have slower growth, which does not require such high P-rich rRNA content (fig. 3). Global demonstrations that growth rate is correlated to average body mass of species individuals have been published since the 1980s (Peters, 1983). Various organisms, including micro-organisms, poikilotherms, homeotherms, tetrapods, mammals, and fish, exhibit analogous declines in specific growth rates as species size increases. These declines share a common slope, approximately -0.25. The growth rate hypothesis has later been developed to link body P content to growth rate through rRNA content (Elser et al., 2000; Isanta-Navarro et al., 2022). Overall, as body mass increases, growth rate decreases, as does P body content, which results in an increase of body N:P with body mass (fig. 3). This relationship has been shown across different but close species (Elser et al., 2006) as well as within species either along ontogeny or when facing different levels of P limitations (Elser et al., 2003; Kyle et al., 2006). However, the increase of P body content with body mass, spanning the entire body size spectrum, is only valid in invertebrates. Indeed, vertebrates which comprise the biggest animals, possess P-rich bones, which proportion increases with body mass. Skeleton represents 3.8% of body mass in shrews and 13.6% in elephants (Calder, 1996; Prange et al., 1979; Martin-Silverstone et al., 2015). As such, larger vertebrates have higher P content and therefore lower N:P than smaller ones (fig. 3).

Since body N:P content is expected to control waste stoichiometry, and body size impacts body N:P content, a link between body mass and waste N:P has been posited. Specifically, since we should expect a negative relationship

between body N:P and waste N:P, the relationship between body mass and waste N:P should be negative in invertebrates, and positive in vertebrates (fig. 3). A large synthesis in the aquatic realm has concluded that the general relationship between body mass and waste N:P was positive, but without investigating the relationship separately for vertebrates and invertebrates (Vanni and McIntyre, 2016), and the same synthesis notes a weak negative effect of body N:P on waste N:P after body mass is accounted for. One of their interpretations is that the relationship between body mass, body N:P, and waste N:P is only valid if the organism is growing, which might not be the case for significant parts of their data (Vanni and McIntyre, 2016). Indeed, the correlation between body N:P and waste N:P was a result of a model for growing animals (Sternler, 1990), but it did not include the possibility of an "adult" animal.

In the terrestrial realm, several papers have been recently published on the relationship between body mass and waste N:P. A first paper in 2020 applied the theory to faeces (not total waste) of large African herbivores. It tended to support the view that faecal N:P indeed increased with body mass (le Roux et al., 2020a) as predicted by the decreasing body N:P, but it was later corrected due to erroneous data, and specified that faecal P was not related to body mass (le Roux et al., 2020b). A reply to this article pointed out that a decrease, instead of an increase, of faecal N:P with body mass was visible in one other dataset, while in three others, no significant relationship emerged (Sitters and Venterink, 2021). In a second reply (le Roux et al., 2021), le Roux et al. suggest that more comprehensive datasets are needed to make further investigations on the effect of body mass on the stoichiometry of recycled wastes.

Overall, both the theory of consumer-driven recycling, which focuses mainly on N, and the broader stoichiometric framework that includes interactions between several nutrients investigate the problem of nutrient cycling mostly through the lens of herbivore-induced effects. However, the role of higher trophic levels is much less considered. All animals have a high demand for proteins and thus N and must sustain low body C:N levels (compared to plants). Herbivores have only access to resources very high in C, and relatively poor in N (Robbins, 2012; Karasov and Martínez del Rio, 2007), which is not the case for carnivores, which consume resources much closer to their own body composition. As a result, they produce wastes of different chemical compositions (Frank et al., 2017; Reese et al., 2018), suggesting a different impact on nutrient

recycling through wastes. The predator-induced effects on nutrient cycles beyond their direct impact on prey population has only recently started to be investigated (Schmitz et al., 2010).

The effect of carnivores on nutrient recycling can vary and take different paths. For instance, insectivorous predators can increase N and P concentration in leaves and litter in forests through the deposition of waste, compared to situations where the predator is absent (Sin et al., 2007). Predators can also move nutrients from a source ecosystem where they feed to a recipient one where they produce wastes. For instance, it was found that urban forests housing crow roosts (*Corvus corone* & *Corvus macrorhynchos*) received 2.6 times more allochthonous P and 0.66 times more N through the presence of birds than through other pathways, which was not the case in forests without crow roosts (Fujita and Koike, 2009). Other examples make the case of nutrients transported from aquatic ecosystems to terrestrial ones through predators. In a temperate forest, the presence of the fish-eating great cormorant (*Phalacrocorax carbo*) increased mineral soil N and P, and decreased litter decomposition due to the increase of lignin-like substances complexed with excreta-derived N (Hobara et al., 2005; Osono et al., 2006). Brown bears can transport N from marine to riparian forests through predation on salmon (Hilderbrand et al., 1999). Several studies also highlight the transport of N and P from the ocean to islands through predation on fish and subsequent guano release (Barrett et al., 2005; Croll et al., 2005; Maron et al., 2006; Fukami et al., 2006), with large functional effects on these islands.

The review from Schmitz et al. (2010) acknowledges that these mechanisms are poorly considered in models and calls also for more efforts to be made on the role of predators in nutrient cycling. Particularly, how carnivore wastes compare to that of herbivores in terms of stoichiometry is poorly characterized in terrestrial ecosystems. In 2017, Frank et al. analyzed the chemical composition of faeces in 23 vertebrate species (7 carnivores, 6 omnivores and 10 herbivores), to investigate dung beetle preferences. Large variations in faeces C:N among herbivores and carnivores were found. The C:N ratio of mammal carnivore faeces in this study was around 5, which was 5 times lower than that of herbivores, and 2 times lower than that of omnivores, reflecting the effect of resource C:N ratio (Cross et al., 2005). Strikingly, body C:N in animals is also 5 (Andrieux et al., 2021), suggesting that carnivore faeces and animal carrion compare in terms of decomposition and the amount of N

remineralized. However, the low sample size of [Frank et al. 2017](#), as well as the lack of data on P impedes more general comparison with herbivores and the inclusion of N:P stoichiometry.

In order to answer the need expressed in various papers for a general test of the relationship between body mass and waste stoichiometry ([le Roux et al., 2021](#); [Sitters and Venterink, 2021](#)), as well as the interesting venue to include carnivores in the waste nutrient recycling framework, I present a database in Chapter 1, in which we collated waste stoichiometries over a large range of terrestrial animals. The database includes herbivores, omnivores, and carnivores, as well as a few detritivore species, and data on waste C, N, P and other nutrient content. In this first chapter, we present the methodology to construct the data synthesis, its broad structure and its important features. I also discuss the remaining gaps. In Chapter 2, I analyze this database with regard to the relationship between waste CNP stoichiometry, body mass and trophic guild (herbivore, omnivore, carnivore), and discuss the applicability of our results to ecosystems, with a focus on the balance between mineralization and immobilization. This database and its analysis highlight general patterns of inter-specific variation in waste stoichiometry related to body mass and trophic guild.

Most of the content discussed above is often approached through the study of inter-specific variation within the terrestrial realm. For instance, differences in diet, within herbivores, between grazers and browsers, is variation associated with species identity ([Codron et al., 2007](#)). Similarly, the difference in nutrient recycling due to body size has often been associated with species identity ([le Roux et al., 2020a](#)) and not with body mass variation during ontogeny. However, intra-specific variation, and especially in traits related to the individual stoichiometric "signatures", are observed but understudied ([Jeyasingh and Weider, 2007](#); [Jeyasingh et al., 2014](#)) despite empirical works showing that inter-specific variation in nutrient recycling can sometimes compare to intra-specific variation ([Villéger et al., 2012](#)). In turn, these intra-specific variations can influence ecosystem function as has been shown in aquatic settings ([Bassar et al., 2010](#); [El-Sabaawi et al., 2015](#); [Roches et al., 2017](#); [Leal et al., 2017](#)). Therefore, mechanisms generating intra-specific variation in stoichiometric traits are relevant to the study of consumer-driven nutrient recycling ([Villéger et al., 2012](#)).

Predictors used to explain the stoichiometric ratio of wastes at the inter-specific level, like body N:P, have been shown not to be as powerful at the intra-specific level (El-Sabaawi et al., 2015, 2016; Tobler et al., 2016). Factors like genetics, sex, age, gut microbiome, individual diet preference, resource quality and availability likely influence the elemental composition of egestions and excretions within the same species. Thus, two sources of intra-specific variation can be distinguished. First, intra-specific variation can be due to genotypic variations associated with stoichiometric traits like acquisition, assimilation, allocation, composition or excretion in homogeneous conditions (Lemmen et al., 2019). Second, this variation can be due to phenotypic plasticity, defined as the ability of an individual to change its phenotype or physiology in response to changes in environmental conditions (Leal et al., 2017).

In ecological stoichiometry, phenotypic plasticity is sometimes implicitly incorporated into models. For example, the gross growth efficiencies of nutrients are varied in Sterner's model of growth depending on the animal's stoichiometric requirements (Sterner et al., 2002a). If resource C/X is higher than what is required, the gross growth efficiency of X is maximized, whereas that of C is such that C/X ratio matches the consumer needs (Sterner et al., 2002a). Therefore, the organism is able to dynamically adapt one of its physiological parameters to the environmental conditions. The stoichiometric theory of consumer-driven nutrient recycling has mainly considered the effect of variation in the quality of the food supply on these dynamical aspects of absorption (Sterner et al., 2002b). However, it has far less considered the effect of varying food quantity on physiology, which has mainly been modelled in other frameworks like nutritional geometry or optimal foraging theory (Burian et al., 2020). Yet, food quantity is obviously key for animal survival and growth (McCue, 2010). Starvation and periods of reduced intake are ubiquitous in nature (McCue, 2010) and can simply be triggered by low resource availability (Dunham et al., 1989; Karasov, 1986; Nagy et al., 1999). However, competition in a resource-limited context can also drive more intense food limitation for lower competitor individuals (Carson and Root, 2000; Bonsall et al., 2003; Long et al., 2003), when the best competitors feed at higher rates than poorer competitors to obtain a higher proportion of available resources, which creates differences in intake rates (Mccarthy et al., 1992). The effect of food availability has recently been investigated in a model incorporating both stoichiometry and metabolism (Burian et al., 2020) and stresses that *"the impact of food quantity on trophic transfer and emerging structural ecosystem*

properties thus critically hinges on behavioural and physiological responses of consumers”.

Food shortage or imposed lower intake might induce plastic responses to buffer this stress. If food is scarce, an individual might trigger physiological adaptations to better digest food in order to extract as many nutrients as possible from the scarce resource, whereas when food is abundant, individuals might invest less in digestion efficiency. Low intake should increase gut passage time, which in turn should passively enable better digestion of food (Mitra and Flynn, 2007), but active mechanisms of digestion efficiency improvement are also described (Mattila et al., 2015). Other theoretical studies have shown that maximal yield of absorption is not possible at high intake (Jumars, 2000; Mitra and Flynn, 2007). These models on absorption efficiency tend to suggest that maximal absorption efficiency is not attainable at any intake rate (Jumars, 2000; Mitra and Flynn, 2007). This contradicts simple models in ecological stoichiometry that assume that a maximal absorption efficiency of limiting nutrients is possible at any intake rate (Sturner et al., 1992).

On the experimental side, absorption efficiency has indeed been shown to decrease with prey abundance and presumably ingestion rate, in numerous zooplankton species (Montagnes and Fenton, 2012), and in marine carnivorous mammals (Trumble and Castellini, 2005). However, some studies suggest that it is not a universal law (Clauss et al., 2014; Conover, 1966a; Barthel, 1983; Besiktepe and Dam, 2002; Rosen et al., 2000; Lawton, 1970; Cymbaluk et al., 1989). For instance, for the copepod *Acartia tonsa* feeding on each of five different autotroph species, only in two cases was absorption efficiency related to food concentration (Besiktepe and Dam, 2002). Ingestion (Bamstedt et al., 2000) and egestion (May and El-Sabaawi, 2022) are not easily measured at the individual scale in aquatic environments, which, along with population dynamics-oriented studies, may motivate the use of food concentration instead of ingestion rates in these studies (Montagnes and Fenton, 2012). Nevertheless, the data suggest that absorption efficiency is sensitive to intake rate or food abundance. However, the chemical analysis of excreta and egesta is particularly challenging when faeces are released into water (May and El-Sabaawi, 2022). This results in few studies having investigated how the absorption efficiency of specific elements varies with ingestion rate. Yet such studies are needed to make predictions about the effect of food abundance on the specificities of nutrient cycles. Population-level measurements of

the absorption efficiency of P in *Daphnia*, however, seem to indicate that it indeed decreases at higher food concentrations which should correlate with ingestion rate (He and Wang, 2007), suggesting a lower fraction of ingested P being recycled at low food abundance. For another element, Ca, this does not seem to hold (He and Wang, 2009). In terrestrial consumers, chemical analysis of faeces is easier, and thus so is the computation of absorption efficiencies for the various elements. In terrestrial environments, studies on the effect of food restriction on absorption efficiency are less common than for aquatic ecosystems and report mixed effects of intake rate on total absorption efficiency (negative in Hubbell et al. 1965; Wellard and Hume 1981, positive in Rosen et al. 2000; Lawton 1970; Cymbaluk et al. 1989; Clauss et al. 2014). The variation of elemental absorption efficiencies as a result of varying food quantity has however received surprisingly little attention, but we can expect that similar physiological plasticity exists in terrestrial fauna, suggesting that food abundance also controls elemental absorption efficiency and thus the fraction of recycled nutrients.

As intake rate variations are imposed on organisms, and consequently also on their growth rate (Lewis and Emmans, 2020), other physiological adaptations could modify not only the absorption efficiency but also their body and waste stoichiometry. Under food restriction, metabolic costs typically decrease, presumably to save energy (Naya et al., 2009; Auer et al., 2015, 2016; Zeng et al., 2018), which should be associated with lower C consumption due to reduced respiration (Bohrer and Lampert, 1988; Lukas and Wacker, 2014; Lampert, 1986; Urabe and Watanabe, 1990). On the other hand, higher intake rates, associated with higher growth rates, can make the organism prone to somatic growth dilution, whereby growth rates differ between elements owing to differential tissue growth, resulting in varying stoichiometric content at different individual growth rates (Karimi et al., 2010). As we saw earlier, the absorption efficiency of nutrients could increase at lower food concentrations, but the waste stoichiometry in this case depends on the ratio of the absorption efficiency among the different elements, ratios which may not be constant across the intake level spectrum. Overall, the simultaneous effects of food quantity on absorption efficiency, metabolic rate and growth rate may have effects on body and waste stoichiometries that are not easy to predict (Sperfeld et al., 2017). It is known that fasting or starved animals (with a complete arrest of intake) can shift in body stoichiometry (Hirche and Kattner, 1993; Chen et al., 2005; Molnar et al., 2006). However, this effect has been poorly

documented for animals feeding at reduced intakes that still allow growth to take place. Moreover, shifts in waste elemental composition in response to food abundance have, to our knowledge, only been tested once in a fish (Moody et al., 2018), but never in a terrestrial organism.

To investigate intra-specific variation in elemental absorption efficiencies, and differences in body and waste elemental content driven by plasticity in the face of intake reduction, we used an experimental approach (Chapter 3), by quantifying nutrient fluxes and stocks of a terrestrial consumer, *Spodoptera littoralis*, submitted to different levels of food restrictions. The routes that nutrients take, and the functions they serve in the organism, are, however, not easy to assess using only gravimetric methods of mass balance. In terrestrial invertebrates, especially, egesta and excreta are mixed together as frass, with no gravimetric method to decipher the provenance, egesta or excreta, of nutrients analyzed within this matrix. Recycling of nutrients, however, in part depends on the relative rates of these processes (Sitters and Olde Venterink, 2021). Excreta is primarily composed of inorganic molecules, readily available to plants (e.g. ammonia), whereas nutrients in egesta are contained in more complex macromolecules that need first to be degraded before autotroph nutrition (Halvorson and Atkinson, 2019; Sitters and Olde Venterink, 2021).

Moreover, mass balance does not tell, for example how N from proteins is used within the organism, should it be used for catabolic processes (through gluconeogenesis) or for biosynthesis during growth (muscle growth). These distinctions are important since catabolic products will generate excretion, whereas growth will be integrated into food webs (Cebrian, 1999). In this regard, isotopic ecology helps decipher the relative extent of nutrient routing (Karasov and del Rio, 2007). Stable isotopes differ slightly in mass, so that the rates of reaction during biochemical processes vary slightly from one isotope to another (Ohkouchi et al., 2015). This helps assess the acquisition and absorption of various elements (DeMott et al., 1998) and the allocation rates of elements to specific tissues (Bearhop et al., 2002). Combined with mass balance, it is also possible to estimate the excretion rate of elements using stable isotopes (Fowler et al., 1975).

During starvation, excretion rates have been reported to increase (Goodman et al., 1984; Pusey, 1986; Chereil et al., 1992; Nordøy et al., 1993), decrease (Runcie and Hilditch, 1974; Owen et al., 1979; McCue, 2006) or remain un-

changed (Weber and O'Connor, 2000). However, most studies are performed in animals experiencing a total arrest of intake. When intake is only reduced at various intensities, the variation of protein catabolism and subsequent excretion is only poorly documented. The analysis of trophic fractionation, the difference in isotopic content between food and the consumer's body, can give information about the extent to which proteins, and thus N, are used for catabolic processes Martínez del Rio et al. (2009).

Similarly, lipids typically contain proportionally less ^{13}C than proteins and carbohydrates (DeNiro and Epstein, 1977; McConnaughey and McRoy, 1979), and an increase in their fraction can therefore be detected using stable isotope analysis Martínez del Rio et al. (2009). Lipids contain C, but neither N or P, and constitute the main reserve of energy for animals (Franzmann, 2018). The increase of these reserves can result in somatic growth dilution, where N and P content shrink as a result of lipid accumulation (Karimi et al., 2010). However, elemental analysis alone is not able to decipher whether C is found mostly in complex carbohydrates or in lipids. Stable isotope analysis can therefore complement mass balance by revealing some of the biochemical processes of proteins and lipids that result in C and N dynamics. In chapter 4, we make use of stable isotopes analysis made during the experimental work of Chapter 3, where larvae of the moth *Spodoptera littoralis* are submitted to various feeding levels, to decipher some of the N and C routes taken during intake level restriction.

In this PhD dissertation, I investigate the effect of animals on nutrient cycling in terrestrial ecosystems at two levels of organization: first at the inter-specific level, focusing on the effect of trophic guild and body mass, and second at the intra-specific level, focusing on the effect of resource availability.

In Chapter 1, I describe a database containing waste chemical composition and stoichiometry in terrestrial animal species associated with species-level body masses and trophic guild.

In Chapter 2, I analyse this database with a focus on the effect of body mass and trophic guild on waste nutrient content. I hypothesize that body mass should have effects on waste nutrient content through its effects on growth and on metabolism. Trophic guild should have effects through its correlate with resource quality and feeding dynamics. I use the tools provided by ecological stoichiometry to answer these questions.

In Chapter 3, I focus on the intra-specific phenotypic plasticity in nutrient fate triggered by variation in feeding levels in *Spodoptera littoralis* larvae. I hypothesize that intake rate should have effects on elemental absorption efficiency and, therefore, on the nutrients' fate during growth.

In Chapter 4, I make use of stable isotope analysis to better understand the protein and lipid physiological adaptation of *Spodoptera littoralis* larvae submitted to various feeding levels. I hypothesized that intake should change the amount of lipidic reserve and the mobilization of protein for metabolism, with effects on the carbon and nitrogen content of larvae and wastes.

Part I

Exploring waste composition in terrestrial fauna: effects of diet and body mass

The first sample collected during my PhD was a rather prestigious one. I quickly needed dung samples to start establishing a laboratory protocol, but Paris is not, as you might expect, the best place to search for this kind of matrix. However, not far from Jussieu, on the other side of the Seine, in the Quartier des Célestins, is a peculiar unit of the French National Gendarmerie. I reminded of the mounted guards who can sometimes be seen around Jussieu. I took a chance and contacted the Guard by email. I quickly had an answer and could enter the stable to collect a fresh sample from one of their horse a few days later.

The story behind this database, however, began earlier than that. Before me, students paved the way, exploring the literature, collecting samples and synthesising some data, among whom, Anne-Cécile Vain and Lucile Serre. The nearby Ménagerie of the Paris natural History Museum had already contributed some samples, but the collaboration network was about to broaden to 15 structures housing terrestrial fauna. From sample handling to chemical and data analyses and collaboration network animation, I have learned a lot. I had the chance to work with veterinarians around France and to gain skills in chemical analyses, especially with elemental analyses, under the supervision of Maryse Rouelle, Véronique Vaury, Magloire Madeng, Mélanie Longchamps and David Carmignac. I also had the pleasure of supervising two master students within this project, Inès Préval and Marie-Amélie Pussacq, who helped me work with the samples from thawing to chemical analyses.

1

A global dataset on waste composition in terrestrial fauna

Samuel Charberet, Isabelle Gounand, David Carmignac, Véronique Vaury and Jérôme Mathieu.

The effect of animals on nutrient cycles partly relies on the fate of their waste. Ecological stoichiometry suggests that the content of waste, including faeces and urine, and their amount, drives their decomposition rate and their role in element cycles. However, to date, we lack a global picture of the effect of animal waste on nutrient cycles, beyond the mammal herbivores. Here, we compiled a global database of waste elemental composition in terrestrial animals. Our database gathered 5844 observations on 266 species. Species-level body mass averages and categorical diets were added to the database to enable the exploration of traits-driven variation in waste chemical composition. The taxonomic coverage of the database includes insects, millipedes, spiders, malacostracans, springtails, birds, mammals, squamates, amphibians, turtles and gastropods. This dataset enables comparative analyses of waste chemical composition across multiple hierarchical levels, ranging from individual organisms to populations. However, taxonomic coverage is uneven between clades, with an overrepresentation of mammals and birds, and a lack of data on insects and other invertebrates. In mammals, the lack of data on urine also prevents a thorough investigation of

the effects of this waste on nutrient cycling. Despite these limitations, this work contributes to a more holistic understanding of the impact of animals on nutrient cycling in terrestrial ecosystems.

1.1 Background & Summary

Terrestrial animals participate in nutrient recycling, particularly through their egesta and excreta (faeces and urine, respectively, [Hobbs 1996](#)). In general, faeces tend to release nutrients more rapidly than plant litter, resulting in accelerated turnover ([Bakker et al., 2004](#)). However, just as different types of plant litter are decomposed at different speeds ([Enríquez et al., 1993](#); [Coûteaux et al., 1995](#); [Sturner and Elser, 2002](#)), wastes from different animals should affect soil nutrient pools differently. Indeed, it has been shown that differences in C:N:P waste stoichiometry can affect nutrient release rates in soils such that poor waste show slower relative release ([Sitters et al., 2014](#)). Waste poor in N, for example, show lower relative release of N into soils ([Kagata and Ohgushi, 2011b](#)). The variable waste nutrient release rates have been shown to be responsible for changes in plant community structure in experimental settings ([Valdés-Correcher et al., 2019](#)), suggesting that complex feedback can emerge from the interplay between plant diversity and waste composition.

The chemical composition of these wastes can vary a lot between animals from different species, owing to their trophic guilds ([Frank et al., 2017](#)) and different physiology ([Sitters et al., 2017a](#)), or between seasons ([Verheyden et al., 2011](#)). The species traits that could help predict egesta and excreta chemical composition are still under investigation. Whereas food nutrient content, and hence trophic guild (herbivore, carnivore) should clearly influence it ([Sturner et al., 1992](#); [Sturner and Elser, 2002](#)), body mass has recently drawn much attention ([le Roux et al., 2020a](#); [Sitters and Venterink, 2021](#); [le Roux et al., 2021](#)) since it should affect body composition ([Elser et al., 1996](#)), especially that of P, and in turn, waste composition. Body P should be negatively correlated to waste P. Yet, it has been proposed that body P is constrained by growth rate and bone content. Growth rates are higher at small body sizes, while bone content increases with body size in vertebrates. Growth rate is correlated with rRNA content, while bone contains P-rich apatite. We, therefore, expect a positive relationship between body size and waste P in invertebrates and a humped-shaped relationship between body size and waste P in vertebrates, owing to the double effect of growth rate and bone presence.

If this hypothesis is confirmed, changes in community body mass spectra, as witnessed in several contexts (Dirzo et al., 2014; Hempson et al., 2017; Ripple et al., 2015), are expected to have significant consequences on nutrient cycling. Having a database providing information on the variation in the chemical composition of waste attributable to body size and other species traits would then be an essential tool. A more precise and exhaustive assessment of the variation in chemical composition of egesta and excreta, as well as an assessment of its drivers, would allow more elaborate models of consumer-driven nutrient recycling to be derived. Global estimation of nutrient fluxes through egesta and excreta are lacking despite their probable importance at those scales Doughty et al. (2013); Doughty (2017), which can, in part, be due to a lack of centralization of the existing literature. To fill this gap, we compiled data on the chemical composition of egesta and excreta, along with species-level traits from various terrestrial animals that can help address these questions.

Data was mainly derived from the literature and completed with measurements done purposely by our team. The database is structured to integrate all the elements relevant to assess the data quality. Individual animal traits, taxonomic identification, sampling environment, and sample chemical analysis are precisely described when available. Furthermore, a large set of unique identifiers connects data, such as different measurements done on the same sample or different samples related to the same individual or population. This allows to include time series of waste elemental composition and food - waste relationships. Data synthesized from the literature included 95 articles and contained 5004 observations on 190 species. We added to this database a set of 840 new data points from 76 species by sampling waste from captive animals, on which we carried out extensive chemical analyses.

1.2 Methods

1.2.1 Literature data extraction

To build the data synthesis, we focused our search effort on terrestrial animals or animals that spend at least one of their life stages on land (therefore, amphibians and some marine birds and mammals). Three types of data were searched for in published literature: waste elemental content (*e.g.* %C in faeces), chemical fluxes (*e.g.* N quantity egested per day per individual), and

nutrient release rate (*e.g.* P quantity egested in faeces per unit body mass) on various types of matrices: urine and faeces (mammals), guano (birds), and frass (arthropods).

We conducted the search across Web of Science and Google Scholar to aim at a global coverage of relevant literature. Our search strategy involved employing specific keywords and search terms, combining ‘faeces chemical composition,’ ‘frass chemical composition,’ ‘guano chemical composition,’ or ‘urine chemical composition,’ each with ‘terrestrial animals,’ ‘insects,’ ‘birds,’ ‘reptiles,’ or ‘mammals.’ Furthermore, in pursuit of maximum coverage, we performed a rigorous screening process by examining the reference lists of the selected articles to identify any additional papers that might contain relevant data. The keyword-based and citation-driven approaches allowed us to retrieve a diverse array of studies relevant to our research objective. Articles included as sources in the database are listed in Appendix A table A.1.

To uphold data quality, studies relying solely on indirect methods for calculations of chemical concentrations were excluded from our analysis (*e.g.*, total N inferred from separate organic and inorganic N measurements, defecation fluxes estimated from average defecation rate and average defecation weight). When we could not associate data with methods used, or when methods gave unplausible values (*e.g.* 0% N in faeces), the data was also excluded. Additionally, articles without precise species names, studies focusing on ileal digesta measurements (materials taken into the gut), or those presenting data from other studies but without citing the source were omitted from the final dataset. Throughout the search process, we considered only papers written in English and only included original data, thereby avoiding data pseudo-replication when using other data synthesis or meta-analysis results. We did not include all retrieved papers related to domesticated fauna to avoid bias in our dataset in this direction.

In total, this first dataset gathers 5004 observations from 95 articles (see table A.1) and 190 species.

1.2.2 Complementary new measurements

Although much data were available in the literature, not all diets were represented equally, nor were major nutrients systematically measured in consid-

ered animal wastes. Carnivore faeces have generally more rarely been studied than herbivore waste, and the waste contents in nutrients other than C, N and P are rarely given. To fill this gap, we collected new samples from a variety of targeted animals (fig. 1.4). To do this, we established a network of collaborations with structures keeping captive fauna in France, including zoological gardens, associations, and research institutes, which list is available in Appendix A (table A.3). Although the nutritional properties of diets can vary between captive animals and wild counterparts (Clauss, Marcus et al., 2007), the use of standardized and informed diets prevents variation and can limit health issues. Veterinary staff performed fresh faeces and food sampling with gloves, plastic bags and 50 mL tubes. Samples were quickly stored in freezers until they were transported in dry ice to our lab, where samples were stored at -30 °C until further analysis. Upon thawing, they were autoclaved in beakers to ensure sterile and secure working conditions. Quickly after autoclaving, samples were homogenized using scissors and dried for three days at 60°C in an oven. Each sample was then separately ground finely using a mill (80µm sieving, Retsch ultra centrifugal mill ZM 200) and stored in plastic tubes. Afterwards, the subsamples were measured for C and N using an elemental analyser, with aspartic acid as a standard. Subsamples were also mineralized in the microwave with HNO₃ and HCl through a cycle with gradual temperature rise until reaching a plateau at 185°C for 45 min. P, K and Mg were measured using inductively coupled plasma optical emission spectroscopy (ICP-OES) using pork muscle (ref. ERM-BB384) as a standard. This procedure was performed for 177 samples in total.

1.2.3 Species' traits data

We extracted the average body mass and diet of species present in the database from two main databases and from various papers. We chose to describe diet as a categorical variable with four levels: herbivore, carnivore, omnivore, and detritivore, to avoid diet subclasses with only a few data points. Herbivory was defined as the exclusive consumption of plant materials, carnivory as the exclusive consumption of animals, detritivory as the consumption of dead material, and omnivory as some combination of the three others. We used Elton traits (Wilman et al., 2014) and the amniote life-history databases (Myhrvold et al., 2015) to extract most body masses and diets. If no such information was available in the databases, we looked for it in peer-reviewed articles, which list is available in Appendix A (table A.2).

1.2.4 Taxonomical data

Each species encountered in the data extraction process was manually searched for on the Global Biodiversity Information Facility Backbone Taxonomy (gbif.org). This taxonomy is based on 105 different sources and is regularly updated (GBIF, 2023). The accepted species name was extracted, as well as the species API key. The full phylogenetic information was then automatically extracted from accepted species names using the "taxize" package in R (Scott Chamberlain and Eduard Szocs, 2013). We only retained data at the species level, and we screened species names so that no names are species synonyms of accepted species. Our code pipeline also allows taxonomic information to be updated every three months (see the following section).

1.2.5 Data processing and database structure

The data processing procedure was designed to allow voluntary contributors to add and analyze data easily through a make-like pipeline executable with only one line of code in the repository R project. Each data source (e.g., article) has its own separate folder, which includes the file containing the raw data in its downloadable form when available, the extracted data in its database form, as well as a descriptive "readme" file describing the digitizing process or possible communications with the studies authors.

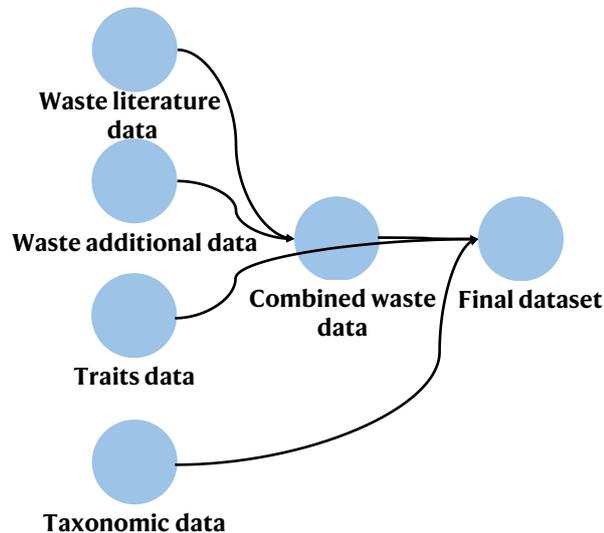


Figure 1.1: Data processing pipeline. Main data processing nodes are shown as circles. A full data processing network, including secondary functions and nodes, can be visualized using the "tar_visnetwork" function (Landau, 2021).

Data from articles are extracted from the literature in separate table sheet files based on the same template (see section 1.3 for an overview and table A.5 for a complete description). All files are then concatenated after a compatibility check through our computational procedure. This step builds the waste dataset (fig 1.1) and allows the listing of species present in the database, which generates a data trait file to be filled when adding new species. Since not all species are present in global traits databases (e.g. [Wilman et al. 2014](#)), we needed to fill in body mass averages and diet while sourcing these additions (table A.2).

If taxonomic names are given at a taxonomic rank other than species, or if the taxonomic name is inaccurate, these data are removed and an error is thrown to warn the user. As described above, taxonomic data are downloaded from the GBIF if new species are added, and at least every three months to follow any taxonomic update.

Literature data extraction generated variation in the vocabulary used to designate similar molecules, methods, units, and in general, in all string variables. This variability is addressed in a homogenizing step. Importantly, all values are converted using a common set of units. Values expressed in moles are converted back into mass using published molar masses. C, N, P, K, Mg and S are expressed as % content in the sample. Because the content in the following elements is very low: Ca, Na, Fe, Si, Al, Cl, Ti, Zn, Mn, Mo, Cu, B, Cr, Pb, As, Cd, Ni, V, Hg, Co, Se, Sr and Ba, we expressed them into ppm. We homogenized extraction and measurement methods to keep only : elemental analyser, autoanalyzer, atomic absorption spectroscopy, ICP-OES, ICP-MS, micro-kjeldahl, macro kjeldahl, kjeldahl, spectrophotometry, molybdenum blue, micro-ascorbic acid and Walkley-Black methods.

The nutrient content data, and the traits and taxonomy at the species level are then combined to form the final dataset (fig. 1.1). Since C, N, and P content data are most relevant to the questions conveyed in the Background & Summary section, we chose to generate datasets one these variables at the species level. These datasets are analyzed in chapter 2.

1.2.6 Data reproducibility

All data processing operations, including digitizing methods and code execution, are available on Git Hub upon inquiry to the authors and will be released publicly upon publication of the present work. The procedure to add data and execute the script is clearly explained on the GitHub repository. Code has been designed to allow global contribution from the scientific community. The use of a make-like pipeline tool ([Landau, 2021](#)) allows contributors with no coding skills to reliably reproduce our analysis.

1.3 Data records

The final dataset comprises a single data table containing 95 entries subdivided into 14 categories (see table A.5). Each data record thus contains information about the literature source (4 entries), the digitizing process (2 entries), and the sample type (5 entries). The body mass of the consumer(s) if available (8 entries), its age(s) (7 entries), sex (1 entry), sampling conditions (10 entries), and species name (5 entries) are precisely defined. The samples are identified through unique numbers (4 entries), and their nature is described with details (10 entries), including, in particular, their observation resolution. The element or molecule measure characteristics are described (11 entries), as well as the measurement methods (13 entries). These entries are described individually in table A.5. Species-level body mass average (given in grams) and diet (carnivore, herbivore, omnivore, detritivore) each comprises one entry. Finally, taxonomy comprises 11 entries and includes ranks from the phylum to the species.

When waste data were associated in the article with data on the chemical composition of food eaten by animals or with body chemical composition, we also extracted them. To ensure clarity and transparency in our findings, we included detailed descriptions of the observational resolution for each data (fig.1.6). The observations were either unique measures or averages over several measures. Each observation was therefore categorised as originating from either individual-level or population-level observations, where the chemical measurements were sourced from a single individual or pooled from multiple individuals, respectively. In cases where the data were an average over several measurements, we explicitly noted the type of error associated with the average, which included intra-individual (same individual measured multiple times), inter-individual (average over several individuals), intra-population

(same population measured multiple times), and inter-population errors (average over several populations). Error types, such as standard deviation, variance, coefficient of variation, mean absolute error, and standard error of the mean, were documented when available, along with the number of measures contributing to the average.

1.4 Results

1.4.1 Overview

We were able to gather data on 11 different classes on terrestrial animals (fig. 1.2): Insecta, Diplopoda (millipedes), Arachnida (spiders), Malacostraca (including isopods), Collembola (springtails), Aves (birds), Mammalia, Squamates (snakes and lizards), Amphibia (*e.g.* frogs), Testudines (turtles), Gastropoda (*e.g.* snails). The body mass coverage included animals from milligrams to tons and pertaining to 4 different trophic guilds: herbivores, omnivores, carnivores, and detritivores (fig. 1.2). The number of species included in the database varied among classes, from 1 for Arachnida to 160 for Mammalia. Similarly, the number of observations per class varies from 6 for Collembola (springtails) to 3717 for Mammalia (fig. 1.2). Most data contained in the dataset are elemental content or stocks (*e.g.* % C in a sample of faeces). A few data were fluxes and rates (297 and 429 observations, respectively). Moreover, note that diets are unevenly distributed among classes, with some classes covering only one diet (*e.g.* detritivore Diplopoda). In contrast, others, such as mammals, birds, and squamates, are more diverse in terms of diets.

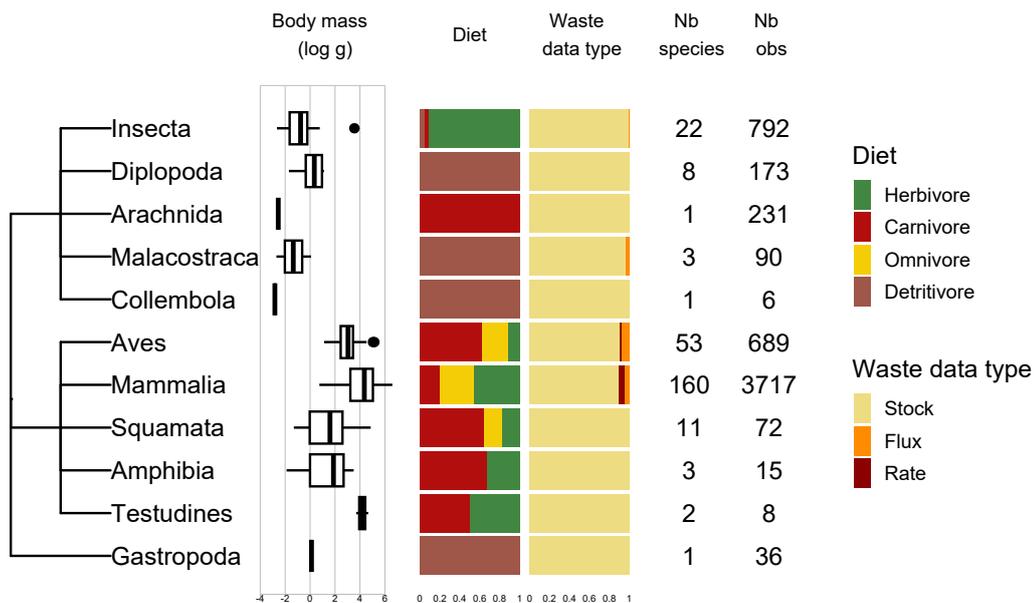


Figure 1.2: Phylogenetic tree of species included in the dataset in the level of the Class. The distribution of body mass is given for each class. The proportion of each trophic guild represented in each class is provided. The waste data type, either stocks (chemical content), flux (mass \times time⁻¹) or rate (mass \times mass⁻¹ \times time⁻¹) are also shown. The number of species for each class, along with the number of observations, are given.

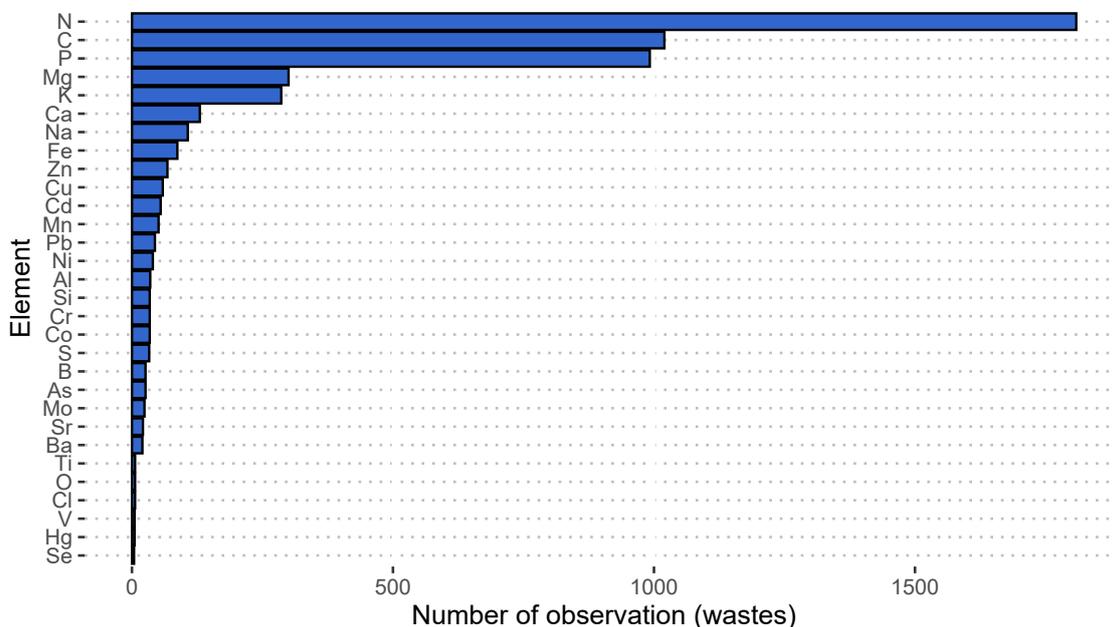


Figure 1.3: Number of observations per elements. C: Carbon, N: Nitrogen, P: Phosphorus, O: Oxygen, K: Potassium, Mg: Magnesium, S: Sulfur, Ca: Calcium, Na: Sodium, Fe: Iron, Si: Silicon, Al: Aluminum, Cl: Chlorine, Ti: Titanium, Zn: Zinc, Mn: Manganese, Mo: Molybdenum, Cu: Copper, B: Boron, Cr: Chromium, Pb: Lead, As: Arsenic, Cd: Cadmium, Ni: Nickel, V: Vanadium, Hg: Mercury, Co: Cobalt, Se: Selenium, Sr: Strontium, Ba: Barium

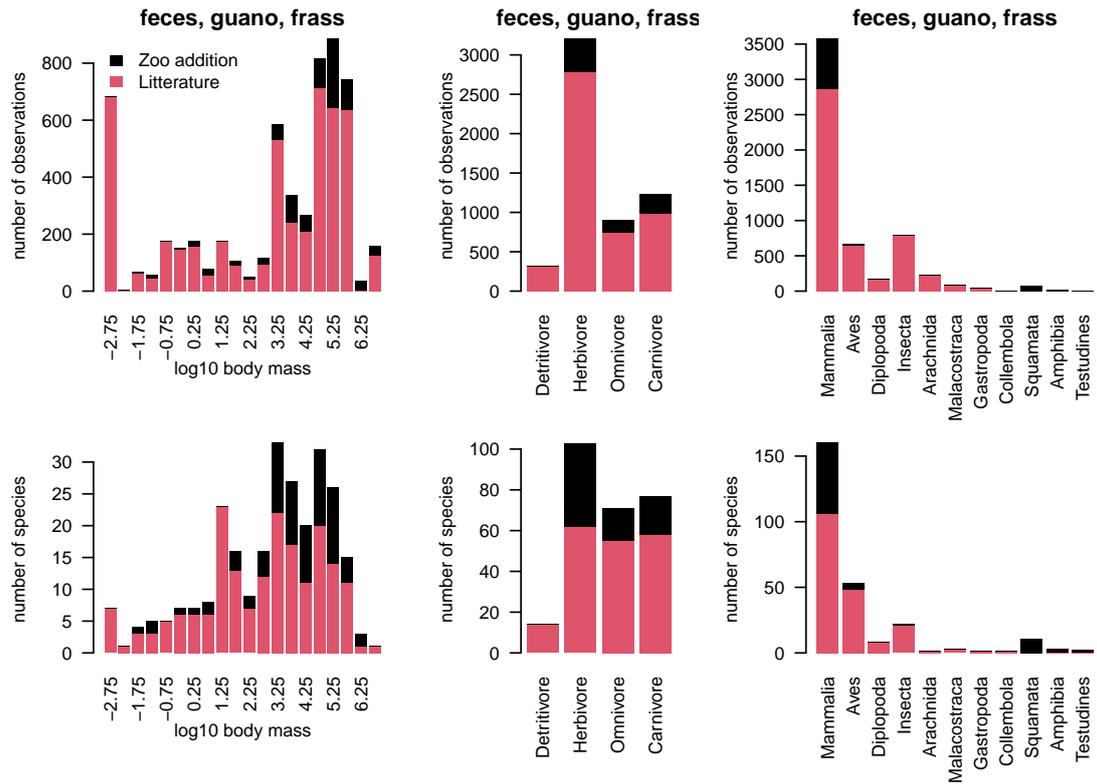


Figure 1.4: Relative contribution of literature and addition from captive animal measures performed by the authors (in feces, guano, and frass samples). The number of observations (top panels) and the new number of species (bottom panels) added to the literature data are shown in the body mass spectra, the diet categories, and the taxonomic classes of animals.

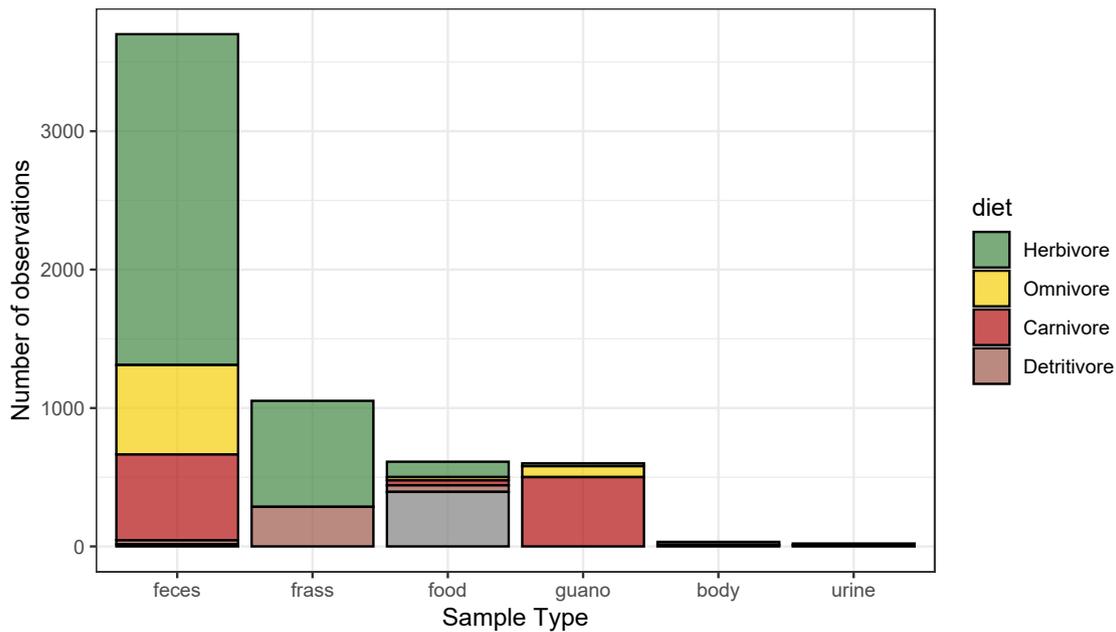


Figure 1.5: Number of observations for each type of sample. Either faeces in mammals, frass in arthropods, or guano in birds. Also shown is the number of reported cases where food composition was concurrently given with waste composition. Grey parts in food samples indicate samples with no specific diet associated.

1.4.2 Inventory of elements

We were able to gather data on 30 different elements, including all macronutrients (C, N, P, O, Ca, Mg, K) as well as micronutrients (Na, Fe, Cu, Cl, Zn) and metals (Pb, Cd etc.). The most often measured element was N (~1800 observations), followed by C and P (~1000 observations each).

1.4.3 Addition from new measurements

A summary of the addition of data from captive fauna samples analyses that we performed is shown in fig. 1.4. These additions constituted 14 % of all observations and 28 % of all species. Importantly, we were able to cover a large body mass range, as well as all diets apart from detritivores. Noteworthy, we also added samples from classes absent from the literature data synthesis: Squamata, Amphibia and Testudines.

The type of sample of "stock" observations, *i.e.* chemical content of samples, are given in fig. 1.5, including mostly faeces, guano, food and frass. A vast majority of observations were made on mammal faeces, and particularly on mammalian herbivores (~3500 observations). It was followed by invertebrate

frass (~1000 observations comprising Insecta, Diplopoda, Arachnida, Malacostraca, Collembola, Gastropoda). Food chemical composition paired with an associated waste composition represented ~600 observations. Birds guano, mostly originating from piscivorous or insectivorous birds (classified here as carnivores) amounted to ~600 observations. Body composition associated with waste composition was rare. Importantly, mammals' urine chemical composition in terms of elements was also very scarce in the literature that we examined (fig. 1.5).

1.4.4 Species body masses

The body mass distribution of species shows a trimodal distribution corresponding roughly to large herbivorous mammals (around 100 kg, peak at larger body mass on the right of fig. 1.7), smaller mammals (1 kg), and birds (10 - 100 g, peak in the middle of fig. 1.7). Herbivores spanned all the body mass spectra, whereas detritivores were centralised at small body masses (fig.1.7). Omnivores were restricted to intermediate body mass, and the maximal carnivore body mass was smaller than that of herbivores (fig.1.7).

1.4.5 Observation resolution

Each waste observation was associated with a resolution that informed the meaning of the associated error (fig. 1.6). Most waste chemical composition measurements were done at the individual level (40 %), with each observation corresponds to a single measure done on a single individual (and hence no error associated with the observation). The second most common resolution is at the level of a population (20%), where the observation originates from a single measure done on wastes produced by a collection of individuals. Most detritivores fell into this category since frass is often pooled to reach measurable amounts. A minority of observations were given as averages of several measures with associated errors, either representing intra-individual, inter-individual, intra-population or inter-population variation (see Methods, fig.1.6).

1.4.6 Sampling environment

Each observation was associated with a sampling environment including the wild, laboratories, zoological gardens and farms. In our database, most observations come from *in natura* samples (~3000 observations), followed by samples originating from animals kept in laboratories (~2000 observations), zoos (~1000 observations), and finally farms (fig. 1.8).

1.4.7 Chemical measure methods

The various elements were measured according to diverse methods. In fig. 1.9, we highlight the measure methods for C, N and P. For C, the most common method was elemental analysis. For N, elemental analysis, but also autoanalyze and Kjeldahl methods were the most common methods. For P, autoanalysis and ICP (inductively coupled plasma) were the most common methods.

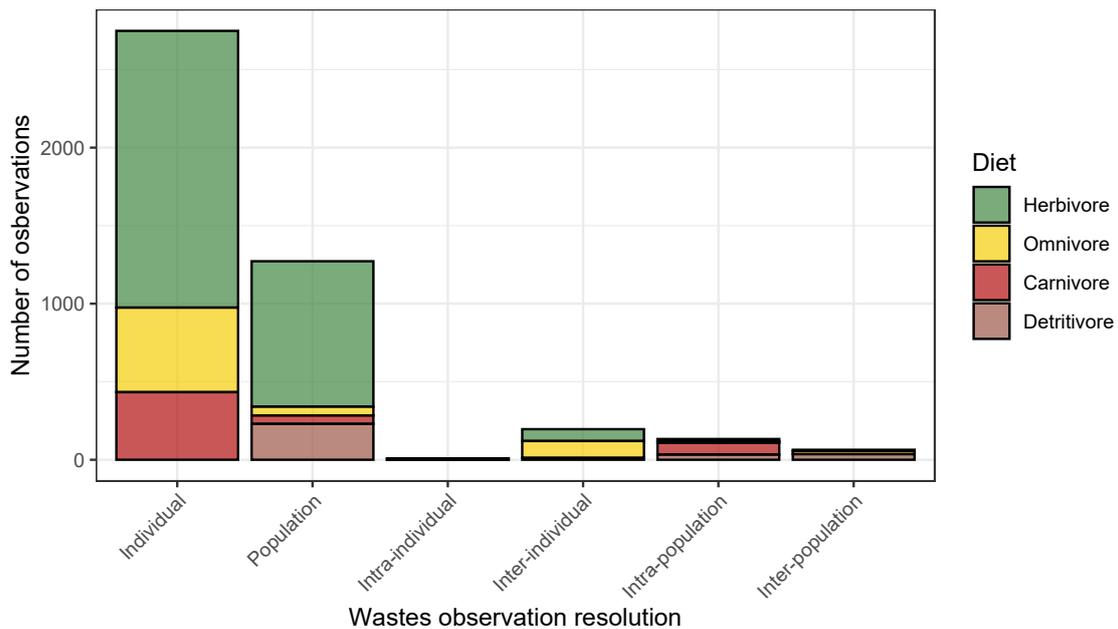


Figure 1.6: Number of observations for each observation resolution in the dataset. "Individual" corresponds to measures done once, at the level of one individual. "Population" correspond to measures done once at the level of a group of individuals. "Intra-individual" corresponds to several measurements done repeatedly on the same individual, giving an average and an error. "Inter-individual" corresponds to several measurements done on different individuals, giving an average and an error. "Intra-population" corresponds to several measurements done repeatedly on the same population, giving an average and an error. "Inter-population" corresponds to several measurements done on different populations, giving an average and an error. Note that authors don't give enough information for some measurements to decide which class the measurement pertains to.

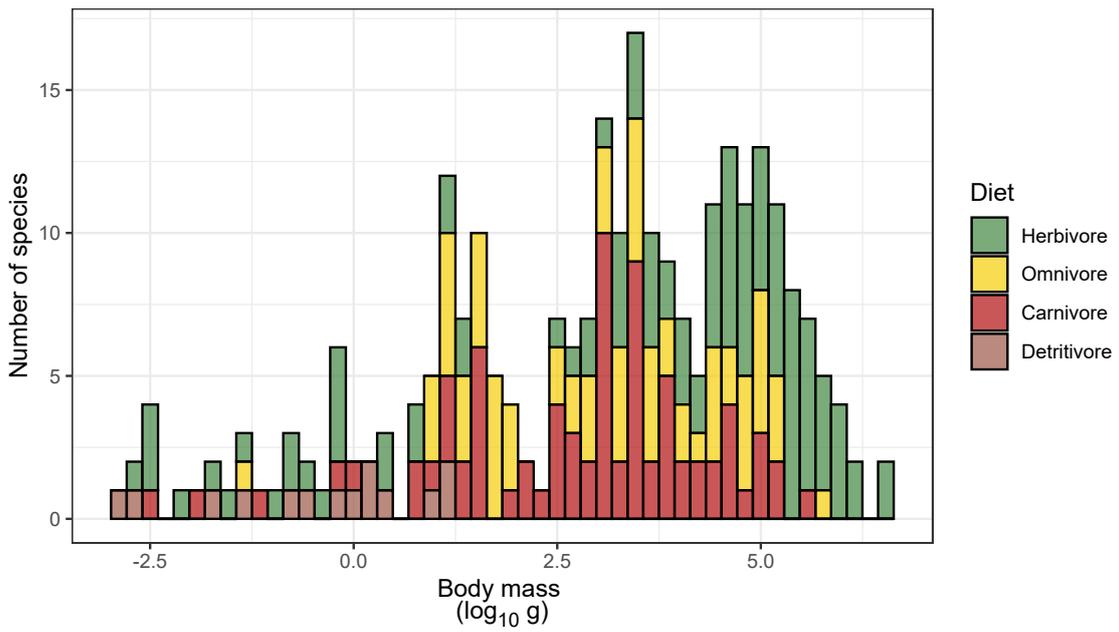


Figure 1.7: Histogram of the number of species according to their body mass. In each body mass class, the proportion of each diet is shown. Note that detritivores are mainly small species. Carnivores span all body sizes except for the largest, where there are only herbivores.

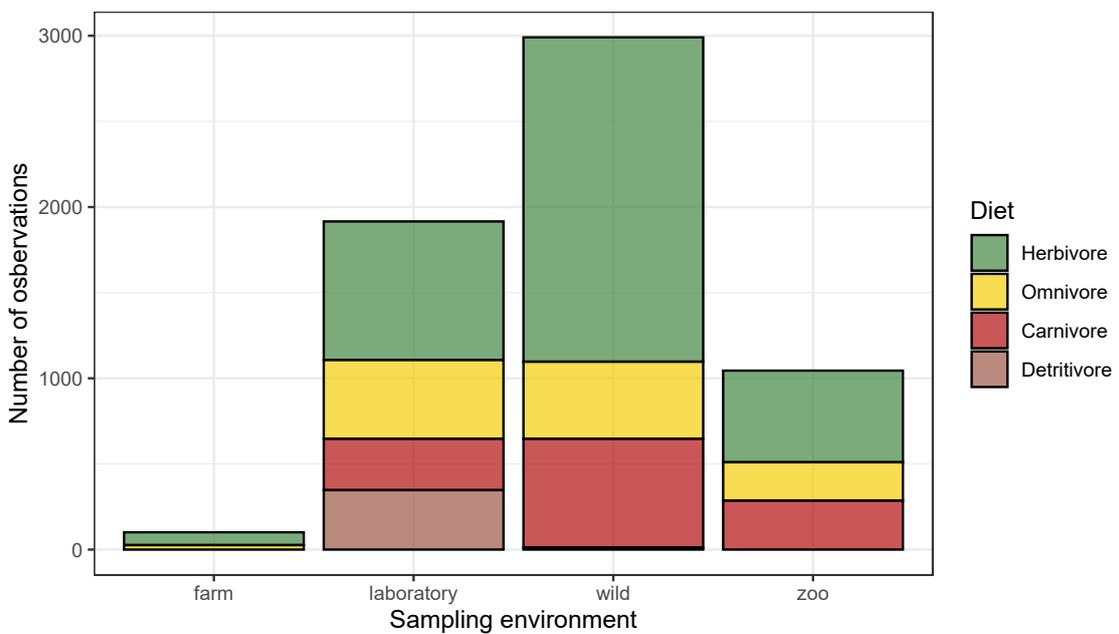


Figure 1.8: Number of observations in the various sampling environments.

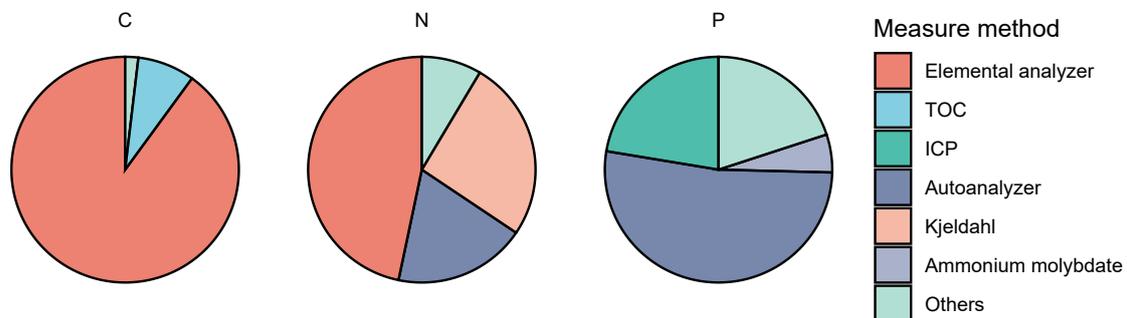


Figure 1.9: Chemical measure methods for C, N and P. TOC stands for total organic carbon (reviewed in [Bisutti et al. 2004](#)), ICP stands for inductively coupled plasma (optical of mass spectrometry, see [Soltanpour et al. 1996](#)). The Kjeldahl method is described in [Bremner \(1960\)](#).

1.5 Discussion

This database represents the first effort to gather data on waste composition from a large diversity of land animals. This synthesis effort should advance the understanding of animal's impact on nutrient cycles in terrestrial ecosystems. However, several limitations exist, that we shall present in the following.

1.5.1 Under-representation of fluxes and rates

A thorough investigation of animals' impact on nutrient cycles inevitably requires estimates of nutrient fluxes and rates that transit through these animals ([Loladze et al., 2000](#); [Schiettekatte et al., 2020](#); [Zehnder and Hunter, 2009](#)). However, most of the data that we were able to find in the literature were waste chemical content. Chemical composition controls processes such as mineralization and immobilisation, and such data are thus important to assess the release rate of nutrients from these wastes. However, ecosystem-scale estimates of recycling by animals need to include the quantity of waste produced by individuals, and making a link with population dynamics requires estimates of quantities produced per unit body mass and time, *i.e.* rates. Due to the challenges of measuring fluxes in wild animals in their natural habitat, the most fea-

sible option currently available to estimate these fluxes involves utilising indirect measurements. This can be achieved by calculating the weight and quantity of waste released combined with chemical data provided by our database. Such examples exist in the literature, where continental scale N fluxes generated by mammalian herbivore populations are computed (Abbas et al., 2012). Another option is to conduct measurements on captive fauna as is done in numerous studies (Clauss et al., 2007, 2013), while concurrently performing chemical analysis. When combined with density population estimates (Santini et al., 2018), it would then be possible to achieve ecosystem-scale assessments of nutrient recycling. We suggest that more such measurements be done, and we hope that our database, designed to host such data and to be curated, will constitute a starting point for a larger and more exhaustive repository.

1.5.2 A gap in non-mammals data

Most observations on wastes in the database were from mammals (fig. 1.2). Although mammals and, in general, megafauna represent substantial nutrient waste fluxes in ecosystems (Enquist et al., 2020; Doughty et al., 2013; Berzaghi et al., 2018; Hulot et al., 2019), there are indications that smaller animals like insects generate as much waste (Hatton et al., 2019; White et al., 2007; Loeuille and Loreau, 2006), possibly being equally important to nutrient cycling (Weisser and Siemann, 2008). Our database includes a substantial variety of mammals (160/5000 species described) but inadequately records information on insect diversity (22/1 million species, Scudder 2009; Wheeler 2009). In general, the lack of data on invertebrates is likely grounded in methodological limitations. These small animals generate few wastes and there is an intrinsic difficulty in measuring chemical content in samples less than 100 mg, typically frass from very small animals. Moreover, many of these invertebrates spend a significant amount of time inside soils, where it is challenging to locate and sample very small faecal pellets.

Data from arachnids are crucially lacking in our dataset. Their small body size and carnivorous lifestyle would have been interesting to complement the carnivores' body mass coverage. Arachnids generate large global impacts on insect populations, amounting to twice the amount of food consumed by human societies according to some estimates (Nyffeler and Birkhofer, 2017). They eat nutrient-rich prey, which generate rich and small-sized wastes that should be easily decomposed and mineralized. Their impact on nutrient

cycling has been assessed in several ecosystems (Curry, 1986; Van Hook Jr., 1971), but the chemical fluxes generated were not estimated.

The lack of data pertaining to animal classes engaged in detritivory, such as Diplopoda, Malacostraca, Collembola, and Gastropoda, represents a noticeable gap in our database. Data either do not exist, are difficult to find or our research process did not allow us to encounter them. The effect of detritivore species on speeding up nutrient cycling has been repeatedly investigated and in various biomes (Joly et al., 2020; Filipiak, 2016; Sagi et al., 2019; Slade et al., 2016; Joly et al., 2018; Daufresne and Loreau, 2001a). They hold the peculiar function of moving detritus from the surface to deeper soil layers, thereby mixing the input nutrients to the rhizosphere where it can be accessed by plants (David, 2014; Frouz et al., 2015). An interesting characteristic of some detritivore species is their coprophagous lifestyle, particularly dung beetles, which feed upon mammalian faeces and are key to their fragmentation and soil incorporation. But the chemical assessment of waste produced from this consumption of faeces is missing from the literature on their important function (Nichols et al., 2008; Veldhuis et al., 2018; Frank et al., 2018; Brown et al., 2010; Raine et al., 2018; Slade et al., 2016; Milotić et al., 2018; Manning and Cutler, 2018). More generally, it would be interesting to include detritivore animals from other clades: plathelminthes, annelids (for which a meta-analysis exists in Van Groenigen et al. 2019), onychophores, tardigrades and nematodes.

1.5.3 In mammals, a lack of data on urine

Data on the chemical composition of waste included faeces, frass, and guano, but mammal urine was crucially missing. Most studies that include urine data focus on domesticated species with restricted body mass and diet (cows, pigs, sheep, goats) and very often in agricultural contexts (Powell et al., 1998; White-Leech et al., 2013; Deenen and Middelkoop, 1992; Saarijärvi and Virkajärvi, 2009; Haynes and Williams, 1993). Moreover, domesticated fauna often receives supplements that greatly influence urine chemical composition and which is therefore not representative of what could be found in non-agricultural settings (Vu T. K. V., 2010). Urine has very different chemical properties compared to faeces, in particular in regards to its N:P ratio (Sitters and Olde Venterink, 2021). Urine contains very little P, but is very rich in N, resulting in N:P ratio over 500, whereas that of faeces is rather around 2-3. Particularly N in urine is found in inorganic forms, sometimes directly available to plants

(Haynes and Williams, 1993), but also prone to ammonia volatilisation (Ruess and McNaughton, 1988). This gap in the literature has already been highlighted by Sitters and Olde Venterink; Sitters et al., and can be explained by the difficulty of sampling fresh urine in field settings.

1.5.4 Conclusion

In conclusion, the compilation and synthesis of data on waste composition in terrestrial fauna presented in this paper represent a pioneering effort in the field of ecological stoichiometry and consumer-driven nutrient recycling. While challenges and gaps remain in the estimation of nutrient release rates, the inclusion of small species and of nutrients found in urine, this database provides a valuable resource for researchers seeking to unravel relationships between animals, their waste, and nutrient cycling in terrestrial ecosystems. We hope it will serve as a basis for future investigations towards a more holistic understanding of the impact of diverse animal species on nutrient dynamics.

In Nature, nothing is wasted, not even waste

Jones (2017)

2

Terrestrial fauna waste composition: patterns and implications

Samuel Charberet, Isabelle Gounand and Jérôme Mathieu.

Terrestrial metazoans produce wastes, faeces and urine, which contain significant amounts of key nutrients. However, their role in nutrient cycles remains inadequately understood. Waste chemical composition is critical to nutrient release rate, but its drivers are poorly characterized in terrestrial ecosystems. We have assembled a large database of the chemical composition of animal wastes combined with diet and body size, in 198 terrestrial species representative of the major clades. In our dataset, diet determines most interspecific variation in waste chemical composition, while body size has a comparatively small effect. Thus, herbivores, omnivores, and carnivores produce wastes of contrasting compositions. We discuss how these differences in waste stoichiometry might impact subsequent use by micro-organisms and plants in light of soil microbiology. While it was known that wastes are generally better decomposed than litter, our analysis highlights that the trophic position of terrestrial animals should be important to explain the distinct effect of animals on nutrient cycling. These results provide a better understanding of animal impacts on terrestrial ecosystems.

2.1 Introduction

Animals consume food resources which are further processed through digestion. Some of the ingested food, and the nutrients that compose it (*e.g.* C, N, P) quickly return to the environment in the form of faeces, while the remaining part is absorbed and used for metabolism and growth. The return of nutrients and energy to the soil participates in numerous ways in the functioning of terrestrial ecosystems. Bacteria, fungi, and eventually plants can further use the nutrients and energy contained in faeces and urine for growth after proper decomposition (Hawke and Summers, 2006; O'Brien and Hatfield, 2019). The fluxes brought by animal waste can, in some cases, represent a crucial contribution to the nutrient return pathway. For instance, in Yellowstone National Park, nitrogen fluxes through animal waste have been shown to exceed nitrogen fluxes through falling litter (Frank et al., 1994). In oceanic islands, the input of nutrients brought by marine birds can have large effects on primary productivity and ecosystem type (Croll et al., 2005). These wastes create local hotspots of nutrients in soils (Whitworth et al., 2019) or result in a redistribution of nutrients in the landscape through movement (Doughty et al., 2013) and, therefore, also influence the spatial distribution of nutrients.

The nutrient composition of wastes influences local scale nutrient release dynamics. Indeed, decomposition (Aarons et al., 2004; Sitters et al., 2014), immobilisation, and mineralisation by micro-organisms (Güsewell and Gessner, 2009) depend on the wastes' chemical composition and elemental stoichiometric ratios due to variation in microbial dynamics at various substrate stoichiometry (for C/N and C/P, see Arenberg and Arai 2019, for N/P see Güsewell and Gessner 2009 and more generally see Cherif and Loreau 2013). As a result, soil nutrient availability depends on waste stoichiometry, among other factors. In turn, plant diversity and community dynamics can respond differently to wastes of contrasted stoichiometry (Gillet et al., 2010; Valdés-Correcher et al., 2019). A finer description, as well as a global assessment of the role of animal wastes in nutrient cycles, is thus crucial to understanding the functioning of terrestrial ecosystems. However, this requires a better knowledge of how the chemical composition varies among species and according to which factors.

Terrestrial animals release their waste in two major ways. Either in the form of separated faeces and urine in mammals, or both mixed together in all

other terrestrial animals, which have a cloaca, including arthropods (frass), birds and squamates (guano). Some nutrients are excreted in urine (or excreta) preferentially (N, [Sitters and Olde Venterink 2021](#)), while others are mostly released in faeces (P, [Sitters and Olde Venterink 2021](#)). Whether both egesta and excreta are released together or not thus modifies the stoichiometry of the local patch of deposited wastes (richer or not in N, respectively). In mammals, physiology suggests that the chemical composition of faeces (egesta) should be explained by the digestibility of the food, which mainly depends on its composition. In non-mammals, the total waste (faeces + urine) should be close in composition to diet because apart from C, which is released as CO₂, all other ingested nutrients will end up being either egested or excreted in a non-growing and stoichiometrically constant animal. However, although the variation in egesta and excreta stoichiometry has been thoroughly studied in aquatic ecosystems, it is not the case for terrestrial ecosystems. Arguments developed in ecological stoichiometry in the context of aquatic systems and giving satisfactory predicting power ([Vanni and McIntyre, 2016](#)) can also be applied to the terrestrial realm ([Sitters et al., 2017a](#)).

Ecological stoichiometry predicts that waste stoichiometry should be driven by body and food stoichiometry ([Sturner et al., 2002a](#)). If the C/X resource ratio is higher than required, X's absorption is maximised, while C's absorption is adjusted such that the absorbed C/X ratio aligns with consumer requirements ([Sturner et al., 2002a](#)). Thus, there should be a positive relationship between food and waste stoichiometry and a negative relationship between body and waste stoichiometry (see Introduction, fig. 2). Therefore, trophic guild (herbivore, omnivore, carnivore), which affects resource stoichiometry ([Cross et al., 2005](#); [Andrieux et al., 2021](#); [Tian et al., 2019](#)), should trigger differences in waste stoichiometry. In addition, body N/P has also been hypothesized to be related to body mass through correlates with growth rate (*i.e.*, the growth rate hypothesis) and bone content (see also Introduction). On the one hand, because biosynthesis machinery has high P requirements, the growth rate hypothesis states that smaller animals, which grow faster, are richer in P, resulting supposedly in lower P in faeces ([Sturner et al., 2002a](#)). On the other hand, in vertebrates, the increasing relative mass of phosphorus-rich skeleton at higher body masses ([Calder, 1996](#); [Prange et al., 1979](#); [Martin-Silverstone et al., 2015](#)) is supposed to increase the requirements for P at high body mass, which should lower the faeces P content ([le Roux et al., 2020a](#)). We therefore expect a positive relationship between body mass and waste N/P in inver-

tebrates and a relationship in vertebrates which direction depends on the relative contribution of the effect of skeleton and the effect of growth rate. Overall, trophic guild and body mass are two traits that should influence waste stoichiometry and, therefore, the fate of the nutrients within the local patch scale.

The effect of body mass has been investigated on herbivorous mammal faeces but received contrasted results in the terrestrial realm, from being confirmed (le Roux et al., 2020b) to being invalidated (Sitters and Venterink, 2021), but no general test on a larger set of species has been undertaken. Moreover, the effect of the trophic guild on waste stoichiometry has been poorly documented in terrestrial systems besides within herbivores where the browser grazer dichotomy has been tackled and theorized (Sitters et al., 2017a; Sitters and Andriuzzi, 2019), in which browsers and grazers have been associated to deceleration and acceleration of nutrient cycling, respectively. Studies indicate that the C/N ratio of mammal carnivore faeces increases from carnivore, to omnivore and to herbivores (Frank et al., 2017), but the effect of body mass, and the inclusion of animals other than mammals is rarely to not explored.

Stoichiometry alone, however, is not sufficient to understand the quantitative effects of animals on recycling. We also need to analyse the fluxes in which animals participate. The ideal situation would be to compare egestion/excretion fluxes with ingestion fluxes at the nutrient level. This would describe how animals are repacking nutrients from biomass in terms of bulk processing and differential speed of nutrient release. However, data on ingestion and egestion fluxes on the same individuals are rarely given in the literature. As an alternative, we can use the large amount of data existing on absorption efficiency, which is defined as the amount of ingested material not retrieved in faeces (Richard et al., 2017). Elemental absorption efficiency (see methods) allows a digestion balance to be performed at the level of the animal but ignores fluxes in excretions. Data on N shows that absorption efficiency decreases at low nutrient content in the resource, owing to the prevalent role that digestive obligatory losses play (Richard et al., 2017). As a result, it happens that in herbivores consuming resources poor in N, the absorption efficiency decreases (Richard et al., 2017). On the other hand, for carnivores, the absorption efficiency of N is high due to the high N content in the resource (Richard et al., 2017). The more nutrients are absorbed, the slower they are

recycled since they will be excreted later or kept in the body for a longer period. Therefore, resource nutrient content could play a role in recycling processes through its effect on absorption efficiency.

In order to test the effect of bodymass and diet on waste CNP composition and absorption, we analysed a part of a global dataset that we built based on a literature search and also on complementary new measurements that we presented in Chapter 1). This dataset includes the waste C/N/P stoichiometry of 195 terrestrial animal species from various taxa (mammals, arthropods, birds, reptiles, amphibians, and gastropods) spanning major diets (herbivores, carnivores, omnivores, detritivores) and with a good representation of ex-tant body masses (mg to ton). The analysis shows that diet better explains waste content in C, N and P chemical composition than body mass. We also compiled another dataset of absorption efficiencies for five nutrients (P, Mg, Ca, K, Na), giving a total of 656 observations on herbivores, omnivores and carnivores consuming diets of contrasted nutrient content. The hypothesis on endogenous-loss-induced control of absorption efficiency is confirmed for most nutrients (P, K, Mg, Na), highlighting the importance of resource nutrient content on the relative fluxes generated by animals.

2.2 Materials and methods

The primary objective of the study was to investigate the determinants of waste nutrient content. We, therefore, gathered data on waste nutrient composition as well as animal traits, at the species level, body mass and diet, in a wide range of terrestrial animals (see chapter 1). The dataset encompasses arthropods, birds, reptiles, mammals, amphibians and gastropods (fig.1.2). Because only a limited amount of data on fluxes were found (see results in chapter 1), we built a second dataset that focused on absorption efficiency, a measure of relative ingestion and egestion fluxes.

2.2.1 Data selection and processing

Unfortunately, the amount of data for urine (in mammals) gathered for our study was not high enough to allow statistical analyses. We, therefore, focused our analysis on the chemical composition of faeces in mammals and on the total waste (egesta + excreta) produced by non-mammals. Based on the dataset presented in Chapter 1, we selected only data on C, N and P stocks, that is, chemical

content expressed in % dry weight in either mammal’s faeces or non-mammal total waste (excreta + egesta). We computed species-level averages content for C, N and P, by averaging the content over all the observations made on the same species. We then computed the ratios of these average elemental contents (C/N, C/P, N/P) for each species. The number of species for each nutrient content and stoichiometric ratio is given in table 2.1.

	C	N	P	C/N	C/P	N/P
Mammal species	90	121	110	89	85	91
Non-mammal species	54	81	60	54	34	55

Table 2.1: Number of species for each nutrient content and stoichiometric ratio.

2.2.2 Absorption efficiency data

In order to investigate how trophic groups, characterized by their diet resource quality, absorbed nutrients, we made use of the abundant literature on absorption efficiency (also termed apparent digestibility). Indeed, since egestion fluxes greatly depend on ingestion fluxes, we used this normalised metric to investigate their balance. Absorption efficiency quantifies the relative input and output nutrient fluxes from the guts of animals, not considering excreta (urine). Specifically, absorption efficiency (AE) is defined as the proportion of intake which is not egested over a period of time longer than digestion:

$$AE(x) = \frac{\text{intake}(x) - \text{egestion}(x)}{\text{intake}(x)}$$

We searched for elemental absorption efficiencies coupled with resource nutrient content (P, K, Ca, Mg, Na). When treatments testing the effect of supplementation were applied to animals, we selected only data from the control group. A total of 43 articles were selected, which contained 656 absorption efficiency observations on 18 mammal species and one bird species (for which egesta was selectively sampled), representative of three trophic guilds (herbivores, omnivores, carnivores). The number of observations for each element and trophic guild, as well as species names, are given in table 2.2. Sources are given in table A.4. These absorption efficiency data are given at the individual level as single measures done on one individual.

	P	Ca	Mg	K	Na
Herbivores	115 (115)	134 (134)	32 (32)	36 (36)	37 (37)
Carnivores	25 (25)	23 (23)	16 (16)	7 (7)	11 (7)
Omnivores	58 (53)	58 (53)	40 (35)	33 (33)	21 (21)

Table 2.2: Number of absorption efficiency observations for each element and each trophic guild. The number of observations for which the elemental composition of the diet is available simultaneously is given in parentheses. Herbivores: *Procapra capensis*, *Equus caballus*, *Gallus gallus*, *Odocoileus virginianus*, *Capra hircus*, *Rangifer tarandus*, *Bos taurus*, *Rhinoceros unicornis*, *Equus caballus*, *Elephas maximus*, *Oryctolagus cuniculus*, *Ovis aries*, Omnivores: *Sus scrofa*, *Sus domesticus*, *Erinaceus europaeus*, *Rattus norvegicus*, Carnivores: *Felis catus*, *Canis lupus*, *Chrysocyon brachyurus*

2.2.3 Statistical analysis

Nutrient content and stoichiometry. Regarding the analysis on waste stoichiometry, we carried out separate analyses for mammals and non-mammals at all steps of our analysis to avoid comparing non-comparable wastes. We first assessed the general and interacting effects of body mass and diet on C, N, P contents and the stoichiometric ratios using ANCOVAs for each response variable (C, N, P, C/N, C/P, N/P). Stoichiometric ratios were log-transformed to avoid numerator/denominator variation biases (Isles, 2020). When the ANCOVA was significant, we investigated further the separate effects of diet and body mass. We tested the effect of diet with non-parametric ANOVA Kruskal–Wallis H test after the removal of diet groups containing less than five species to avoid poor statistical power. When Kruskal–Wallis H test were significant, we carried out post-hoc pairwise comparisons to determine which trophic groups were different from one another. The diet groups were compared by pairs for each nutrient and each stoichiometric ratio using Holm-corrected Mann–Whitney U tests. Similarly, the effect of body mass was assessed inside each diet through linear regressions of nutrient content against the logarithm of species’ body mass (base 10).

Absorption efficiency. Elemental absorption efficiencies were assessed against resource elemental content. According to the endogenous loss hypothesis (Richard et al., 2017), a constant loss term is applied at all resource levels. We therefore fitted a non-linear model using the nls function in the stats R package to assess the quality of this model, where:

$$AE(X) = \frac{k_X \cdot I \cdot R(X) - E}{I \cdot R(X)}$$

with $AE(X)$ the absorption efficiency of the nutrient X , $R(X)$ the level of X in the resource (measured in % dry weight), I the mass-specific ingestion rate, here considered constant among all species (being fed *ad libitum*), E a constant loss term, and k_X a constant representing the "true digestibility" ($AE(X) = k_X$ when $I \cdot R(X) \rightarrow +\infty$).

2.3 Results

2.3.1 Chemical composition of wastes

According to the ANCOVAs (table 2.3), body mass and diet explained a significant part of the variability of the waste chemical composition in all but two models, namely the P content and the N/P ratio in non-mammal waste (table 2.3). We proceeded with in-depth investigations on the separate effects of diets and of body mass within each diet group. In-depth ANCOVA analyses are available in table B.1 and B.2.

Diet showed a marked effect on waste composition (figs.2.1, 2.2). In mammals, the faeces of herbivores were always different from carnivores in terms of C, N, and P and their ratio (figs.2.1). Specifically, herbivores had higher C, C/N, C/P and N/P, but lower N and P than carnivores (figs.2.1). Omnivores were generally in between herbivores and carnivores, except for N/P, where it was the highest among all diets (figs.2.1.f). However, differences between omnivores and herbivores, or between omnivores and carnivores, were not always significant.

In non-mammals, diet also affected total nutrient content, with herbivores having lower N and P and higher C/N and C/P than carnivores. However, the C and the N/P ratio were not different between herbivores and carnivores (fig.2.2.b). Moreover, the C content does not seem to vary from one diet group to another in non-mammals (fig.2.2.a). N waste content increased from herbivores and omnivores to carnivores. Also, N content was equivalent between detritivores and herbivores (fig.2.2.b).

Group	Variable	Adjusted r ²	sigma	Statistic	p-value	df	AIC	BIC	Deviance	n observations
Mammals	C	0.375	5.6	11.7	1.41E-08	5	573	591	2630	90
	N	0.586	2.03	35	1.29E-21	5	523	542	474	121
	P	0.53	1.56	25.6	9.79E-17	5	417	436	251	110
	log ₁₀ C/N	0.475	0.456	16.9	1.64E-11	5	120	138	17.2	89
	log ₁₀ C/P	0.527	0.806	19.7	1.06E-12	5	212	229	51.3	85
	log ₁₀ N/P	0.356	0.65	11	3.73E-08	5	188	205	35.9	91
	C	0.149	12	2.33	0.0403	7	431	449	6590	54
	N	0.386	5.06	8.19	2.45E-07	7	502	524	1870	81
	P	0.0161	3.26	1.14	0.354	7	322	340	553	60
Non-mammals	log ₁₀ C/N	0.478	0.906	7.93	2.75E-06	7	152	170	37.8	54
	log ₁₀ C/P	0.348	1.65	3.52	0.00862	7	139	153	70.7	34
	log ₁₀ N/P	-0.0377	1.49	0.719	0.656	7	209	227	104	55

Table 2.3: ANCOVA results on C, N, P and stoichiometric ratios with body mass and trophic guild as explicative variables. The analyses were ran separately for mammals and non-mammals.

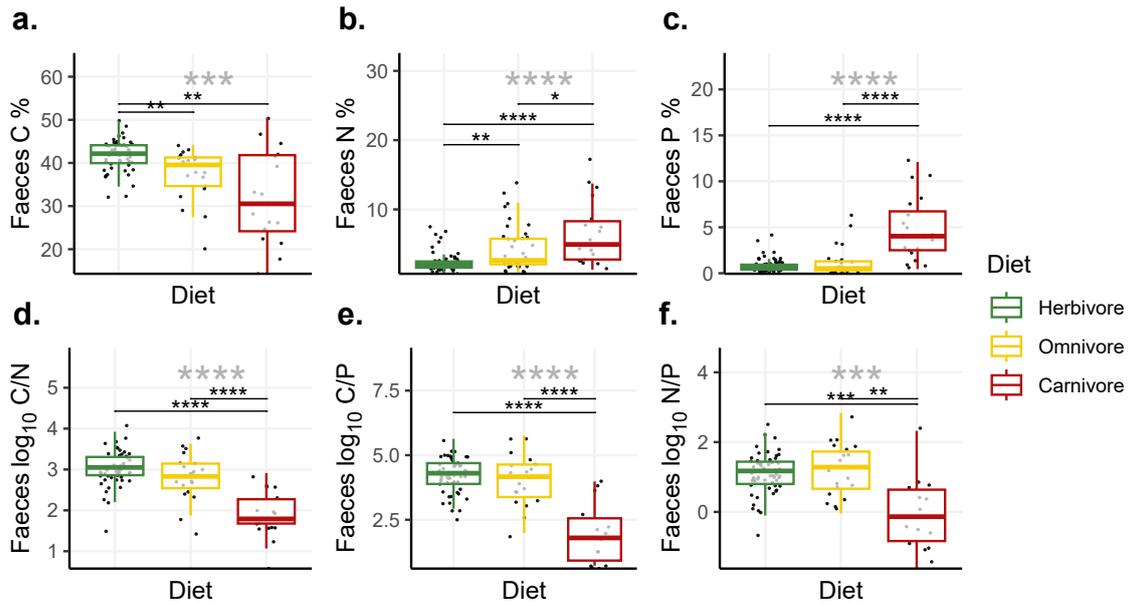


Figure 2.1: Effect of diet on CNP absolute concentration and ratios (mass ratios) in mammal faeces. Each point represents the mean for a given species. Grey stars show the significance of the Kruskal–Wallis H tests. Black stars show the Holm-corrected significance of Mann–Whitney U tests.

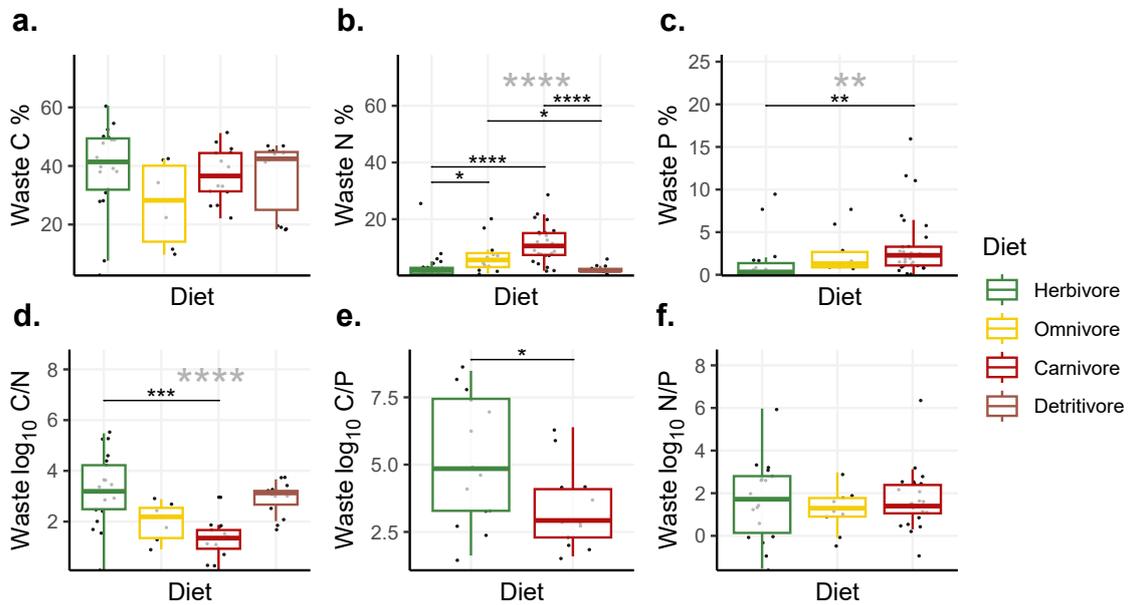


Figure 2.2: Effect of diet on CNP absolute concentration and ratios (mass ratios) in non-mammals total waste. Each point represents the mean for a given species. Grey stars show the significance of the Kruskal–Wallis H tests. Stars show the Holm-corrected significance of Mann–Whitney U tests.

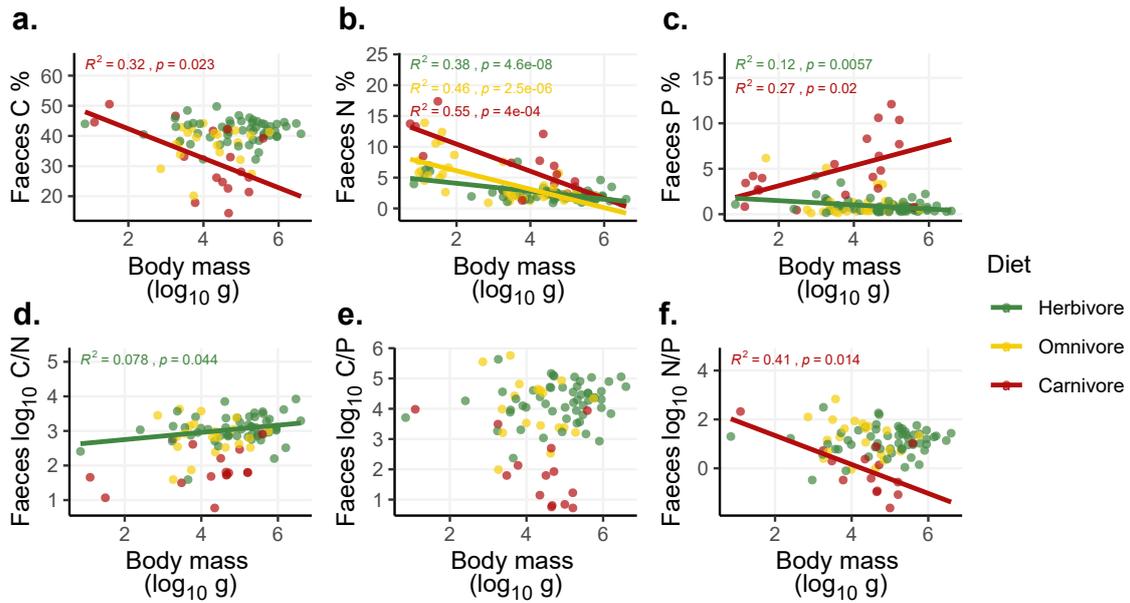


Figure 2.3: Effect of body mass on CNP absolute concentration and ratio (mass ratios) in mammal faeces for each diet. Each point represents the mean value for one species. Only significant relationships are shown.

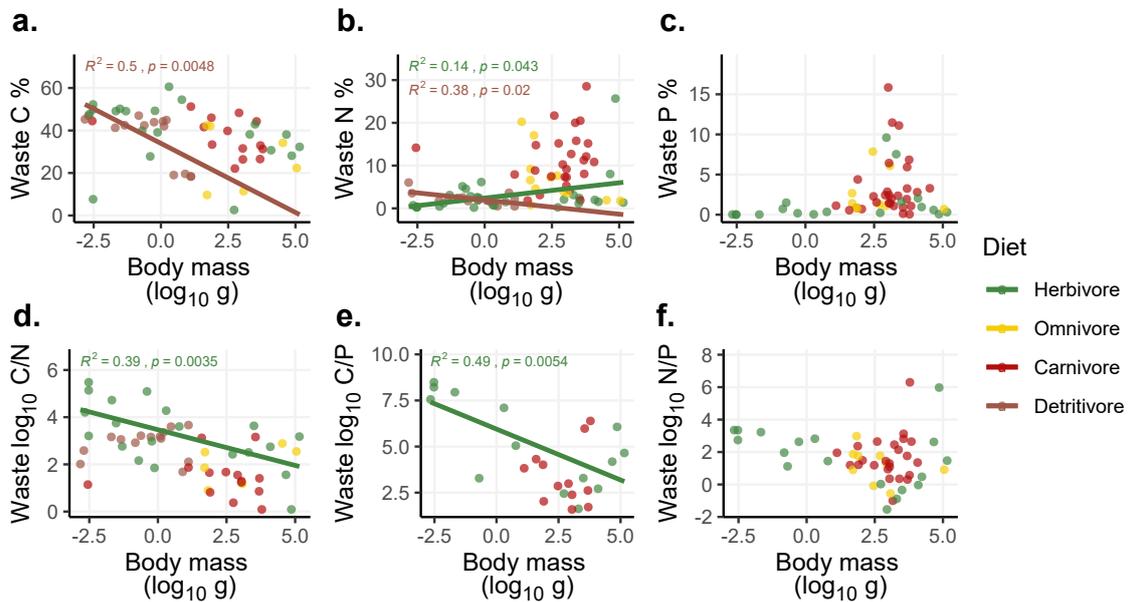


Figure 2.4: Effect of body mass on CNP absolute concentration and ratio (mass ratios) non-mammals total waste for each diet. Each point represents the mean value for one species. Only significant relationships are shown.

Body mass exhibited contrasted effects on waste composition inside trophic guilds (figs. 2.3, 2.4). The N content decreased with body mass in all diet

groups in mammals (fig.2.3.b). In mammalian herbivores, P decreased with body masses (fig.2.3.c), whereas it increased in carnivores. In carnivores, C, N, N/P decreased whereas P content increased with bodymass (fig.2.3.a, b, c, e). In omnivores, both N and P content decreased with body mass (fig.2.3. b and c)

In non-mammals, body mass also had little effect. No correlation between waste content or stoichiometric ratios and body mass was found for omnivores nor carnivores in non-mammals. Non-mammalian herbivores exhibited a positive relationship for N, and negative relationships for C/N and C/P with body mass. Detritivore waste C and N decreased with bodymass (fig.2.4.a).

2.3.2 Chemical fluxes in mammal faeces

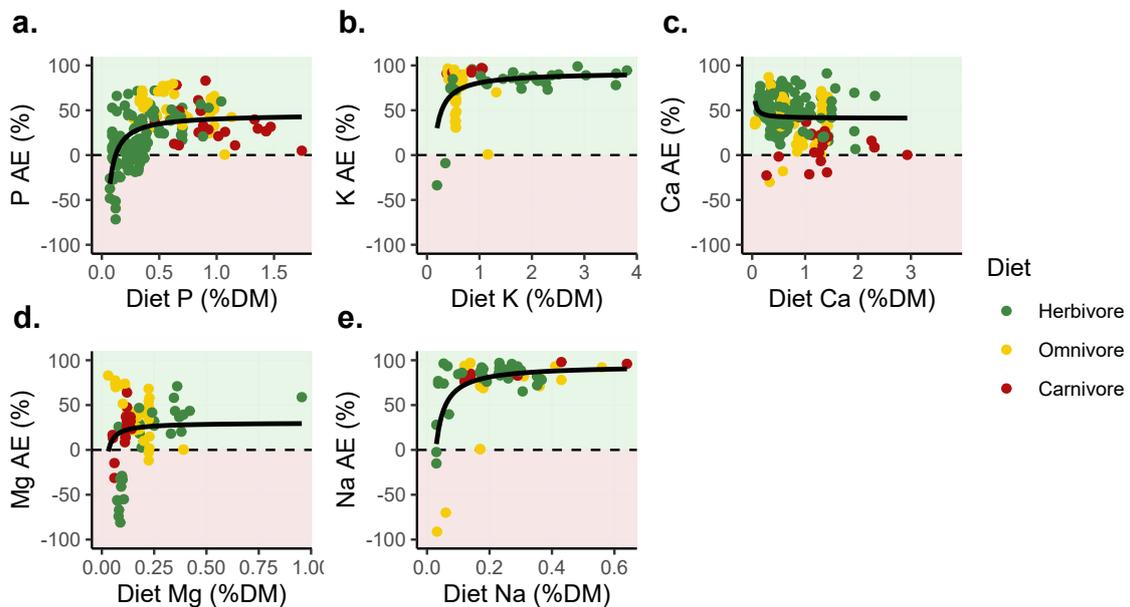


Figure 2.5: General relationship between absorption efficiency and the content of elements in food for P, K, Ca, Mg and Na, at the level of an individual. The red area represents the state at which the animal eats less of the element than it withdraws in faeces, the animal being an overall source of the element. In the green area, the animal can be at equilibrium, considering urine is not shown, or even be a sink of nutrients. For each plot, the regression line follows a theoretical relationship $y = \frac{kx-E}{x}$, with E an obligatory loss constant.

The absorption efficiencies for P, Mg, Na, K were affected by the resource elemental content. The richer the resource was in P, Na, Mg, and K, the higher the absorption efficiency was. Concurrently, the lower the resource was in these elements, *i.e.* in herbivores, the lower was absorption efficiency. For very low elemental content in the food, which mainly occurred in herbivores (fig.2.5),

absorption efficiency can even be negative, meaning that the element is more egested than ingested during the period of measurement (also see table B.3 for modelling details).

2.4 Discussion

Overall, our study shows that wastes' CNP chemical composition is primarily influenced by the animal's diet, being higher in C and lower in N and P in herbivores than in carnivores, both in mammals and in non-mammals (figs. 2.1, 2.2). Body mass had relatively fewer effects on waste nutrient content (figs. 2.3, 2.4). Nonetheless, faeces of larger mammals had lower N content than smaller ones in all diets (fig.2.3.b). We also found that when a resource is too poor in P, K, Na and Mg, the animal can lose more nutrients than it gains through ingestion (fig.2.5) as it has already been shown for N (Richard et al., 2017).

2.4.1 Diet explains most of faeces' content and stoichiometry differences

The variation in waste nutrient content was mostly associated with diet, which can be attributed to both the variety of resource quality among diets and the physiological differences of species between trophic guilds. Herbivores tend to eat poorer resources, composed of poorly digested, complex carbohydrates and polyphenols (cellulose and lignin, respectively, Redjadj et al. 2014). Food is typically ingested at high rates in herbivores to get sufficient amounts of proteins from the N-poor plant (Mattson, 1980). Because they mostly retain N from their food and release the indigestible C in excess there is a high C content (figs. 2.1.a, 2.2.a), and low N content in their wastes (figs. 2.1.b, 2.2.b). On the other hand, carnivores and omnivores have access to readily digested food composed of proteins and close in composition to their own (Sturner et al., 2002a; Andrieux et al., 2021). Because of the high digestibility and energy content of their food, intake and defecation rates are lower in carnivores (De Cuyper et al., 2020). The higher N and P contents of carnivores' faeces relative to that of herbivores (figs. 2.1, 2.2) can be attributed first to the higher nutrient content of their food, but also likely to constitutional losses from the gut that accumulate for a longer time between defecations events (De Cuyper et al., 2020).

2.4.2 Contrasting support of growth rate and skeleton hypotheses among mammals in %P waste content

There has been a claim that large-body mass vertebrates require more P because of relatively larger skeletons and thus should have less P in their faeces (le Roux et al., 2020a). On the other hand, it can be noticed that, in principle, small and fast-growing animals should also require more P than large species to fuel their growth. Differences in body mass should thus translate into variation in waste N/P. Our analysis supports the growth rate hypothesis but not the skeleton hypothesis for mammalian carnivores, for which we observe that faeces become richer in P when bodymass increases, while N/P ratio decreases with body mass. On the opposite, P content in herbivorous mammal faeces rather supports the skeleton hypothesis with a slightly negative relationship between faeces P and body mass (fig.2.3.c). However, we didn't find any relationship between body mass and faeces N/P in mammalian herbivores, which corroborates the absence of a relationship in African herbivores already found (Sitters and Venterink, 2021). The difference in slope for the relationship between faeces P and bodymass between herbivores (negative) and carnivores (positive) suggests that other factors influence the P content in faeces. Particularly, the authors noticed the presence of undigested bones in carnivore faeces, as has already been documented in wild fauna (Stiner et al., 2012). This could explain this trend since bones contain 13% P by mass. It is possible that smaller carnivores, because of mechanical constraints during feeding, avoid ingesting bones. However, studies suggest that it might also be linked to the age of the prey (Stiner et al., 2012), which we did not control for.

In non-mammals, body mass seemed to play little role, especially for N/P, for which none of the diet groups were affected. The growth rate hypothesis did not seem to play a role in our dataset. However, it might be linked to a moderate statistical power. A more exhaustive analysis of invertebrates might be fruitful since these organisms have been shown to be more prone to the growth rate hypothesis than larger vertebrate animals (Isanta-Navarro et al., 2022). Note that the model of Sterner and Elser positing a negative relationship between body N/P and waste N/P is valid only for a growing animal (Elser et al., 1996; Sterner et al., 2002a). Consequently, the absence of growth at the time of waste sampling might explain the lack of a relationship between body mass and waste N/P in our dataset. Nuanced effects of body size on waste N/P have also been found in aquatic ecosystems and interpreted in the same manner

(Vanni and McIntyre, 2016).

2.4.3 Nitrogen content of waste decreases with body size in mammals

Noteworthy, the wastes' N content decreased with body mass within trophic guilds across mammals (fig.2.3). Large body size is supposed to be accompanied by smaller mass-specific metabolic rate, which can be associated with the tolerance of lower food quality and, therefore, lower faeces N content. A better ability to digest proteins at high body mass is also possible, but this view is disputed since no difference in gut passage time, a crucial parameter in protein digestion, is found across herbivore body masses (Clauss et al., 2007). However, this could explain the negative relationship between body mass and faecal N content in herbivores in our dataset. But for carnivores and omnivores, in which the negative relationship is even steeper and which consume easily digested N-rich resources, the picture is less clear. Moreover, C content also seemed to decrease with body mass in carnivores, so that the relative N content at high body mass can not be explained by a higher C content.

However, our study does not account for N deposition through urine in mammals, which represent 80 % of a mammal's N output. Urine is expected to be phosphorus-limited when used as a substrate for micro-organism sources of nutrients (Sitters and Olde Venterink, 2021). But urine N can be subjected to substantive volatilization (up to 60 %, Clough et al. 1998; Wachendorf et al. 2005), suggesting that the "free", usable N is split almost equally between faeces and urine, given that faeces N is less prone to such losses (Sitters and Olde Venterink, 2021). A recent study suggests that supplying urine and faeces in the same place reduces plant N and increases plant P absorption, respectively (Li et al., 2021), suggesting that the cross biogeochemistries of N and P vary depending on the waste-producing behaviour of species,

2.4.4 Potential consequences of waste C/N on N fate

At the ecosystem scale, the quality of wastes has been shown to affect nutrient fate, which can be either immobilised or mineralised by micro-organisms (Robertson and Groffman, 2015; Arenberg and Arai, 2019; Güsewell, 2004). This dichotomy is crucial since immobilised N or P becomes inaccessible to plants, whereas mineralised nutrients are available to plants, opening the way to complex feedback between plants' and animals' nutrient fluxes. We hereafter use our results to conceptually explore the effects of animal waste on

these processes.

Litter C/N ratio under 25 has been shown to stimulate mineralisation and, when above 25, to stimulate immobilisation (Robertson and Groffman, 2015), a “threshold” that relies on microbial biomass requirements. Although this threshold could be marginally different for faeces, studies have indeed shown that faeces’ nutrient release rate depends on stoichiometry as does litter (Sitters et al., 2014). All of the diet averages in mammals show C/N ratios lower than 25 (fig.2.1.d), suggesting that mammal faeces N primarily stimulate mineralisation and increases plant-available N. However, some wastes from herbivore and omnivore species exceed this value of 25 (fig.2.1.d). Depending on diet, immobilisation could thus play some role. In carnivore faeces, this limit is never reached so most of its N is expected to be mineralised. Interestingly, the C/N of carnivores’ faeces (around 10) is very close to that of microbial mass (Andrieux et al., 2021), suggesting ideal conditions for microbial growth in carnivore wastes. On average, animal body C/N, which is around 4, but prone to variations (Andrieux et al., 2021), can thus lower than that of carnivore egestion, suggesting that carnivore faeces and the prey that otherwise would have survived can be prone to contrasted decomposition. Comparing the effect of predation and subsequent egestion on nutrient recycling to other sources of prey mortality (illness, starvation) might require comparing the decomposition processes between carnivore faeces and carrion. It is known that decomposing microbial communities can adjust to their substrate stoichiometry, owing to competitive exclusion, and it might also be the case between carrion and wastes (Barton et al., 2012; Danger et al., 2008). Experimental works on the differences between decomposition kinetics could help include these processes in parametrized models.

In non-mammals wastes, the C/N threshold of 25 is sometimes vastly exceeded, reaching a value of 100 for some species (fig.2.2.d). This is likely due to the very high C/N ratio of the resources consumed by some of these species (termites). The termites play an important role in various ecosystems through the consumption of dead plant material, such as wood, bark and straw, which would be very much longer to decompose without them. Numerous termite species can digest woody fibers with the aid of gut microbiota, which supplements their endogenous enzymes (Bignell, 2011), but they still produce very high C/N wastes.

Moreover, body mass did not significantly influence faeces' C/N ratio neither in mammals nor in non-mammals except for herbivorous non-mammals (figs. 2.3.d, 2.4.d). There may thus be no effects of animal body mass on the relative importance of mineralisation vs immobilisation of produced waste. However, herbivores being generally larger than carnivores ([Price and Hopkins, 2015](#)), there is a net effect of body mass through its correlation with diet (table B.1).

2.4.5 Potential impacts on P cycling

The fate of P in litter is known to depend on the C/P ratio, as does the fate of P found in faeces ([Sitters et al., 2014](#)). Generally, for litter, mineralisation occurs below 200:1 and immobilisation above 300:1 ([Arenberg and Arai, 2019](#)). Although more carbon can sometimes result in a priming effect, whereby carbon input increase microbial activity, it was shown that higher C/P result in a lower P release rate from faeces ([Sitters et al., 2014](#)). Again, in mammals, most of the species averages have waste C/P below 200 (fig.B.2.e), suggesting a dominance of faeces P mineralisation over immobilisation. The few data points in non-mammals prevent any conclusion from being firmly drawn, but the few existing points for termites (fig.B.3.e) show very high C/P, suggesting an immobilisation of P from these wastes. These results have to be nuanced with the variations observed in immobilisation/ mineralisation processes due to other factors, such as temperature, moisture, pH, and soil parent material ([Dalal and Hallsworth, 1977](#); [Sharpley and Smith, 1989](#)). This complex control of P mineralization likely results from a wide range of microbial C/P ratios, suggesting a lot of variation in microbial requirements regarding P, and, therefore, in the threshold for mineralization to occur, as well as from the microbial adaptation to nutrient-deficient environments ([Manzoni et al., 2010](#)).

2.4.6 Potential effects on plant communities

Soil N/P ratio has been suggested to influence plants' growth since it controls which nutrient is limiting ([Elser et al., 2007](#)). N/P ratios below 10 or above 20 tend to be associated, though not always, with limitations in biomass production due to inadequate levels of nitrogen and phosphorus, respectively

(Güsewell, 2004). Moreover, faeces N/P tend to influence plant community diversity. N/P ratios typically ranging from 10 to 20 seem to support the most diverse plant communities in mesocosm experiments (Valdés-Correcher et al., 2019). The mammal faeces in our dataset typically range from 1 to 10 (fig.2.1.f), suggesting that most plants growing on it would be limited by nitrogen. However, we stress that these N/P critical ratios for limitation depend on total N and P supply (Güsewell and Gessner, 2009), suggesting a more complex picture. Carnivore faeces N/P were around 1, whereas that of animal body N/P is around 3 (Andrieux et al., 2021). This can be explained by the presence of undigested bony tissues in carnivore wastes (Abraham et al., 2022; Stiner et al., 2012). Microbes' N/P is around 10, a higher value than carnivore waste, which suggests a limitation by N. Similarly, plants might be limited by N at such low N/P ratios (Güsewell, 2004). However, phosphorus in bone apatite is not easily taken up by microbes, and this also could trigger limitations. Specialized fungi are able to mineralize phosphorus from apatite (Gadd, 2010; George et al., 1995; Stevens et al., 2018), but with slower kinetics than other phosphorus forms. Carnivore faeces could, therefore, release P at longer timescales than herbivore faeces. Altogether, we suggest that the presence of recalcitrant P should be accounted for when studying the effect of carnivore waste on nutrient recycling.

Overall, our results are in agreement with previous research showing that the deposition of egesta and excreta should stimulate nutrient mineralization and nutrient cycles, at least locally (Frank and McNaughton, 1992; Van Der Wal et al., 2004; Fornara and Du Toit, 2008), suggesting an important role of animals in speeding up nutrient cycles (Veldhuis et al., 2018; Sitters et al., 2017b). However, the effect of wastes is to be related to other factors when assessing the overall role of animals in biogeochemical cycles. Soil temperature, humidity, and micro-organism abundance, as well as consumption of one part of the primary productivity and resource choice, can vary as a result of the activity of animals, like burrowing, soil compaction or social nests (Bardgett and Wardle, 2010). Sometimes, the combined effect of these factors results in a slowing down of nutrient cycles (Sitters and Andriuzzi, 2019).

2.4.7 Effects of food quality on absorption efficiency

Absorption efficiency of nutrients varied a lot at low nutrient contents in food, even being negative in certain cases (fig.2.5). The maximal efficiency of absorption varied among nutrients, being high for K and Na (80 %), lower for P and Ca (40 %), and even lower for Mg (25 %). K and Na are easily absorbed through pumps and channels in the gut (Rajendran et al., 2018), whereas P can be contained in phytates, which poorly digested (Abbasi et al., 2019). Mg can be contained in chlorophyll, and Ca can be found in plant cell walls; therefore in complex molecules harder to digest. The possibility of "negative" apparent absorption occurs because, when the resource is too poor, even if the animal feeds at a maximal rate, the nutrient requirements are not fulfilled, yet endogenous losses including bacteria (Stephen and Cummings, 1980; Watson et al., 2019), epithelial cells (Phillipson, 1971; Shah et al., 1982) and intestinal secretion (Tamminga et al., 1995) are still being released (Richard et al., 2017; Rodehutsord et al., 2000; Schuba et al., 2017; Tayo et al., 2009). Therefore, at low nutrient content, the animal can transiently become a nutrient source. This source, however, is temporary because nutrient loss from the body pool would be lethal if prolonged. If the resource is sufficiently rich in the nutrient, the animal can be at equilibrium, ingesting as much of the nutrient as it releases into the environment. But the animal can also be a sink of the nutrient, which occurs in a typical growth situation where biomass is accumulating (Sternner et al., 2002a).

Cases of animals being transient sources of nutrients in nature have been reported and were typically associated with low resource availability and body mass loss. For instance, Bornean orangutans have been found to be in negative nitrogen balance due to seasonal low fruit availability in their diet (Vogel et al., 2012). Several isotopic studies also suggest that reindeer can experience tissue wasting resulting in transient negative nitrogen balance (Parker et al., 2009; Vogel et al., 2012; Chan-McLeod et al., 1999; Gustine et al., 2011; Barboza and Parker, 2006). In a species of snail, nitrogen is accumulated in tissues during growth in spring and is subsequently lost in summer when primary production declines and snails undergo tissue loss (Hill and Griffiths, 2017). Our results suggest that endogenous losses of nutrients can participate in negative nutrient balance, not only for N as has been already shown (Richard et al., 2017), but also for other nutrients (P, Na, K, Mg).

Therefore, the effect of resource nutrient content on absorption efficiency depends on the richness of the resource. In this regard, atmospheric CO₂ fertilization could pose a threat to herbivores adapted to eat low-quality forage by decreasing its N/C ratio and potentially preventing them from acquiring sufficient nutrients even at maximal feeding rate [Cotrufo et al. \(1998\)](#). Research has indicated that a decline in absorption efficiency among herbivorous insects exposed to experimental CO₂ fertilization is indeed possible ([Srinivasa Rao et al., 2012](#)).

2.4.8 Perspectives

Our data synthesis, however, highlights ongoing gaps in the literature that need to be filled. First and foremost, more data in C, N and P waste composition for non-mammals could improve our estimation of the effect of body mass and trophic guild. These organisms are the most diverse and abundant and probably represent high fluxes of biomass in terrestrial ecosystems ([Sheldon et al., 1973](#); [Loeuille and Loreau, 2006](#)). Moreover, they have high metabolic rates and growth rates, reproduce fast and have very diversified diets. As such, these small body-sized animals are likely to be highly important when it comes to nutrient cycles. We emphasise that more research is needed on the digestive physiology and waste composition and fluxes of these animals. A second gap in our analysis was the lack of data on urine in mammals. Yet, urine contains a significant part of released nutrients, especially N ([Sitters and Olde Venterink, 2021](#)), and their inorganic forms can make them more biologically reactive, sometimes being easily accessed by plants, contrarily to faeces. The factors associated with the variation of mineral excretion are not well known in mammals, and the subsequent nutrient fate has been only poorly described ([Steinauer and Collins, 2001](#)).

The exploration of the intricate relationship between waste stoichiometry, nutrient release rates, and absorption efficiency stands as a compelling research perspective yet to be fully completed. Integrating these three elements is vital to comprehensively understand the impact of animals on nutrient recycling within ecosystems. Waste stoichiometry, influenced by diet, plays a pivotal role in determining nutrient release rates upon waste decomposition. However, coupling this understanding with insights into absorption efficiency, how efficiently organisms utilize and allocate these nutrients, is crucial. Combined with nutrient release rates, which can inform on the magnitude of nutrient

fluxes through animal populations, these factors intertwine to shape the fate of nutrients, impacting their availability for microbial processes, plant uptake, and subsequent ecosystem functioning.

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Part II

**Feeding rate as a key factor
affecting nutrients and isotopes fate
in consumer-driven recycling**

A pressing wish to do experiments had followed me since the beginning of the PhD. Among the numerous mechanisms that could trigger changes in waste chemical composition, intake level seemed a reasonable possibility. Once the hypotheses were set, we started looking for a model organism with my supervisors. Field cricket was the first candidate. As I began my search for climate chambers to house the crickets, I paid a visit to the sensorial ecology lab led by David Siauxsat, conveniently located on the floor beneath my workspace. Their model, *Spodoptera littoralis*, a moth, could also be a very good solution. We were warmly welcomed to collaborate with them, and quickly, these colleagues became a second team for me. In the early stages of the process of learning rearing protocols, Annick Maria has been a golden mine of information and help. This model turned out to be very practical for our question. Initially thought to be an experiment to test the effect of intake rate on waste composition only, we realized that nutrient fate, the efficiencies of absorption and growth were profoundly impacted by intake level, broadening the study to other but neighbouring questions.

This experiment also allowed isotopic analyses which were used to conclude about lipidic and protein dynamics in the larvae during food limitation. We wish to thank Magloire Mandeng-Yogo and Mélanie Longchamps for their help with chemical and isotopic analyses.

Both Chapter 3 and 4 are based on the same experiment led in December and January 2022. In Chapter 3 are developed aspects relative to C, N, P and other nutrients. In Chapter 4, you will find mechanistic insights and aspects of protein and lipid dynamics provided by isotopic analyses.

I speculated whether a species very linked to repeated and great changes of conditions might not assume a fluctuating condition ready to be adapted to either condition.

Charles Darwin, letter to Karl Semper, 1881

3

Feeding rate influences waste composition and nutrient fate in a terrestrial consumer

Samuel Charberet, Jérôme Mathieu, Annick Maria, David Siaussat, Magloire Mandeng-Yogo, Mélanie Longchamps and Isabelle Gounand.

Animals that are not in a growth stage and receive adequate nutrition uphold a state of nutrient equilibrium, in which their intake equals output fluxes, including egestion, excretion, and respiration. However, it is not the case of growing animals, nor the case of animals facing food restriction. Food shortage is common in nature, but its cascading effects on the strength of trophic links and nutrient trophic transfer are still elusive. Here, we investigate animal's role in nutrient cycling by quantifying how a herbivorous insect growing under food restriction transforms food into either body mass, which will climb up the food chain, or waste, which will be decomposed and remineralized at shorter timescales. The efficiency of absorption of C, N, P, Na, Mg, S, K and Ca decreased with intake rate along with their retention times inside the consumer. Waste and body chemical composition also changed with intake level. Growth efficiency was constrained by maintenance at one end of the intake spectrum and by low absorption efficiency at the other, resulting in a humped-shaped relationship between growth rate

and growth efficiency. The highest growth efficiency is reached at intermediate levels of resource availability, where absorption efficiency is high and provides sufficient nutrient levels for food to exceed uncompressible maintenance requirements. These results highlight that resource availability modulates the interplay between nutrient retention and release at the individual level, which might affect nutrient recycling when upscaled at the ecosystem level.

3.1 Introduction

At the core of predicting how food webs influence biogeochemical cycling in ecosystems lies an understanding of the fate of the consumed resources (Cebrian, 1999; Elser and Urabe, 1999; Hessen et al., 2004). Ingested food can take various routes, such as being expelled in the form of faeces, excreted as either inorganic or organic substances, or integrated into the food web as growth. Establishing a mechanistic connection between individual and ecosystem processes requires an understanding of how consumers distribute their dietary intake between these routes through absorption and egestion, growth, excretion, and respiration (Hessen et al., 2004). Trophic transfer, the quantity of energy and nutrients transferred between trophic levels, and nutrient cycling ultimately depend on these individual allocations (Allen and Gillooly, 2009).

Conversion efficiency (or gross growth efficiency), the fraction of consumed food converted into growth, is central in theoretical ecology because it influences food chain length (Post, 2002a; Yodzis, 1984). Growth efficiency directly depends on absorption efficiency, the fraction of ingested food that is absorbed for further use, since biosynthesis requires building blocks that should first be absorbed. However, it does not equal absorption efficiency, the fraction of consumed food effectively absorbed, since parts of the absorbed nutrient can be excreted or respired rather than included in new body mass. At the intraspecific level, growth efficiency is, in most models, considered constant (Barbier and Loreau, 2019; Montagnes and Fenton, 2012). However, intake (or ingestion) rate has been acknowledged as a potent driver of absorption efficiency among conspecific individuals confronted with various resource levels (Andersen et al., 2009; Mitra and Flynn, 2007; Fenton et al., 2010; Montagnes and Fenton, 2012), suggesting that it could also drive growth efficiency (Li and Montagnes, 2015; Almeda et al., 2009).

These works associated high intake rate with low absorption efficiency. A mechanistic explanation proposes that in animals feeding *ad libitum*, a high intake rate typically optimizes the absorption rate at the expense of efficiency. High intake rates inherently cause ingested material to pass quickly through the gut, leading to inefficient use (Mitra and Flynn, 2007; Flynn, 2009). During food restriction, increased absorption efficiency due to slower gut transit time enables the consumer to extract the highest possible amount of energy and nutrients from the scarce food (Jumars, 2000). Increased absorption efficiency can induce higher growth efficiency, resulting in a higher fraction of consumption being transferred to the upper trophic level. On the flip side, higher absorption efficiency results in a smaller fraction being recycled at the time scale of the individual and possibly longer nutrient retention times inside consumers (DeMott et al., 2010). This suggests that intake rate can control the fraction of consumption routed to trophic transfer or nutrient recycling with large potential effects on ecosystem functioning (Flynn, 2009).

As revealed by the long-standing literature on functional responses, intake rate is largely controlled by food availability (Suzuki-Ohno et al., 2012; Li et al., 2011). Periods of low food availability are frequent in ecosystems (McCue, 2010; Dunham et al., 1989; Karasov, 1986; Nagy et al., 1999), suggesting that intake rates can also be often reduced at the individual level. Intake rate can also be reduced by intra-specific competition, whereby dominant individuals monopolize most of the available food, while other individuals receive less (e.g. Mccarthy et al. 1992). Several studies have indeed revealed that absorption efficiency can increase when the food is less abundant, as in systems of copepods and algae (Gaudy, 1974; Landry et al., 1984; Besiktepe and Dam, 2002; Kiørboe et al., 1985; Thor and Wendt, 2010; Santer and van den Bosch, 1994). The same trend is observed in other zooplankton (Evjemo et al., 2000; Urabe and Watanabe, 1991), in bivalve larvae (Sprung, 1984), fish larvae (Boehlert and Yoklavich, 1984) and tunicates (Lombard et al., 2009). However, this prediction does not always hold in these species of copepods (Conover, 1966b; Barthel, 1983; Besiktepe and Dam, 2002; Wendt and Thor, 2015), and its test has been lagging behind in terrestrial ecosystems.

In the terrestrial realm, the intake - absorption efficiency relationship has received relatively less attention and encountered contrasted support, from being reported as negative in isopods, insects, fish and mammals (Hubbell

et al. 1965; Zheng et al. 1993; Solomon and Brafield 1972; Wellard and Hume 1981, respectively), to positive or null in insects and mammals (Lawton 1970; Cymbaluk et al. 1989; Clauss et al. 2014). The outcome of these investigations, in aquatic or terrestrial settings, might depend on the range of food availability investigated in the experiments and on the way food availability is reported (food concentration, intake rate, predator-prey ratio) so that general conclusions are not easily drawn from this ensemble of studies.

While growth efficiency represents what is absorbed and subsequently converted to growth by the consumer from the lower trophic level, waste production is what is not absorbed and is excreted or egested by the consumer and subsequently participates directly in nutrient recycling. If a higher proportion of nutrients are diverted to growth in the consumer biomass, or kept for a longer time before excretion, the cycling of nutrients is slowed down (DeMott et al., 2010). Changes in the fraction of intake ending up in egestion and excretion might have noticeable consequences at the ecosystem level since the nutrients they contain constitute an important cycling path for terrestrial primary producers and decomposers. Indeed, the consumer recycling path is usually faster than that of terrestrial plant litter, which is more slowly decomposed (Steinauer and Collins, 2001; de Mazancourt et al., 1998). As a result, the amount and quality of consumer wastes should strongly influence autotroph growth both in terrestrial (Carline et al., 2005; Frank, 2008; Daufresne, 2021) and aquatic ecosystems (Andersen 1997; Sterner 1990; Sterner et al. 2002b, also see the General Introduction). In particular, ecological stoichiometry predicts that the quality of wastes should depend on both the body stoichiometry and on the food stoichiometry, particularly in nitrogen (N) and phosphorus (P) (Sterner et al., 2002a).

Making predictions about nutrient cycles requires data on how efficiently the different elements are absorbed, which may differ among elements and from the total absorption efficiency reported in most studies since the various elements are not absorbed with equal kinetics (Bielik and Kolisek, 2021). Ecological stoichiometry has focused chiefly on C, N and P for their crucial role in physiology and tendency to be limiting in various environments (Sterner and Elser, 2002). However, the limitation can be triggered by other elements, such as Mg, Ca, K, and S (Baribault et al., 2012; Naples and Fisk, 2009; Lapis et al., 2013). Hence, recently, ecological stoichiometry has started to include elements beyond C, N and P, such as other macronutrients (K, Mg, Ca), and

micronutrients (Cl, Fe, Al, Mn, [Hopper et al. 2021](#); [Peñuelas et al. 2019](#)). Even the absorption of C, N and P are not independent of other nutrients ([Couzy et al., 1993](#); [Fairweather-Tait and Hurrell, 1996](#); [Kiela and Ghishan, 2016](#); [Goff, 2018](#)) since proteins (containing N), ATP (containing P), but also ionic gradients (K, Ca, Na, Mg, etc.) are essential to the proper functioning of digestion and absorption ([Sans et al., 2021](#); [Jeyasingh et al., 2023](#)). Below a certain threshold, the acquisition of a plentifully available nutrient could be impaired by the absence of another one needed for absorption (for instance, Na see: [Kaspari 2020](#) and [Sehested et al. 1996](#); for Ca see: [Liesegang et al. 2007](#) and [Kodama et al. 2003](#)), suggesting that non-linear effects of intake are to be expected on the absorption efficiencies of particular elements. It is known from aquatic studies that phosphorus ([He and Wang, 2007](#)) and nitrogen ([Kiørboe et al., 1985](#)) absorption efficiencies can decrease at higher food concentrations. However it is not known how the extent of this decrease in absorption, which means more recycling, compares between elements. The link between intake rate and absorption efficiency, including the elemental partition of absorption across the food intake gradient, is poorly documented for a range of terrestrial consumers. Studying these mechanisms becomes crucial as resource scarcity becomes more frequent with global change ([O'Connor et al., 2009](#); [Parmesan et al., 2000](#); [Maron et al., 2015](#)).

Variations in elemental absorption efficiencies also affect body and waste composition. If an element is better absorbed than another for a given level of food availability, the body content in the first should increase relative to the other, affecting body chemical composition, and a similar reasoning applies to wastes. Such changes in body stoichiometry have been repeatedly highlighted in consumers ([Simpson et al., 2002](#); [Persson et al., 2010](#); [Hessen et al., 2013](#); [Wei et al., 2022](#)), and can affect the dynamics of the predator by changing food quality relative to the predator requirements ([Greenstone, 1979](#); [Jensen et al., 2011](#)). And, as discussed in chapter 2, the chemical composition of wastes has large effects on the immobilisation / mineralisation rates due to microbial growth requirements ([Güsewell and Gessner, 2009](#); [Arenberg and Arai, 2019](#)). Several studies find that intake reduction changed body composition ([Hirche and Kattner, 1993](#); [Chen et al., 2005](#); [Molnar et al., 2006](#)), but the existing data syntheses on the variation of waste N/P ratio in aquatic animals don't assess the effect of intake rate. However, they emphasize that this is an important research direction ([Vanni and McIntyre, 2016](#)).

To better understand the interplay between intake rate, absorption of nutrients, and growth efficiency, we experimentally submitted larvae of the moth *Spodoptera littoralis* to various food intake levels. We tested the hypothesis that resource scarcity increases the absorption efficiency of 8 chemical elements (C, N, P, Na, Mg, S, K, Ca), possibly at different extents, which, in turn, would increase growth efficiency. We assessed whether the chemical composition of wastes and organisms would vary under various intake levels due to the unequal retention of individual elements. Our results show that intake rate differently affected nutrient absorption efficiency resulting in changes in stoichiometry of both body and waste.

3.2 Materials and methods

3.2.1 Study system

We used the polyphagous lepidopteran species *Spodoptera littoralis* for its size, which enabled measurements of intake and frass output, and during the intense growth period of the seventh instar, in which body mass can increase by a factor of 4, which eases the growth properties estimation. Its waste, called "frass", comprises both digestive and excretory waste, which facilitates the determination of mass and nutrient budgets. Larvae from a laboratory strain were reared at 23 °C, 60–70% relative humidity, and a 16:8 light/dark cycle (Hinks and Byers, 1976). During the feeding trial, they were provided with a semi-artificial diet prepared at the laboratory with composition given in table C.1 (76 % water and 43 % C, 4.2 % N and 0.5% P in proportion of dry weight, also see fig. C.7). Under these rearing conditions and with uninterrupted access to food, the larvae undergo seven instars prior to metamorphosis (chrysalid stage). For the purpose of experimentation, 400 sixth instar larvae were isolated in individual 30 mL circular polypropylene containers. They were provided *ad libitum* food until the completion of the sixth moult (start of the seventh instar). The newly moulted seventh instar larvae, weighing 311 ± 66 mg (mean \pm standard deviation see fig. C.2), were used for the study.

3.2.2 Experimental design

We randomly assigned each of the 400 seventh instar larvae to one of five food provision levels: 120, 240, 360, 480 or 900 mg of food per day (fresh weight). We had beforehand estimated that the maximal individual intake rate was 595

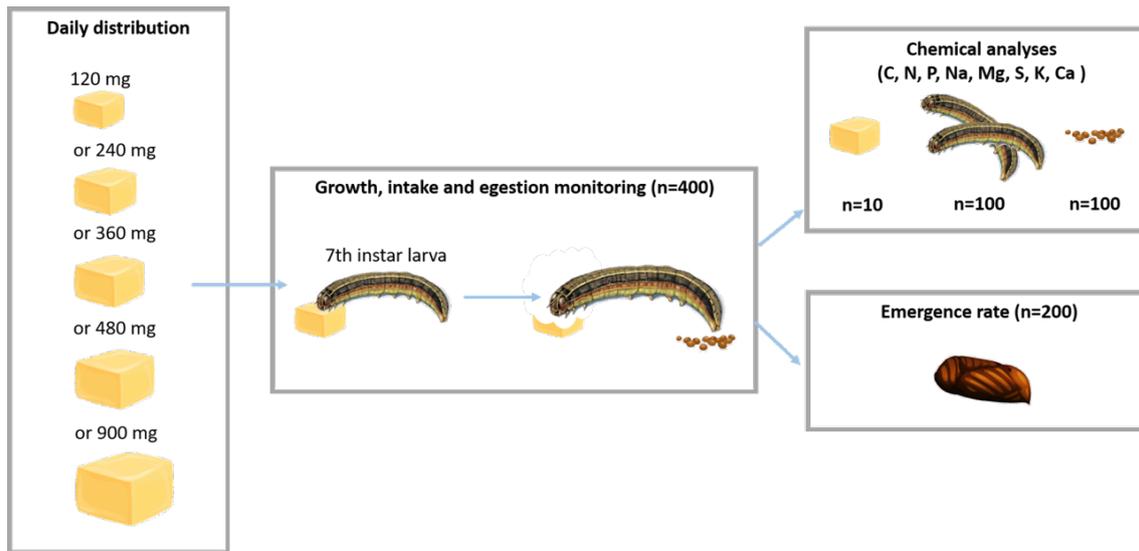


Figure 3.1: Methods overview. Yellow cubes represent food; masses are given in fresh weight. Pooled samples of frass from 4 caterpillars were used for chemical analyses. Groups of two caterpillars were used for chemical analyses.

\bar{x} 43 mg/day, meaning that larvae receiving 900 mg per day were fed *ad libitum*, while the other larvae were not. Each food intake level was tested on 80 individuals. We conducted this study over ten weeks (ten temporal blocks, for which initial larvae masses were not significantly different see fig.C.2), working with 40 individuals each week, 8 for each food intake level. Larvae were allowed to feed over a period of two or three days, depending on the timing of pre-pupation, which varied among the larvae. Body mass measurements, frass and food leftover collections were carried out daily during this period. Pre-pupation, triggered by visible water loss, either occurred on the third day of the seventh instar, in which case measures were taken over a period of two days, or later, in which case measures were taken over a period of three days.

3.2.3 Experimental workflow

Throughout the experiment, food was prepared for each temporal block and conserved in a fridge. Each larva was provided with a specific quantity of freshly prepared food and weighed daily. Food subsamples were taken at every food preparation for subsequent chemical analysis (fig. C.7). We also collected and weighed any food leftovers and frass produced by each larvae to determine their actual intake and frass production rates. Food leftovers and frass were promptly stored at -20 °C, and later dried for 72 hours at 60 °C in an oven to measure their dry mass. On the third day, half the larvae were quickly stored at -20 °C, dried for 72 hours at 60 °C in an oven, and prepared for body chemical

analyses. The remaining half was left in the rearing chambers until emergence to examine the impact of food scarcity on mortality, emergence success, and adult body masses. Intake only lengthened the timing of emergence but did not affect success (only two larvae did not emerge, one fed 120 mg per day, and the other fed 900 mg per day). Intake rate increased adult body mass (fig. C.3).

3.2.4 Chemical analysis

Chemical analyses required that we pooled samples to obtain enough mass. Hence, groups of four caterpillars reared over the same week and on the same food provision level were composed. Two individuals were selected for chemical analysis, while the remaining two were left alive until emergence. The analyzed frass was a composite sample sourced from all four individuals.

The dried samples of food, larvae, and frass were ground to a fine powder using a mixer mill (Retsch MM 200). The total carbon and total nitrogen content were determined using an elemental analyzer (Flash HT - Delta V Advantage, ThermoFisher) using aromatic polyimide (EMA-P2) as a standard. The contents of P, Na, Mg, S, K, and Ca were analyzed using ICP-MS after undergoing liquid microwave digestion (Milestone 1200 Mega, Milestone Inc., USA) in Teflon bombs with a 3:1 mixture of HNO₃ and HCl.

3.2.5 Growth and mass budget

Food limitation depends on the balance between intake and requirements, which largely depend on body mass. To remove the dependency on body mass and investigate how processes vary with food limitation, we used the Mass-Specific Intake Rate (MSIR). This metric, calculated as the ratio of food intake to body mass, serves as an indicator of food limitation. Specifically, low MSIR values suggest food restriction, whereas high MSIR values indicate adequate nutrition.

$$\text{MSIR}_i = \frac{I_i}{d_i \frac{ib_i + fb_i}{2}}$$

with I_i the total fresh mass of food ingested by the individual i , in mg, throughout the seventh instar, d_i the number of days spent in the seventh instar before pupation by individual i , ib_i the initial body mass of the individual i , and fb_i the final body mass of individual i , in mg, which are divided by two to obtain an average body mass during the seventh instar.

The Mass-Specific Growth Rate (MSGR) is the growth over the seventh instar divided by the time spent in the seventh instar and the average mass of the individual i . The unit is therefore in $\text{mg} \times \text{mg}^{-1} \times \text{day}^{-1}$. Masses are given in fresh weight since initial bodymass can not be measured in dry weight.

$$\text{MSGR}_i = \frac{fb_i - ib_i}{d_i \frac{ib_i + fb_i}{2}}$$

The absorption efficiency (AE) is the proportion of ingested mass which is absorbed, and not egested nor excreted, over the seventh instar, given here in % dry weight. If intake and frass production rates are equal, the absorption efficiency is 0. If intake is greater than frass production, AE is positive; in the opposite case, it is negative.

$$\text{AE}_i = 1 - \frac{E_i}{I_i}$$

With I_i the total dry mass in mg of food consumed by the individual i and E_i the total dry mass of frass egested by the individual i throughout the seventh instar.

Growth efficiency (GE) is the proportion of ingested mass resulting in growth (expressed as % fresh weight, since dry weight is not available before the growth period):

$$\text{GE}_i = \frac{fb_i - ib_i}{I_i}$$

In the case of a group of caterpillars used for chemical analysis, we also wanted to use mass-specific intake rate as an indicator of low intake, now computed at the level of a group of four caterpillars:

$$\text{MSIR}_j = \frac{\sum_{i \in j} I_i}{\left(\frac{1}{4} \sum_{i \in j} d_i\right) \left(\frac{\sum_{i \in j} ib_i + \sum_{i \in j} fb_i}{2}\right)}$$

With I_i the total fresh mass of food consumed by the individual i from the group j throughout the seventh instar, d_i the number of days spent in the seventh instar by individual i , ib_i the initial body mass of individual i , and fb_i the final body mass of individual i in mg.

For each element (C, N, P, Na, Mg, S, K and Ca) we can compute the absorption efficiency as follows. For the element k and group j the absorption efficiency

AE_{jk} is given by:

$$AE_{jk} = 1 - \frac{C_{Ejk}E_j}{C_{Ijk}I_j}$$

with C_{Ejk} the proportion of element k in the frass of the group j , E_j the mass of frass produced by the four larvae of the group j combined over the experimentation period, C_{Ijk} the proportion of element k in the food of the group j , I_j the mass of food consumed by the four larvae of the group j combined over the same period.

As a whole, we were able to compute growth efficiency, total absorption efficiency, elemental absorption efficiency, as well as body and frass chemical composition.

Retention time (RT) represents the average time an element spends in the body pool in the group of larvae and is computed by dividing the mass of the element in the final biomass by the output rate of the element:

$$RT_{jk} = \frac{C_{Ljk}fb_i}{\left(\frac{1}{4} \sum_{i \in j} d_i\right) E_{jk}}$$

with C_{Ljk} the proportion of element k in the larvae of the group j , fb_i the final body mass of individual i , d_i the number of days spent in the seventh instar by individual i , and E_{jk} the mass of element k egested by the group of larvae throughout the seventh instar.

3.2.6 Statistical analyses and modelling

We assessed the monotonicity between variables using Spearman's rank correlation coefficient (ρ) and the associated significance. When monotonic, we used linear models or loess local regression to highlight non-linearity. When not, we used shape-constrained additive models concave p-spline that allowed for non-monotonicity (Pya and Wood, 2014). We developed a mathematical model of mass fluxes during growth to support our interpretations of the results relative to growth efficiency. The model is presented in Box A and its derivation is detailed in Appendix D.

3.3 Results

3.3.1 Effects of intake on absorption and growth efficiencies

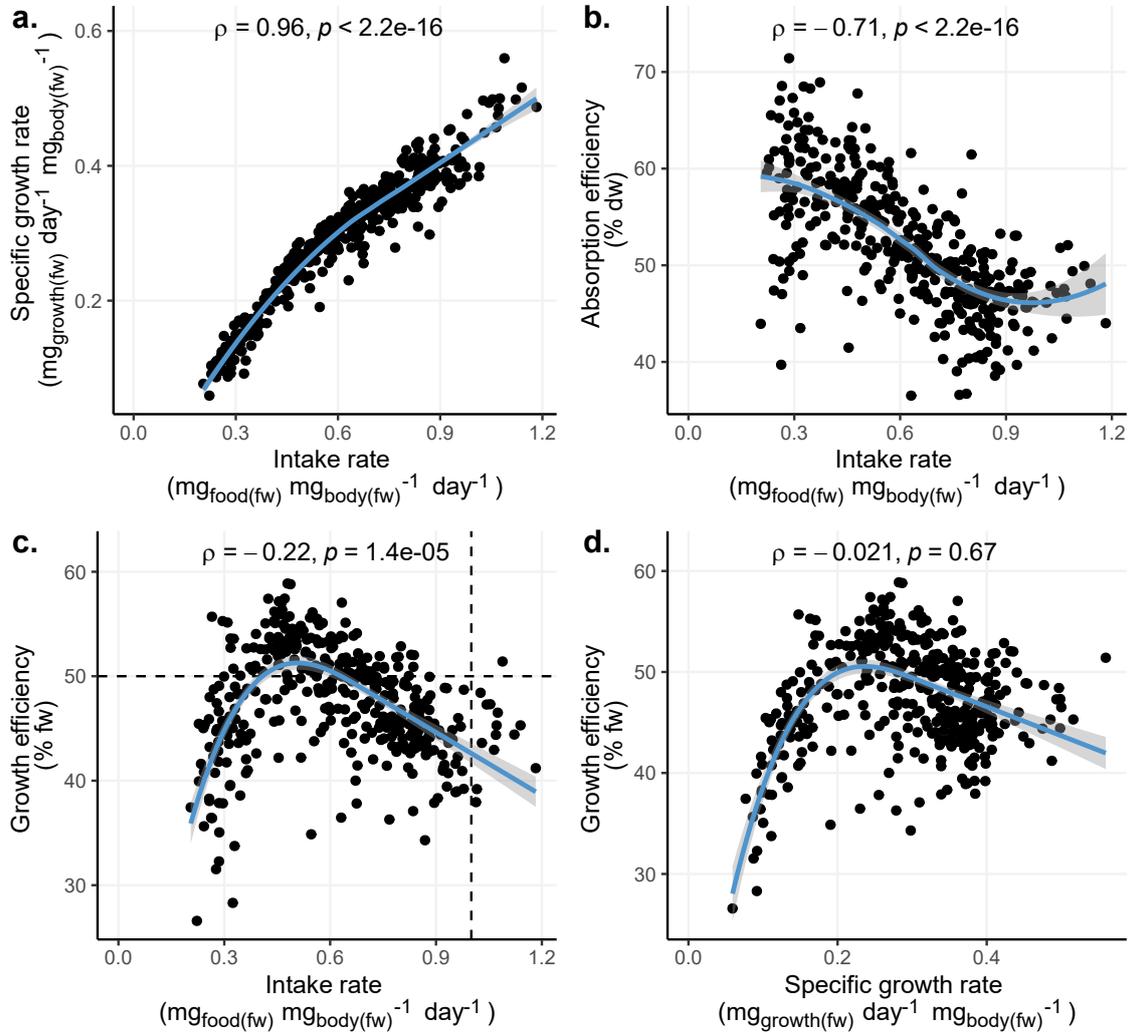


Figure 3.2: Relationships between intake, growth and total absorption in fresh weight. One point represents a measurement taken at the level of one individual. The lines represent local polynomial regression (loess on both top panels, concave p-spline on both bottom panels), and shaded areas are 95% confidence intervals of the mean. (b) Absorption efficiency represents the proportion of ingested food absorbed by the gut. (c, d) Growth efficiency represents the proportion of food resulting in growth. The vertical line in panel (c) represents a rate of 1, for which daily intake is equal to body mass. The horizontal line indicates a growth efficiency of 50%, where half of the intake is converted to growth. The rho correlation coefficients and corresponding p-values for the Spearman test are also provided.

As anticipated, growth rate was positively correlated to intake rate, (fig.3.2.a, $\rho = 0.96, p < 2.2e-16$). However, absorption efficiency decreased with intake rate and was thus higher for underfed individuals (fig.3.2.b, $\rho = -0.71, p <$

2.2e-26). Intake reduction increased absorption efficiency up to 30% compared to individuals fed *ad libitum*. On average, underfed individuals had an absorption efficiency of 60%, whereas well-fed individuals were around an efficiency of 45% (fig.3.2.b). Correspondingly, the proportion of food that was either egested or excreted was lower for underfed individuals than for well-fed individuals.

The relationship between growth efficiency and intake rate, as well as the relationship between growth efficiency and growth rate, were non-monotonic and described by non-monotonic concave relationships (Spearman's $\rho = -0.22$, $p = 1.4e-5$; $\rho = -0.021$, $p = 0.67$, respectively), first increasing, then decreasing. The highest growth efficiency (50 %) was observed at an intermediate intake level ($0.45 \text{ mg} \times \text{day}^{-1} \times \text{mg}^{-1}$) and not the highest one ($1.2 \text{ mg day}^{-1} \text{ mg}^{-1}$). Growth efficiency was lower at both ends of the intake rate span, resulting in a hump-shaped relationship (see fig.3.2.c). We find a similar hump-shaped relationship between growth rate and growth efficiency (fig.3.2.d), meaning that the maximum growth efficiency occurs at an intermediate specific growth rate. See box A and fig.3.3 for our proposed mechanistic interpretation.

Box A: A model to explain non-monotony in growth efficiency

In our experiment, growth efficiency exhibited a non-monotonic relationship with intake rate, first increasing and then decreasing. We speculated that maintenance processes monopolize energy at low intake rates, resulting in a lower relative investment in growth. At high intake, lower absorption efficiency causes growth efficiency to also decrease. We thus wrote a mathematical model with these two assumptions (see full derivation in appendix D), and confronted it with the data. In the model, we assume that absorption efficiency progressively decreases at higher intakes and that what is absorbed is allocated in priority to maintenance processes, which are uncompressible costs, and then to growth. We also assume, based on our data (see fig.C.9), that mass-specific maintenance costs decrease when intake decreases. Growth efficiency, G_e is thus defined as:

$$G_e = \frac{A - M}{I} = \frac{A_0 k}{I} \ln \frac{I + k}{k} - \frac{aI + M_0}{I}$$

with I the intake flux, A the absorption flux, M the maintenance flux. A_0 describes the maximal absorption flux, k the sensitivity of absorption to food restriction, M_0 the maintenance costs of a fasting animal (when $I = 0$), and a the impact of increasing intake on maintenance processes, respectively.

This simple allocation model can reproduce qualitatively the observed hump-shape pattern based on basic underlying assumptions, with higher peaks for higher k , that is for individuals which absorption efficiency is more sensitive to food restriction (fig.3.3). However, when the model is adjusted to the growth efficiency data, the estimation of A_0 , the maximal absorption efficiency, converges to a value higher than 1, which is not biologically relevant (absorption efficiency is bounded $\in [0, 1]$). We think this discrepancy is due to oversimplification in our model that ignores a process important for quantitative predictions. Our data suggest that a decrease in absorption efficiency for animals submitted to very low intake is possible (fig.3.2.c). We suspect that even lower food levels would accentuate this decrease and that integrating such constraints in the model should allow us to provide a better-suited fit to data.

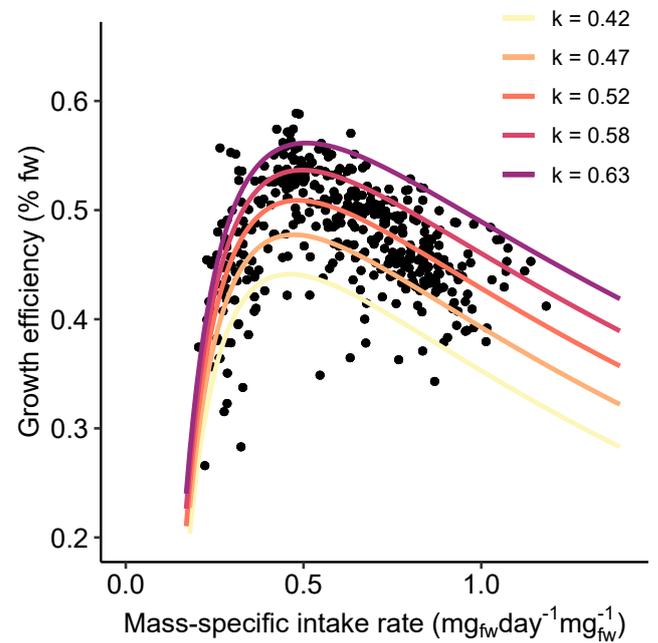


Figure 3.3: Unconstrained model fit to growth efficiency data and an illustration of the effect of k , the sensitivity of absorption to food restriction. Fixed parameters were estimated without constraints, giving $A_0 = 1.57$, $M_0 = 0.14$ and $a = 0.3$.

3.3.2 Impact of intake level on element absorption and retention time

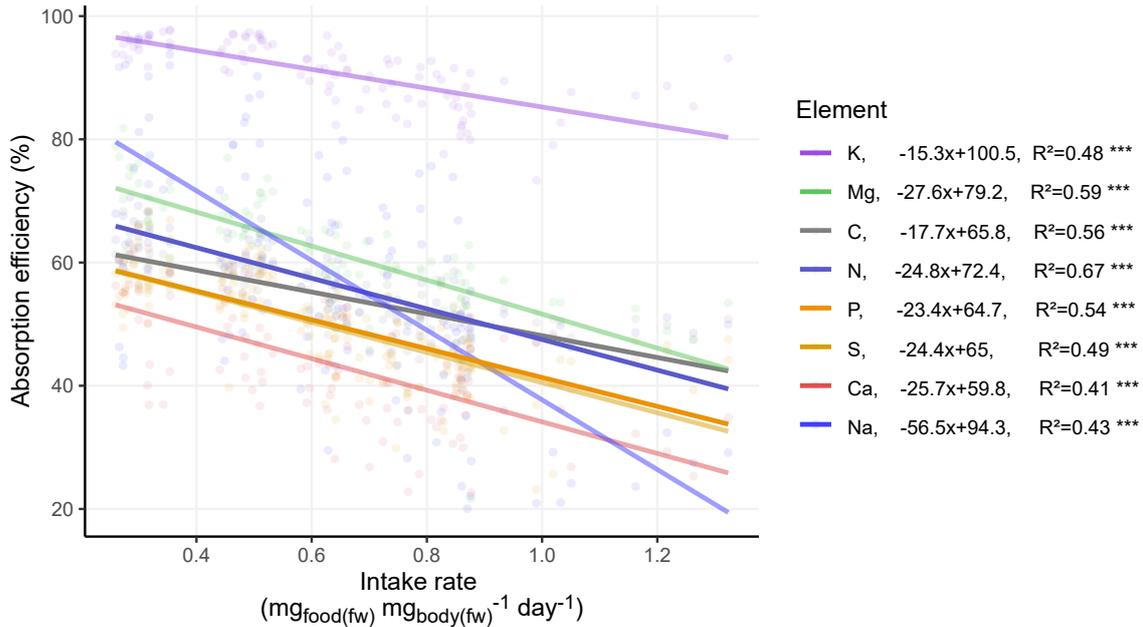


Figure 3.4: Absorption efficiencies (%) of C, N, P, Na, Mg, S, K and Ca according to intake rate (each point represents a pool of 4 individuals, see methods). The lines represent linear regression. The equation depicts the results of linear models, and the stars indicate the significance level following (* = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$)

Results from the previous section show that the total absorption efficiency increases with resource shortage. Here, we detail the relationship for each specific element. Figure 3.4 shows that all elements are better absorbed at lower intake, but the strength of this effect varies among elements, as indicated by the different slopes. Particularly, low intake improved N and P absorption to a greater degree than C absorption (see slopes values in fig.3.4). The average absorption efficiencies also varied among elements, being, for instance, very high for K and rather low for Ca.

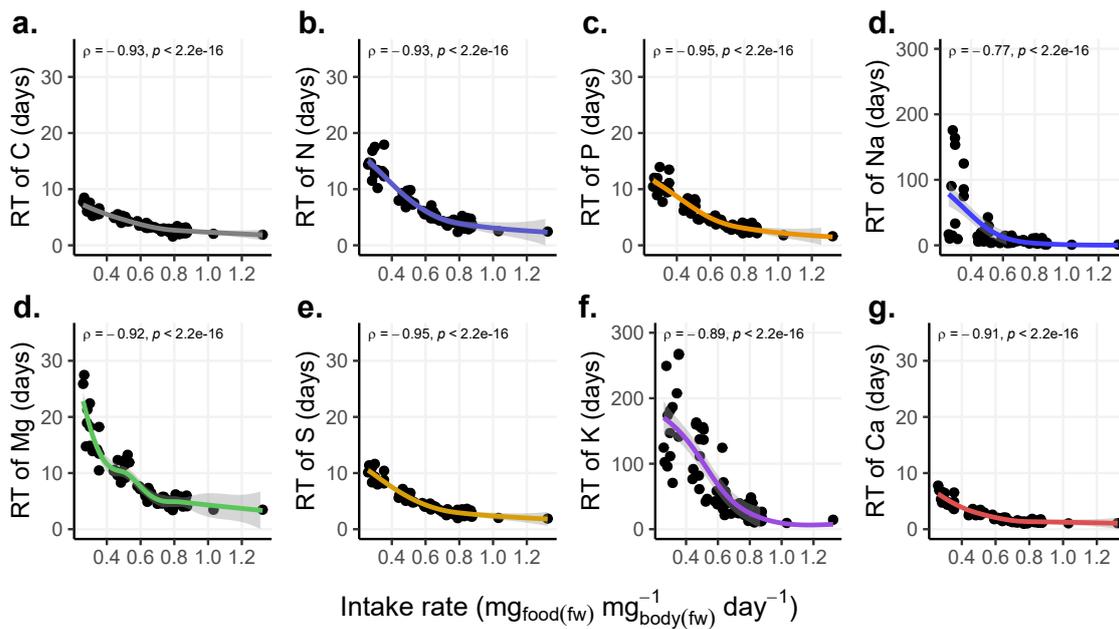


Figure 3.5: Retention times (RT) for each of the eight elements (C, N, P, Na, Mg, S, K and Ca) according to intake rate (computed at the level of a group of 4 caterpillars). Retention time is the average time an atom of the element spends within the larvae pool before being egested or excreted. The lines represent general additive models, and shaded areas are 95% confidence intervals. The rho correlation coefficients and corresponding p-values for the Spearman test are also provided.

The retention time of all nutrients strongly increased with reduced intake rates (fig.3.5). The retention times of C, N, and P were lengthened about 10 times at the lowest intakes, while the retention times of other nutrients were 100 to 200 times longer (for Na and K, respectively).

3.3.3 Impact of intake level on body and wastes CNP composition

Individuals feeding at high rates (*i.e.*, not food-restricted) were generally richer in carbon and hence comparatively poorer in N, P and other elements than underfed animals (fig.C.5). As a result, body C/N and C/P ratios were higher at high intake rates and lower at low intake rates (fig.3.6.a and b). However, underfeeding yielded uneven levels of enrichment for different body nutrients, including N and P, which resulted in body N/P ratio increasing with intake rate (see fig.3.6.c).

Moreover, at low intake rates, frass was poorer in nutrients, including N and P (fig.3.6 and fig.C.6). Not all nutrients were equally rarefied in frass as a result of low intake. For example, frass produced at low intake were of lower

N/P ratios than at high intake (fig.3.6 .f). Of interest is the positive relationship found between body N/P and frass N/P (fig. C.8).

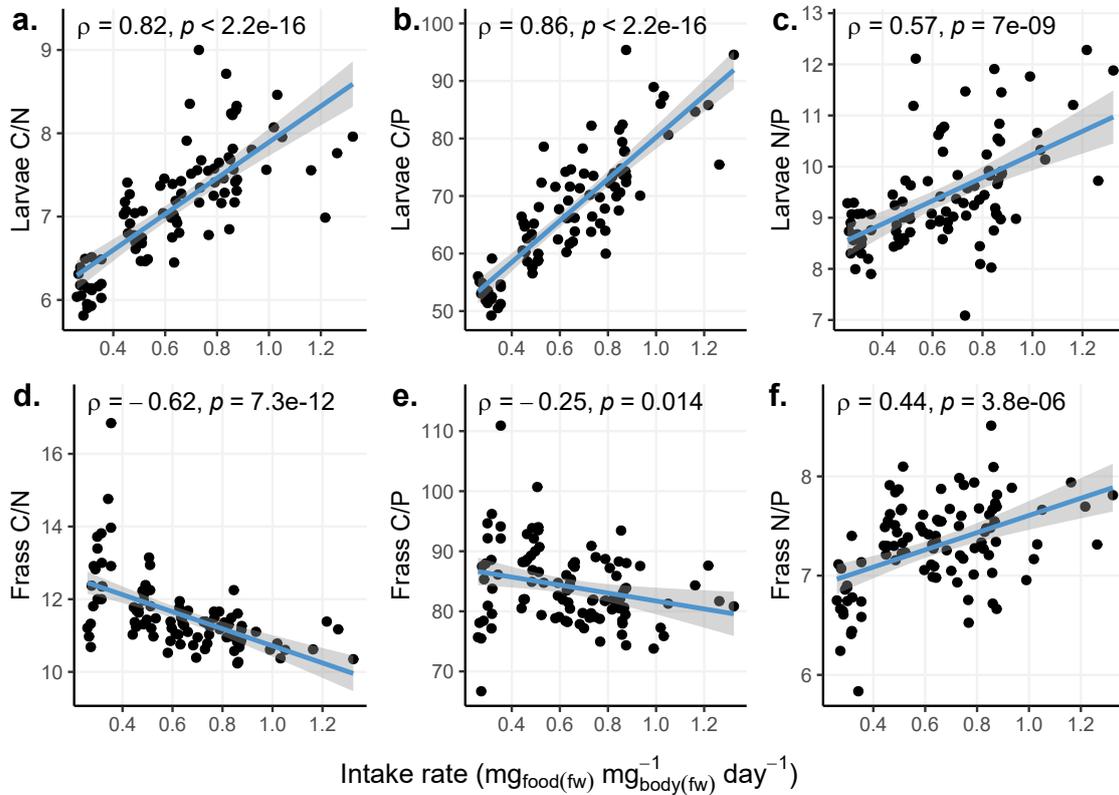


Figure 3.6: Effect of intake rate on body and frass chemical composition illustrated through the massic ratios between C, N and P. Each point is a measure done with pooled samples of 4 individuals for frass and two for larvae. The lines represent linear models. ρ is the Spearman correlation coefficient, and the p-values are those of the associated correlation tests.

3.4 Discussion

Our experiment provides a thorough budget of elemental fluxes and stocks in individuals of a growing herbivorous insect under different levels of food restriction. The results indicate that total food absorption efficiency was reduced when intake was increased. This logically caused the growth efficiency to be reduced at the highest intake rates. However, at the lowest intake rates, growth efficiency was also reduced, which we interpret as an effect of the monopolization of intake towards maintenance processes (e.g., respiration). This resulted in a hump-shaped relationship between intake rate and growth efficiency. Because intake and growth rates are highly correlated, we also observed a hump-shaped relationship between growth rate and growth efficiency, meaning that

both could not be maximized simultaneously. Elemental absorption efficiencies were also improved under restriction to various degrees, resulting in the lengthening of retention times for these elements in the larval pool. Body and waste chemical compositions were also impacted, organisms being richer in C at high intake rates and richer in N and P at low intake rates. Wastes were generally poorer in nutrients, including N and P, at low intake. Below, we discuss these results in the light of existing literature.

3.4.1 Absorption efficiency increases with food restriction

The increase of absorption efficiency at low intake rates is in line with numerous studies from aquatic species (Gaudy, 1974; Landry et al., 1984; Besiktepe and Dam, 2002; Kiørboe et al., 1985; Thor and Wendt, 2010; Santer and van den Bosch, 1994) but also contrasts with other studies both in aquatic and terrestrial species (Rosen et al., 2000; Lawton, 1970; Cymbaluk et al., 1989; Clauss et al., 2014; Conover, 1966b; Barthel, 1983; Besiktepe and Dam, 2002; Wendt and Thor, 2015). The underlying mechanisms that may explain this phenomenon encompass passive and active processes. Indeed, when the quantity of food available in the gut is low during periods of low intake, food is being processed by acids and digestive enzymes for a longer time, causing an overall "passively" improved digestion (Clauss et al., 2007; Jumars, 2000). But low intake can also induce plastic responses that maximize absorption, such as optimization of enzyme or acid secretion, a process involving changes of gene expression, which is thus active (Panserat and Kaushik, 2010; Darchambeau, 2005; Zinke et al., 2002; Chatterjee et al., 2014). Determining the specific processes at play in the increase of absorption efficiency would thus require further physiological studies. Studies which, contrarily to us, found a positive effect of intake rate on absorption efficiency interpreted that food restriction decreases absorption efficiency due to increased endogenous losses or to a limitation of microbial digestive activity at very low intake (see (Bielik and Kolisek, 2021)). It is possible that the extent of the restriction was too low in these studies to induce the physiological reaction that we see or that the diets chosen in these studies were much less digestible than the one we considered, preventing any improvement in digestibility (for instance in mammalian herbivores in Cymbaluk et al. 1989; Clauss et al. 2007).

3.4.2 Absorption efficiency improvement depends on the element

At the nutrient level, organisms better absorb all of the eight tested chemical elements at low intake rates. However, the reduction of intake did not affect the absorption of the various elements equally. The absorption of some nutrients was more sensible to food restriction than others, indicated by a greater slope, whereas the maximal absorption also varied, indicated by the different intercepts (fig. 3.4). The underlying reasons for the variation in absorption's maximum and sensibility to food restriction among elements are likely rooted in the biochemical context in which the elements are absorbed by organisms, as well as by the demand-supply equilibrium.

Indeed, some minerals exist as free ions and are readily absorbed through channels and pumps in the gut (Rajendran et al., 2018). Our data demonstrate that both K and Na are indeed highly absorbed at low intake rates (fig.3.4). However, an increase in intake rate drastically reduces the absorption of Na, and Ca is poorly absorbed at all intake rates (fig.3.4), even though it is unlikely that an efficient absorption could not happen (Stobbart and Shaw, 1974). This suggests that maximal absorption of these ions is not required at all intake rates and that adaptive absorption may play a role in regulating the input of these cations, which are crucial in maintaining chemical osmosis and appropriate signalling (Bradley, 2009; Clapham, 2007; Naikhwah and O'Donnell, 2012). By contrast, other elements occur in complex molecular contexts, such as C, N, P and S, which are found in proteins, carbohydrates, nucleic acids, phytates, and secondary metabolites. Some of these compounds are refractory to digestion, (e.g. complex carbohydrates, phytates (Martin, 1983; Huang et al., 2009)), and this may hinder the proper absorption of these elements, as the lesser slopes of these elements suggest. This challenging digestion might explain the rather low enhancement of C, P and S absorption efficiencies at low intake rates. The different slopes among elemental absorption efficiencies show that relative absorption efficiencies vary between pairs of elements. This means that food restriction will modify the stoichiometry of absorption, and subsequently egestion fluxes, therefore affecting the interactions between nutrient cycles.

There was no obvious peak in elemental absorption efficiencies at intermediate intake rates (fig. 3.4). Under a certain threshold, very low intake rates could theoretically result in a decrease in elemental absorption efficiency (Burian et al., 2020), owing to limitations in other nutrients. When we investi-

gated the non-linearity of absorption efficiencies with intake, some elemental absorptions showed a probable reduction at the lowest of intakes, in particular in P (see fig. C.4). However, gaining an understanding of the precise interrelations between nutrient absorption mechanisms would certainly require independently reducing the availability of individual elements in food and observing the resulting absorption of other nutrients as has been done, for instance, on one occasion between calcium and phosphorus (He and Wang, 2009). It is also possible that such low intake would simply result in death, preventing such an effect from being observable or relevant.

3.4.3 Food restriction increases retention times

Higher absorption efficiencies were accompanied by longer retention times of nutrients in the biomass (fig.3.5). When an individual eats less compared to its mass-specific nutritional requirements, nutrients tend to spend more time in the body. They are excreted or egested after a longer period on average. Hence, animals are transiently immobilizing nutrients that would have otherwise been returned to the soil more rapidly when consumed at a higher intake rate. If we consider the ecosystem scale, ecosystems with low productivity (such as tundra and deserts) or a temporary perturbation that affects productivity would cause consumers to retain nutrients for longer periods. This could potentially worsen the slow cycling of nutrients typical of nutrient-poor ecosystems (Delgado-Baquerizo et al., 2013) and lead to a reduction in productivity due to a negative feedback loop. This only holds, obviously, if the lifespan is not shortened by food restriction, which would instead speed recycling by returning more quickly the whole pool of biomass to the decomposition process. But, on the contrary, many experiments tend to show that moderate food restriction extends lifespan (Partridge et al., 2005; Speakman and Mitchell, 2011), and therefore trigger a slower return of body nutrients, at least at the individual scale. In the kind of organisms we used for our experiment, the change in retention time should have a limited impact on nutrient fluxes since the lifespan is about 40 days. However, we can expect food restriction to induce longer retention times in larger and long-lived animals. In theoretical studies, the return of nutrients through egestion and excretion has been shown to have a small but positive effect on recycling in nutrient-poor systems (Cherif and Loreau, 2013). However, if retention times are lengthened in these situations, this positive effect might be attenuated.

3.4.4 Growth efficiency peaks at moderate food restriction level

Variation of growth efficiency among species or strains has been repeatedly investigated, particularly in unicellular organisms, by considering the interdependence between growth efficiency and growth rate at the inter-specific level (Lipson, 2015; Roller and Schmidt, 2015). Some found a positive relationship between growth rate and growth efficiency (Carlson et al., 2007) interpreted as follows: assuming constant maintenance requirements, as growth rate decreases, a greater proportion of consumed substrate is used for maintenance, hence a decrease in growth efficiency decreases (Wang and Post, 2012; Pirt and Hinshelwood, 1965). Others found a negative relationship between growth efficiency and growth rate, interpreted as resulting from an overflow metabolism (where alternative pathways wastefully consume extra nutrients) limiting efficiency at high growth rates (Beardmore et al., 2011; Molenaar et al., 2009; Maharjan et al., 2013; Wong et al., 2009). A conceptual model combining both views was proposed by Lipson (Lipson, 2015) and later in a mathematical model by Tang (Tang and Riley, 2023). Similarly, in a recent fitness optimization model, such a relationship was also predicted in animals (Burian et al. 2020, fig. 6H). According to Lipson, considering the whole span of resource availability gives a positive relationship followed by a negative one in a hump-shaped curve between growth rate and growth efficiency, owing to both maintenance processes and rate-yield tradeoffs.

In our experiment, the increase in growth efficiency when intake is mildly reduced seems to be due to increased absorption efficiency, providing additional building blocks for biosynthesis. The acute drop in growth efficiency occurring at very low intake levels is likely due to the monopolization of energy for the essential maintenance processes, with little to no nutrients being available for growth anymore. The mathematical model shown in Box A. and fig.3.3 shows that including maintenance processes and decreased absorption at high intake indeed qualitatively predict such effects. In the literature on animals, both positive (e.g. Pandian 1967; Wang et al. 1998) and negative (Bartley et al., 1980) relationships have been found between intake rate and growth efficiency. Our results tend to show that considering a large enough variation in intake allows us to see both effects (fig.3.2.c). Interestingly, this results in the impossibility of maximizing both growth rate and growth efficiency simultaneously. From a selective value standpoint, maximizing growth rate is favoured because it results in a higher reproduction rate (Bernardo,

1993). Growth efficiency can rather be seen as an adaptive process to maintain growth in periods of low resource availability (Roller and Schmidt, 2015). Such an adaptive response to resource availability might have far-reaching consequences on population persistence and community dynamics under a fluctuating environment. For example, during unfavourable seasons or perturbations, buffering stress by improving absorption and growth efficiency could propagate up the food chain, making each trophic level grow less rapidly but more efficiently (Fenton et al., 2010; Montagnes and Fenton, 2012). Our result on retention times suggests that the ecosystem-level corollary could be an amplified slowing down of nutrient cycling.

3.4.5 Response to food restriction modifies body and waste stoichiometries

The quality of both larvae and their frass were also impacted by intake level. At high intake rates, the body nutrient content was lower apart from C (fig.3.6.a and b). This is likely due to the accumulation of C-rich lipidic reserves that increased the C content in well-fed animals. Similarly, the N/P ratio of larvae increased with intake rate (fig.3.6). This result adds to numerous instances of intraspecific variability in consumer stoichiometry (Simpson et al., 2002; Persson et al., 2010; Hessen et al., 2013; Wei et al., 2022). The tolerance in body stoichiometric variation has been associated with a lower sensitivity to elemental deficiencies (Mulder and Bowden, 2007; Seidendorf et al., 2010) and has even proven to be a competitive advantage in some cases (Grover, 1991; Grover and Chrzanowski, 2006).

Moreover, prey body stoichiometric variations induce differences in nutritional and energetic properties that can affect predators' growth, possibly leading to compensatory feeding behaviors in some predators (Sánchez-Vázquez et al., 1999; Mayntz et al., 2005, 2009; Rubio et al., 2003; Jensen et al., 2011). The variation in the carbon-to-nutrient ratio in animals experiencing various intake levels may affect whether energy or nutrients (lipids or proteins, respectively) are limiting for the predator (Elser et al., 2016).

On the other hand, underfed animals' wastes were poorer in nutrients (fig.3.6.c and d, fig.C.5). Wastes are thus produced in lesser quantities and qualities at low intake. Lower nutrient content is known to reduce the decomposition rate of wastes (Zechmeister-Boltenstern et al., 2015; Enríquez et al., 1993; Güsewell

and Gessner, 2009; Wang et al., 2018a; Sitters et al., 2014), slowing down even more the cycling of nutrients at low intake. The waste N/P ratio decreased at lower intake, suggesting that N was poorly excreted, while P, found mainly in egesta, continued to be egested, potentially due to the poor digestibility of phytates. Moreover, contrarily to expectations under the classic stoichiometric model of homeostatic growth (Sturner et al., 2002a), the frass N/P was not negatively correlated to body N/P (fig. C.8). Non-homeostasis caused by variation in intake possibly prevented us from seeing such a relationship due to a decoupling of absorption and body requirements at variable body stoichiometry.

3.4.6 Note on the growth rate hypothesis

Although our experiment was not designed to test the growth rate hypothesis – which states fast-growing organisms are high in P (Sturner and Hessen, 1994; Isanta-Navarro et al., 2022)–, our data allows us to assess the relevance of the theory in the context of a gradient of food availability. We observe a decrease in body P content with increasing intake (fig.C.5.c) while the growth rate is increasing (fig.3.2.a). Body N/P was also positively correlated with intake. This indicates that in our experiment, faster-growing animals were poorer in P than slower-growing ones and had a stronger decrease in P than in N content with growth rate (fig.3.6.c). This goes in an opposite direction than the positive correlation between growth rate and P content found in various studies (Elser et al., 2003, 2006; Kyle et al., 2006), as well as than the negative relationship of growth rate with N/P body ratio (Mckee and Knowles, 1987; Church and Robertson, 1966), of studies which illustrate the theory at the intraspecific level.

Actually, many experiments confirming this theory at the intraspecific level forced the differences in growth by manipulating the P contents of food (Elser et al., 2003, 2006; Kyle et al., 2006). But conversely, we show here that under constant food stoichiometry, a lower growth rate during food restriction does not necessarily imply lower body P and body N/P increase. In our experiment, high intake rates allowed the building of a lot of C-rich lipidic reserves, therefore increasing C-nutrient ratios at high growth rates and diluting P content. At low intake, biosynthesis likely focused on building N-rich proteins to maintain functioning. Variation in lipid storage combined with the absence of P limitation ultimately may have masked the predictions expected

under the growth rate hypothesis.

The insights gleaned from this experiment at the interface of ecophysiology and nutrient recycling offer a compelling foundation for further exploration. One promising avenue lies in delving deeper into simultaneous variations in both the quality and quantity of food resources (Burian et al., 2020). While this study focused on intake levels, manipulating food quality alongside quantity could uncover intricate relationships governing nutrient absorption and utilization. Moreover, investigating the interplay between these factors could shed light on whether the observed hump-shaped relationship between growth efficiency and intake persists or transforms under diverse nutritional landscapes as suggested by Burian et al. (2020). Exploring these interactions will not only advance our comprehension of physiological adaptations to varying nutritional constraints but also pave the way for more comprehensive ecological models, enhancing our ability to predict and manage ecosystem responses to changing environmental conditions.

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Data, script, code, and supplementary information availability

Data, code and supporting information are available at: <https://doi.org/10.5281/zenodo.7824974>.

4

Feeding and growth variations affect ^{13}C and ^{15}N budgets during ontogeny in a lepidopteran larva

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Isotopes are widely used in ecology to study food webs and physiology. In particular, the fractionation observed between trophic levels in nitrogen and carbon isotopes, explained by isotopic biochemical selectivity, is used to estimate trophic levels and probe physiological processes. However, it is subject to important within-trophic level variations, leading to imprecision in trophic level estimation. Understanding the origin of these variations is thus important to improve the study of food webs. In this study, we characterized this variation by submitting *Spodoptera littoralis* larvae to a gradient of starvation levels, a factor that we hypothesized would change the trophic fractionation between individuals. The various growth rates that were induced from these starvation levels resulted in a 1-1.5‰ within-trophic level variation of the trophic fractionation in both carbon and ni-

trogen, which is substantial compared to the 3-4‰ classically associated with between-trophic levels variations. Hence, starved animals sampled in natura may be ranked at a higher trophic level than they really are. We were able to gain an understanding of the effect of growth rate on isotope fluxes between three easy-to-measure biological materials, food, the organism and its wastes (frass), giving insight into physiological processes at play but also conveying helpful information to the sampling framework of field studies.

4.1 Introduction

Stable isotopes are frequently used to understand fluxes of nutrients in ecosystems as well as trophic position and animal body condition (Post, 2002b). The systematic differences in stable isotope levels between the resource and the tissue of a consumer - the trophic fractionation, here denoted $\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$ - are used to estimate the trophic level of consumers. It occurs because isotopes of different masses have slightly different kinetics during biochemical processes (*i.e.*) respiration or absorption, see Fry 2006). The ^{15}N level of the consumer is usually increased by 3-4‰ relative to its resource because animals retain ^{15}N preferentially over ^{14}N (Martínez del Rio et al., 2009). Carbon fractionation, on the other hand, might vary in a population due to differences in the abundance of *de novo* synthesized lipids in the consumer's body (Melzer and Schmidt, 1987). However, the within-trophic level variability of trophic fractionation sometimes impedes accurate trophic level estimation (Martínez del Rio et al., 2009). Understanding the drivers of these variations is crucial to improving our estimations.

Most of the proposed mechanisms to explain $\Delta^{15}\text{N}$ variation involve diet protein quality and metabolism (Starck and Wang, 2005). However, nutritional status, determined by the resource availability in the environment (Doi et al., 2017; Trochine et al., 2019), can influence trophic fractionation. Physiological responses to nutritional stress involve adjustments in digestion, reserve utilization and metabolic rate. As these processes change in rate (see fig.4.1.a and c), biochemical processes that determine absorption, respiration and excretion also change, therefore impacting $\Delta^{15}\text{N}$ and $\Delta^{13}\text{C}$. Total food restriction, which causes weight loss (corresponding to negative growth rates in fig.4.1.b and d), has the overall tendency to increase heavy isotopes content (^{15}N and ^{13}C), leading to an overestimation of the trophic level (Adams and Sterner, 2000; Boag et al., 2006; Gorokhova and Hansson, 1999; Haubert et al., 2005;

McCue, 2008; Oelbermann and Scheu, 2002; Olive et al., 2003; Schmidt et al., 1999). But more rarely has the effect of various feeding levels been considered, with no convincing conclusion to this day (Hertz et al., 2015). To improve the estimation of trophic levels by including these mechanisms, we need a detailed understanding of the relationship between variation in nutritional status and trophic fractionation.

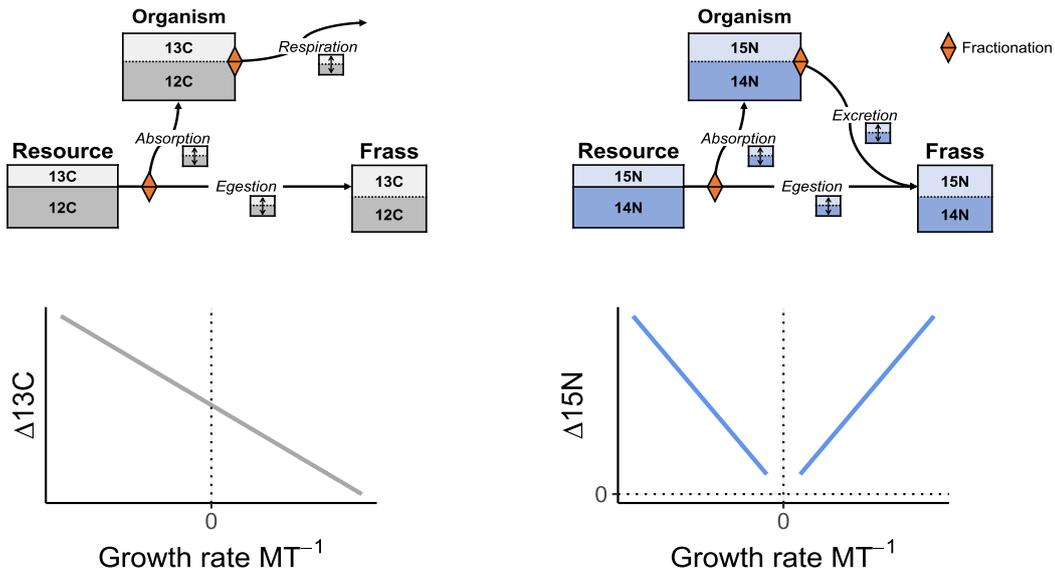


Figure 4.1: Isotopes routing and main hypotheses. a. & c. The three analyzed matrices, their relative (not-to-scale) content of isotopes, fluxes between them, as well as nodes where fractionation can occur (diamonds). The exact proportion of isotopes is not intended to represent reality faithfully but rather to illustrate the dynamical aspect of trophic fractionation. b. & d. Hypothesized relationships between trophic fractionation and growth rate for nitrogen and carbon. a. Most carbon is lost through either respiration or egestion and marginally through excretion. c. On the contrary, nitrogen is solely dropped through either egestion or excretion, with the impossibility of distinguishing their contribution only based on frass analysis. b. The hypothesized relationship between $\Delta^{13}\text{C}$ and growth rate, measured as mass gained per unit of time MT^{-1} . We expect a negative relationship because of the increasing proportion of ^{13}C -poor *de novo* synthesized lipids, thus modulating the respiration fractionation. d. Hypothesized relationship between $\Delta^{15}\text{N}$ and growth rate. High growth rates should increase protein synthesis and breakdown rates, which retain preferentially ^{15}N , and very low intake rates (weight loss) should increase protein catabolism, also increasing $\Delta^{15}\text{N}$, both playing on the excretion fractionation.

Across this gradient in nutritional status, an important threshold is the maintenance feeding level (zero growth rate in fig.4.1.b and d). Below the feeding level required for maintenance, body mass decreases, and adaptations in lipid and protein metabolism are triggered. Lipids typically contain proportionally

less ^{13}C than proteins and carbohydrates (DeNiro and Epstein, 1977; McConnaughey and McRoy, 1979). A shrinkage of body lipid content should thus result in an increase in $\Delta^{13}\text{C}$ compared to high feeding levels (Gaye-Siessegger et al., 2004), where the organism might be able to accumulate ^{13}C -poor lipid reserves, therefore decreasing $\Delta^{13}\text{C}$ (fig.4.1.a).

Regarding nitrogen, low feeding levels are classically associated with an increase in $\Delta^{15}\text{N}$ due to asymmetrical isotopic routing during protein mobilization for energetic catabolism (Hatch 2012; see fig.4.1.c). But high feeding levels, which are often accompanied by high growth rates, can also be accompanied by an increase in $\Delta^{15}\text{N}$ (Sick et al., 1997; Focken, 2001). Indeed, due to an increase in protein synthesis and breakdown rates when the animal is growing fast, removal of ^{14}N is intensified, thus enriching the consumer in ^{15}N and increasing $\Delta^{15}\text{N}$ (fig.4.1.c). As a result, both very low and very high intake rates might increase $\Delta^{15}\text{N}$, but due to different processes, protein mobilization at low intake rates in a weight loss context and protein synthesis and breakdown rates at high intake rates in a growth context.

Moreover, as the gut filling level decreases with underfeeding, the food passage time increases and the biochemical conditions in the gut change. This change in temporal and chemical conditions might alter the isotopic fractionation right from the absorption stage (Schmidt et al., 2015). The relative decrease in the concentration of food in the near-empty gut might increase the enzymes' accessibility and, in turn, the absorption of heavy isotopes. As a whole, trophic fractionation should depend on both nutritional status and body mass dynamics (Sears et al. 2009; Williams et al. 2007, see Hatch 2012 for a review), but these effects remain poorly investigated, especially in varying feeding levels (Gaye-Siessegger et al., 2007).

Elucidating how the nutritional status modifies isotopic fractionation in a growing organism could shed light on the within-trophic level variability of the estimated trophic level and should be of interest for field studies as well. We conducted a feeding level experiment during the larval development of the cotton leaf worm *Spodoptera littoralis*, including severe food restriction, three intermediate restriction levels, and an *ad libitum* level, which corresponded to a range of growth rates. We assessed ^{15}N and ^{13}C budgets, measuring isotopic fractionations between food, body and frass (excreta + egesta).

More specifically, we wanted to test the hypotheses that:

1. $\Delta^{15}\text{N}$ should increase at negative growth rates due to protein catabolism during weight loss and increase at positive growth rates due to faster protein synthesis and oxidation. Around the maintenance level, as these two processes slow down, $\Delta^{15}\text{N}$ should decrease. Overall we should thus obtain a V-shaped relationship between $\Delta^{15}\text{N}$ and growth rate (fig.4.1.d).
2. $\Delta^{13}\text{C}$ should decrease with growth rate because of the accumulation of ^{13}C -poor lipid stores (fig.4.1.c).
3. The relative absorption of ^{13}C might increase at low feeding levels as both gut passage time and digestion efficiency increase.

4.2 Materials and methods

4.2.1 Study system

S. littoralis larvae from a laboratory strain were reared on a semi-artificial diet for the total duration of the experiment. We provide the detailed food composition in Supplementary Information, table 1. The climate chamber was set at 23 °C, 60–70% relative humidity, and a 16:8 light/dark cycle (Hinks and Byers, 1976). In these rearing conditions and with continuous access to food, the larvae go through 7 instars before entering metamorphosis (chrysalid stage). To enable proper mass balance calculation and prevent cannibalism, we isolated the 400 larvae intended for the experiments at the 6th instar in individual 30 mL circular polypropylene boxes. We provided them *ad libitum* food until the 6th moult completion (start of the 7th instar).

4.2.2 Experimental design

We randomly assigned each of the 400 7th instar larvae to one of five food provision levels for the duration of the experiment. Food was kept the same as before the start of the feeding level experiment. The food intake level was fixed to either 120, 240, 360, 480 or 900 mg of food per day (fresh weight), depending on the larva. We had beforehand estimated the average maximal individual intake rate for 7th instar larvae and obtained 595 ± 43 mg/day. There were 80 individuals for each tested food intake level. We conducted this study over ten weeks (10 temporal blocks), performing the experiment with 40 individuals each week, 8 for each food intake level. Individual measurements and sample

collections took place over two or three days depending on whether the larva pre-pupation occurred on the third day of the 7th instar (in which case measures were taken during 2 days) or later (in which case measures were taken during three days).

4.2.3 Experimental workflow

During the experiment, each larva was given the defined amount of freshly prepared food and weighed every day. Food subsamples were taken at every food preparation for subsequent chemical analysis. We collected and weighed daily food leftovers and frass produced by each larva to assess the actual intake and frass production rates. Food leftovers and frass were quickly stored at -20 °C, and later dried for 72 hours at 60 °C in an oven to measure their dry mass. On the third day, half the larvae were quickly stored at -20 °C, dried for 72 hours at 60 °C in an oven, and their dry mass was measured. The other half of the individuals was left in the rearing chambers to later investigate the effect of food restriction on mortality, emergence success and body mass (not analyzed here).

4.2.4 Chemical analyses

Chemical analyses required that we pooled samples to obtain enough analyzable material. Hence, groups of 4 caterpillars reared over the same week and on the same feeding level were composed: two that were pooled together for chemical analysis and two that were left alive until emergence. The analyzed frass was a pooled sample of all four individuals.

All samples - food, larvae, and frass - were ground to a fine powder using a mill. Total carbon, total nitrogen, as well as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were measured using an elemental analyser coupled to a mass-spectrometer (Flash HT - Delta V Advantage, ThermoFisher). We checked for measurement errors using aromatic polyimide (EMA-P2) as standard.

4.2.5 Starvation proxy and isotopic data

Intake rate alone does not accurately represent the nutritional status. Rather, it depends on the balance between intake and requirements, the latter largely depending on body mass. We, therefore, used mass-specific ingestion rate (MSIR) as an indicator of nutritional status. Low values of mass-specific ingestion rate define intense starvation, whereas high values of mass-specific ingestion rate

represent sufficient intake.

$$\text{MSIR}_j = \frac{\sum_{i \in j} I_i}{\left(\frac{1}{4} \sum_{i \in j} d_i\right) \left(\frac{\sum_{i \in j} ib_i + \sum_{i \in j} fb_i}{2}\right)}$$

with I_i the total fresh mass of food ingested by the individual i of the group j over the course of the 7th instar, d_i the number of days spent in 7th instar by individual i , ib_i the initial body mass of individual i , and fb_i the final body mass of individual i .

Pee Dee Belemnite (PDB) and atmospheric nitrogen were used as standards for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Isotopic data for sample s are reported using delta notation:^{13C}

$$\delta^{13}\text{C}_s = 1000 \left[\frac{^{13}\text{C}_s / ^{12}\text{C}_s}{^{13}\text{C}_{\text{PDB}} / ^{12}\text{C}_{\text{PDB}}} - 1 \right]$$

and

$$\delta^{15}\text{N}_s = 1000 \left[\frac{^{15}\text{N}_s / ^{14}\text{N}_s}{^{15}\text{N}_{\text{air}} / ^{14}\text{N}_{\text{air}}} - 1 \right]$$

The trophic fractionation, *i.e.* the difference in $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ between larvae and food, was computed as follows:

$$\Delta^{13}\text{C} = \delta^{13}\text{C}_{\text{larvae}} - \delta^{13}\text{C}_{\text{food}}$$

and

$$\Delta^{15}\text{N} = \delta^{15}\text{N}_{\text{larvae}} - \delta^{15}\text{N}_{\text{food}}$$

We computed the ratio of absorption efficiencies between the two carbon isotopes (thereafter C IAER) to characterize how isotopes are differentially absorbed. This metric characterizes the absorption process, which is one of the two fluxes, along with respiration, determining carbon trophic fractionation (fig.4.1.a). We did not compute this metric for nitrogen because, unlike carbon, nitrogen excretion products also end up in insect frass, and it is, therefore, impossible to disentangle absorption from excretion effects using this metric (fig.4.1.c). Moreover, as samples are heated during drying, some ammonium might volatilize, biasing the mass balance (Harrison, 1995).

$$\text{C IAER} = 1000 \left(\frac{\text{AE}_{^{13}\text{C}}}{\text{AE}_{^{12}\text{C}}} - 1 \right)$$

with AE_i the proportion of ingested isotope which is assimilated, and not egested/excreted, over the 7th instar, given in % dry weight:

$$AE_{jk} = 1 - \frac{C_{Ejk}E_j}{C_{Ijk}I_j}$$

with C_{Ejk} the proportion of isotope k in the frass of the group j , E_j the summed mass of frass produced by the four larvae of the group j and with C_{Ijk} the proportion of isotope k in the food of the group j , I_j the summed mass of food ingested by the four larvae of the group j . Please refer to Appendix E for a detailed calculation of C_{Ejk} and C_{Ijk} .

4.2.6 Statistical analyses

To test the effect of starvation and subsequent variation in growth rate (GR) on the trophic fractionation and relative carbon isotope absorptions, we used linear regressions. We chose to test the effect of growth rates on $\Delta^{15}\text{N}$ and $\Delta^{13}\text{C}$, and the effect of mass-specific intake rate on CIAER. Details on modelling choices are provided in Appendix E.

4.3 Results

Table 4.1: Summary of linear models describing the influence of growth rate (GR) and mass-specific ingestion rate (MSIR) on the trophic fractionation (Δ), and carbon isotope absorption efficiencies ratio (CIAER), respectively.

Equation	n	R^2	F	p-value
$\Delta^{13}\text{C} = -0.0032 \times \text{GR} - 1.7$	92	0.35	48	p<0.01
$\Delta^{15}\text{N} = 0.0054 \times \text{GR} + 0.32$	92	0.53	100	p<0.01
$\text{CIAER} = -0.65 \times \text{MSIR} - 0.97$	100	0.28	38	p<0.01

Despite strong starvation conditions, we were not able to force negative growth rate (fig.4.2.a). We were therefore unable to test the relationships between trophic fractionation - $\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$ - and growth rates for negative growth rates. Here, we describe these relationships for positive growth rates only.

4.3.1 Trophic fractionation

As expected, larvae were always richer in ^{15}N than the food they ate ($\Delta^{15}\text{N}>0$ for all larvae, see fig.4.2.d). There was a clear positive correlation between $\Delta^{15}\text{N}$ and

(positive) growth rate ($F = 100, p < 0.01, R^2 = 0.53$; table 4.1.) in accordance with our hypothesis (right side of the graph in fig.4.1.d). As for carbon, larvae were always poorer in ^{13}C than their food ($\Delta^{13}\text{C} < 0$ for all larvae, fig.4.2.c), and this difference was exacerbated by a growth rate increase ($F = 48, p < 0.01, R^2 = 0.35$; table 4.1.), also in accordance with our hypothesis (fig.4.1.c). In both cases, the $\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$ spanned over a range of ~ 2.5 ‰, of which 1 ‰ in the case of carbon, and 1.5 ‰ can be fully attributed to growth rate variation. These variations are substantial vis-à-vis the one classically attributed to a one trophic level shift (3-4 ‰),

4.3.2 Isotope absorption efficiencies ratio (IAER)

The relative absorption of ^{12}C and ^{13}C depended on the mass-specific intake rate. ^{12}C was systematically better absorbed than ^{13}C , and this effect increased with feeding level ($R^2 = 0.28, F = 38, p < 0.01$, fig.4.2.b).

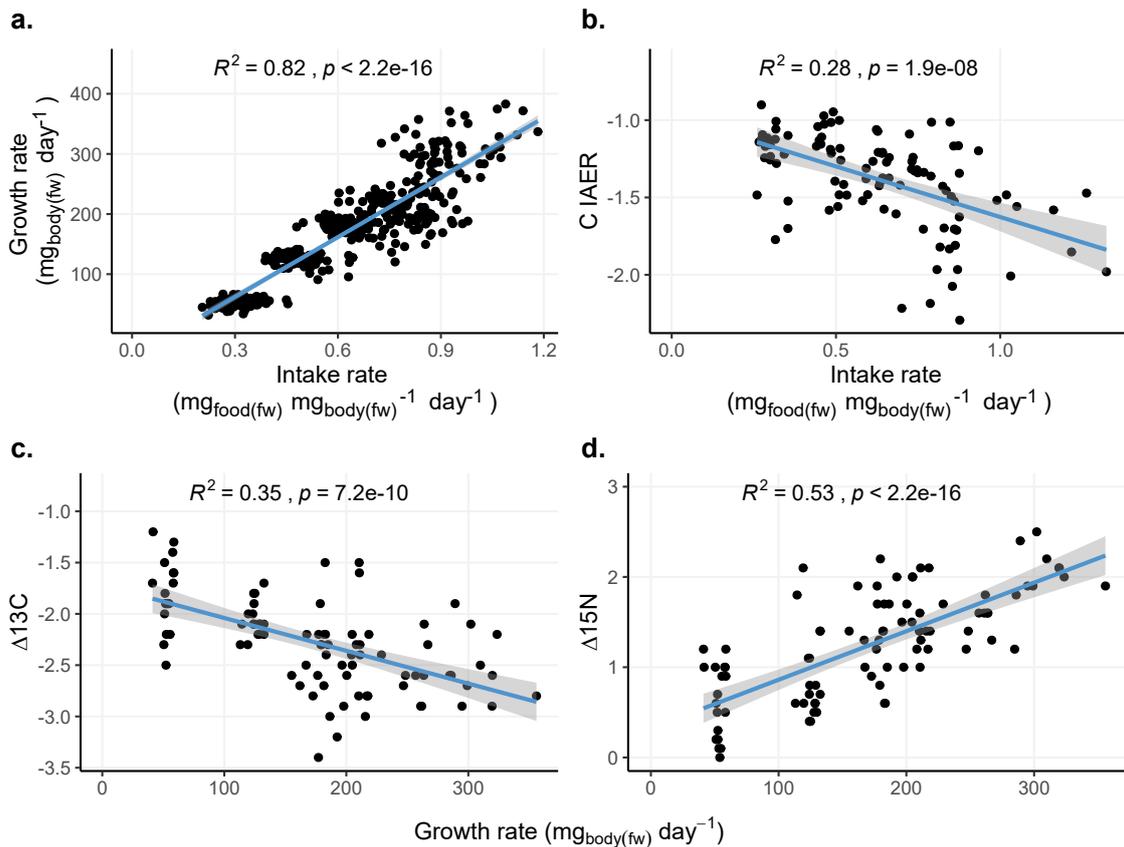


Figure 4.2: Growth and isotopic analyses. a. Individual growth rate as a function of mass-specific intake rate. The fitted curve is a generalized additive model. b. Carbon isotope absorption efficiencies ratio (IAER) as a function of mass-specific intake rate measured at the level of a group of 4 caterpillars. c. Carbon trophic ($\Delta^{13}\text{C}$) fractionation as a function of growth rate. d. Nitrogen trophic fractionation ($\Delta^{15}\text{N}$) as a function of growth rate.

4.4 Discussion

In agreement with our prediction, $\Delta^{15}\text{N}$ increases with growth rate, up to 1.5 ‰, which is substantial compared to differences typically associated with trophic fractionation (3-4 ‰). Our results agree with previous work showing that $\Delta^{15}\text{N}$ is sensitive to growth, at least in some tissues, as highlighted by (Sick et al., 1997). We show that food limitation does not always increase $\Delta^{15}\text{N}$, which rather depends on the underfeeding intensity and whether underfeeding is concurrent with growth. This contrasts with the classic view that $\Delta^{15}\text{N}$ should increase in starved individuals owing to protein depletion for energetic requirements. At least two studies suggested that this increase in $\Delta^{15}\text{N}$ at high growth rates could be due to higher rates of deamination and protein synthesis at higher intake rates (Sick et al., 1997; Focken, 2001). Combining both predictions leads to a more comprehensive view of the effect of feeding level on nitrogen trophic fractionation. Despite very low intake rates, down to 10% of *ad libitum* levels, no weight loss was observed in our experiment, leaving the complete shape of the relationship between $\Delta^{15}\text{N}$ and growth rate only speculative, although the fact that most studies show an increase of $\Delta^{15}\text{N}$ with starvation intensity or fasting duration in a negative growth context, whereas we find the contrary for positive growth rates, suggest such a relationship (Martínez del Río and Wolf, 2005). But whether a V-shaped relation can arise or not requires further investigation.

On the other hand, $\Delta^{13}\text{C}$ were negative at all growth rates. Such negative values of carbon trophic fractionation have been reported elsewhere, especially in invertebrates and in herbivores (Zanden and Rasmussen, 2001; McCutchan et al., 2003). When done at the level of amino acids, trophic fractionation of non-essential amino acids can be negative and depends on the diet (McMahon et al., 2010). Such negative bulk $\Delta^{13}\text{C}$ values could, therefore, be the signature of intense non-essential amino acids biosynthesis during the larva growth. Moreover, $\Delta^{13}\text{C}$ decreased with growth rate and intake level, which is consistent with previous findings (Doi et al., 2017). This is likely due to the possibility of constituting ^{13}C -poor lipid reserves at high growth rates (DeNiro and Epstein, 1977; McConnaughey and McRoy, 1979). On the other hand, long periods of fasting are typically associated with a decrease in lipid content and a corresponding increase in mineral content (Parker and Holm, 1990; Cherel et al., 1992). Our data show that simply reducing intake can also lead to such

effects. To conclude, both $\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$ were affected by feeding level and growth rate. This shows that when assessing trophic levels using isotopic data, the nutritional status of the individual can bias the estimate. Despite being hard to estimate without destructive measurements, at least severe starvation and underfeeding might be detectable through environmental conditions. Physiologically, the nutritional state at which an individual grows can be assessed through age-size comparison, sclerochronology if applicable (Castanet, 1994), or biochemical indicators (e.g. ketone bodies, Shah and Bailey 1976; Chowdhury et al. 2014).

Diet indicators are also prone to estimate error owing to variable nutritional status. The carbon isotopic signature of herbivores is sometimes used to estimate if their diet is composed primarily of C4 plants, rich in ^{13}C (–12 to –20 ‰), or of the ^{13}C -poorer C3 plants (–25 to –32 ‰, O’Leary 1981). Elevated $\delta^{13}\text{C}$ values in the consumer can hence indicate a predominance of C4 plants in the diet. The proportion of C3 in the diet of insects has sometimes been inferred through this tool. It is not clear whether the intensity of isotopic fractionation due to starvation could change as a result of the difference between C4 or C3-based diets, the present case being an example of an artificial diet containing both. Still, starvation is likely to lead to overestimates of the C4 fraction, although not by much (around 10% based on fig.3 in (Fry et al., 1978).

The mass budget of heavy and light isotopes revealed that ^{12}C was more easily absorbed than ^{13}C , which is consistent with the observation of a negative $\Delta^{13}\text{C}$. But as the intake rate decreases, ^{13}C is better absorbed compared to well-fed animals. This indicates that the biochemical environment of the gut varies with intake level, with effects on the processes of digestion and absorption. Moreover, we can also conclude that the respiration fractionation either is negligible compared to the one associated with absorption or that it further decreases the amount of ^{13}C in the organism. But the biochemical origin of this modulation of ^{13}C absorption is unclear. It could be due to longer gut passage time, or to increased food enzymatic availability at low gut filling levels. Our results reveal that the within-trophic level differences in trophic fractionation imputable to nutritional status (1-1.5 ‰) are substantial compared to differences typically associated with trophic level changes (3-4 ‰). Hence, assessing trophic levels *in natura* using isotopic analysis requires caution, especially if the community is perturbed and might be subject to nutritional stress. With the changes in frequency and intensity of drought episodes, one should be

cautious to these potential biases in isotopic trophic ecology.

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Data, script, code, and supplementary information availability

Data, code and supporting information are available at: <https://doi.org/10.5281/zenodo.7824974> (Charberet, 2023).

5

General discussion and perspectives

Throughout the present work, we explored the role that animals play in nutrient recycling in terrestrial ecosystems. Our questions were the following: Do different species have different waste nutrient contents in C, N and P in terrestrial fauna? What is the effect of the animal's diet and body mass on this variation? What can we learn from the joint study of waste stoichiometric ratios? And finally, how do physiological constraints affect nutrient flows inside animals?

Mainly, our answers to these questions proceed as follows (fig. 5.1): diet is the most prominent factor which shapes this composition. Body mass had, contrary to expectations, relatively fewer effects. We also show that intake level has profound consequences on nutrient allocation inside animals, including absorption, body stoichiometry, and waste stoichiometry, with probable effects on the rates of nutrient cycles. In the following, we build on these result to investigate the conditions for a positive effects of animals on nutrient cycling and elaborate a view of animals' ecological stoichiometry that integrate more physiology.

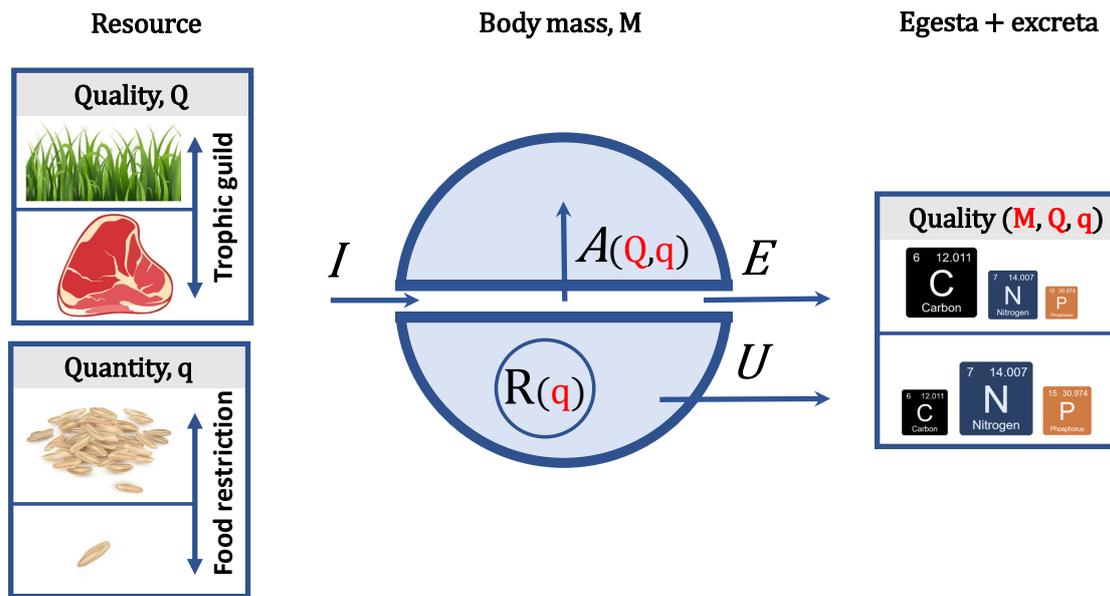


Figure 5.1: Overview of the main results of the dissertation. *I* stands for ingestion, *A* for absorption, *E* for egestion, *U* for excretion, and *R* for reserves. Letters in parentheses represent the test of the effect of quantity (*q*), quality (*Q*) or body mass (*M*) on these processes. Letters in red represent an effect, while letters in black represent no effect.

5.1 Fluxes of energy and structure are plastic

Organisms don't need chemical elements for their "mass" or "structural" aspects only. Chemical elements are contained in molecules that also provide energy to fuel the various metabolic pathways required for survival and growth (fig.C.9). Organisms need to acquire both energy and structural material. However, the relative allocation to growth, maintenance, and output fluxes can vary. Precisely, our experiment shows that the amount of intake devoted to maintenance can vary with intake (fig.C.9) as has already been shown elsewhere (Auer et al., 2015). Similarly, our experiments indicate that body nutrient content can vary at various intake rates (fig. 3.6). Moreover, we show that absorption efficiency can vary with intake but with more or less sensitivity depending on the element (fig.C.4). Research also shows that when resources are lacking, growth can adapt by slowing down (Loewith and Hall, 2011), and maintenance costs can drop (Burggren, 2020; Auer et al., 2015) as we also saw in our results (fig.3.2.a, and C.9). Moreover, if a specific nutrient is in poor quantity in the resource, adaptive processes targeting precisely the assimilation of the lacking nutrient (Boer et al., 2003) or reducing the requirement for it (Boer et al., 2010) can take place. Maintenance is generally a plastic process,

meaning that organisms are not inherently to allocate a specific proportion of their intake resources to energetic or structural processes (Auer et al. (2020), see fig.3.2.a and fig.C.9). Hence, metabolism and growth can adapt in a way that relaxes the stoichiometric constraints on the input and output fluxes determined by intern processes.

However, our simple stoichiometric models of population dynamics don't take this plasticity in allocation into account, nor do they account for constraints of absorption efficiencies of elements along an intake gradient, mostly to keep models mathematically tractable. Strong homeostasis models assume that resource stoichiometry and organism pool stoichiometries are fixed, which results in a fixed consumer stoichiometry (Sousa et al., 2010). On the other hand, weak homeostasis models acknowledge that resource availability influences organisms' composition because reserve varies relative to structure depending on the nutritional status (Sousa et al., 2010). However, strong and weak homeostasis are constructions that ignore that the proportion of resources devoted to structure relative to energy is not fixed, but rather plastic, and can change over time if the organism is confronted with resource-level variability (McCue, 2007; Glazier, 2015). I suggest including maintenance processes and variable assimilation efficiencies of elements in stoichiometric models, along with the variation of allocation between structure and maintenance.

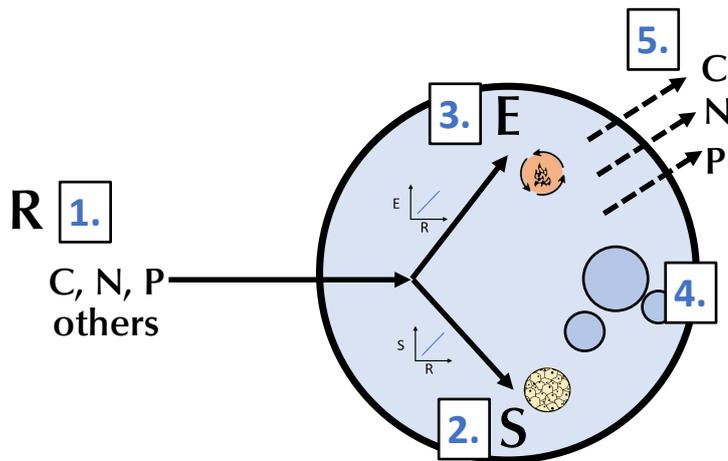


Figure 5.2: Simple model of nutrient fluxes inside animals 1. Acquisition of elements can not (solid arrow) be independent. Once acquired, the resource is either (2.) allocated to structural (S) processes related to biomass construction or replacement or (3.) to energetical (E) processes related to metabolism. Energetical and structural processes are able to adaptively slow down as resource availability (R) decreases, as represented in both graphs. The wastes or reserves compartments can deeply influence an organism’s chemical composition (4.). Generally, elemental withdrawal rates are relatively independent of each other (dotted arrows in 5.).

Stoichiometric mismatches, the difference in stoichiometric composition between the resource and the consumer, can be defined to include both structural and maintenance processes in the definition of ideal resource stoichiometry. It is possible to propose simple allocation models where the resources have to be mostly devoted to building new structures, such as during growth, or to maintenance, such as during adulthood. Moreover, as we saw, growth investment can drop as a result of low resource availability (fig.3.2, and C.9). Additionally, it is possible to include adaptive plasticity to a deficiency in the elemental environment by a lowering of requirement or modifying the nutrient use efficiency (Sinsabaugh et al., 2013). Models with variable assimilation efficiencies have been proposed, but not at the elemental level (Fenton et al., 2010).

5.2 Relationships between requirements, acquisition flux and chemical composition of the resource

A refined perspective of the constraints put on resources is in terms of dynamic fluxes and rates rather than in fixed chemical composition (Sousa et al., 2010). The fundamental challenge faced by an organism is to acquire the amount of energy and nutrients required for a given period of life, expressed in joules or kilograms per time unit (Sousa et al., 2010). Elemental intake rate results from the combination of the resource acquisition rate and its chemical composition. A whole range of combinations of acquisition rate and resource chemical composition are able to meet a given requirement, given that the considered animal can indeed consume the resource (herbivores can not eat meat to increase the N content of their food). For example, if the requirement is 25 grams of carbon /day, acquiring 50 grams/day of biomass composed of 50% carbon or acquiring 100 grams/day of biomass composed of 25% carbon both meet the requirements. Therefore, organisms are not exactly bound to consume resources of a given chemical composition but rather to meet a certain elemental acquisition rate. This is why, even at the maximal rate of acquisition, animals can be limited by an element like in figs.2.5. Therefore, it would be interesting to include resource abundance-richness relationships in models and use optimization models to guide the behavioural choices of animals, which can choose among resources and bounded intake rates to meet their requirements. If an animal indeed meets its requirements, the animal should be able to be at equilibrium or even grow, which has the effect of sequestering nutrients and diverting it temporarily from recycling. Short-time scale effects of animals could, in this way, be explored with more detail.

5.3 Animal impact on cycling could depend on the distribution of nutrients in the resource

This dissertation has explored the effect of low-quality and low-quantity diet on recycling. The classical theory of consumer-driven nutrient recycling has highlighted differences in the effect of animals among nutrient-rich and nutrient-poor systems. Still, the definition of a nutrient-rich or nutrient-poor ecosystem can be refined. The classical theory states that the adverse effects of ani-

imals are due to selective foraging on the richest resource in nutrient-poor systems, leaving only nutrient-poor litter fall (Bardgett and Wardle, 2010). Indeed, some plants in the nutrient-poor ecosystem are rich in nutrients, but they are not abundant. In our analyses, we show that at high availability of nutrient-poor resources, animals could fail to eat sufficient amounts to meet their basic nutrient requirements, and as they still release wastes (excretion, endogenous losses), they can lose more nutrient than acquired (fig.2.5). In parallel, our experiment shows that if nutrient-poor systems mean a low quantity of rich resources, the animal indeed sequesters the rich organic matter that could have been easily decomposed but will even increase its absorption efficiency and retention time, which could reduce recycling at short time scales compared to an ecosystem with no herbivore (fig.C.4). We can suggest defining nutrient-poor ecosystems based on the distribution of nutrients in resources, deciding the effects of animals on recycling: either low amounts of nutrient-rich resources and high amounts of nutrient-poor resources (a.), high amounts of resources of intermediate richness (b.), or low amount of rich resource only (c.). Depending on the situation of the ecosystem, there could be different dynamics triggered by animals.

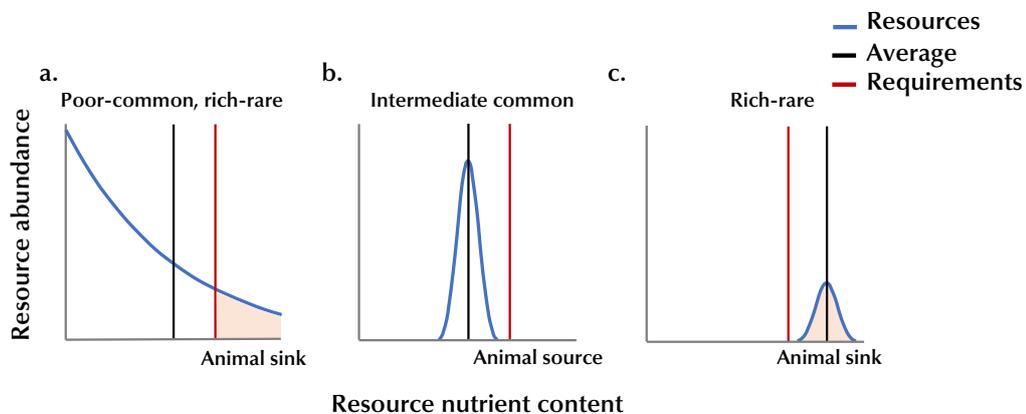


Figure 5.3: The distribution of nutrients among resources in nutrient-poor systems might influence plants-animal feedback in recycling. In a. and b. panels, the average nutrient content in the resource (black line) is the same and is typically low. In the c. panel, there are few resources, but richer. The y-axis is rescaled to see the whole distribution. The requirements are for maximal intake rate. a. The common-poor, rare-rich resource ecosystem still holds some rich resources that animals can selectively feed on, and this is associated with a negative effect of animals on nutrient recycling. b. The prevailing-intermediate resource lacks rich resources. Animals, even at maximal intake, might not meet their requirements while losing nutrients due to maintenance. Hence, they might have a transient, positive impact on nutrient recycling. c. Here, the resources are rich but rare. The animal is able to grow with this resource but might increase absorption efficiency (fig.C.4) and retention time (fig.3.5), ultimately slowing down nutrient cycling.

Indeed, these three scenarios are linked to whether or not animal growth can occur, at which efficiency, but also to the absorption efficiency of the various elements. In the intermediate common scenario, the animal can not grow even at maximal intake since the limiting nutrient can not be found in sufficient amounts. In a. and c. scenarios, growth might occur, as in the experiment of Chapter 3, since there are no nutrient limitations. However, growth efficiency diminishes at low resource availability even when the resource is rich, and it is expected that it could even be negative, provoking body mass loss (see fig.3.2). Differences between a. and c. scenarios might be the amount of litter recycled, which can be high in a., but low in c. owing to the already low availability of resources, but also to efficient absorption by consumers.

5.4 About changing scales

This dissertation has mostly focused on the individual level of organisation. In the light of consumer-driven recycling and soil microbiology, we have been able to derive from our results that animals can have positive effects on nutrient cycles. The next step would be to quantitatively assess the fluxes generated by a population of animals in the ecosystem and how they compare to other fluxes, like litter fall, weathering inputs, or biological fixation. This task requires joint data on population intake, density and dynamics, waste chemical properties and fluxes. Long-term mesocosm experiments seem to be promising in this regard since other confounding factors can be controlled for, and populations can be monitored closely. It would allow assessing the effects of variation in requirements inside populations due to life stages and intra-specific competition.

At the community level, a glaring knowledge gap is the relative importance of species of various body masses in recycling. Damuth's rule of equivalence between energetical flows at all bodymass suggests that all species participate in equivalent recycling (Damuth, 1981), but this has to be put to the test. Some models suggest that smaller species participate in larger energy fluxes (Loeuille and Loreau, 2006). Yet, these animals are precisely the least studied ones regarding nutrient cycling. Again, an experimental approach giving some control might help to decipher cross effects in communities. Starting with small and simple communities in mesocosms seem to be adapted.

At the global scale, assessments of fauna's nutrient recycling, like the one done in (Doughty, 2017; Dangal et al., 2017), are also needed to investigate with scrutiny the changes in nutrient recycling conveyed by current biodiversity changes.

5.5 Conclusions

One of the main lessons of this work is the fundamental link between ecology and physiology. Animals are able to plastically adapt to various conditions, from poor-nutrient forages to low resource availability, by adjusting their internal physiology. These adaptations then reverberate into the fluxes they generate, suggesting that ignoring animal physiology in functional ecology prevents complex and elegant dynamics from being captured. On the flip side, extreme conditions imposed experimentally in ecological settings can lead to interesting discoveries about the surprising animal's physiological capabilities.

As I conclude my doctoral journey, I reflect on the intricate interplay between animal physiology and ecology. Through these years of research, I've studied the deep connection between these two facets of biology, revealing a complex web of adaptations, interactions, and responses within the natural world. This work expands our understanding while highlighting the critical importance of grasping the delicate balance that sustains ecosystems. I hope that these insights will contribute to ongoing scientific progress and foster a deeper appreciation for the richness of our natural environment. As one chapter closes, I eagerly anticipate the fresh perspectives and discoveries that lie ahead in the ongoing exploration of ecosystems.



Data synthesis sources

This section provides sources related to the dataset used in Chapters 1 and 2. You will find data sources for the data syntheses of Chapters 1 and 2 and the list of structures which provided samples for our complementary measurements. The full database entry list is also given.

A.1 Waste nutrient data sources

In table A.1 are listed the article from which data were retrieved for the data synthesis of Chapter 1. Indicated are the types of waste data found.

Author, year	Egesta	Excreta	Diet trial
Sørensen and Fernández (2003)	Yes	Yes	Yes
Valdés-Correcher et al. (2019)	Yes	No	No
Sitters et al. (2014)	Yes	No	No
Chen et al. (2003)	Yes	No	No
Fugler (1985)	Yes	Yes	No
Manny et al. (1975)	Yes	Yes	No

Table A.1 continued from previous page

Author (year)	Egesta	Excreta	Diet trial
Hulot et al. (2019)	Yes	No	No
Emerson and Roark (2007)	Yes	No	No
Tajovský et al. (1992)	Yes	Yes	No
Anderson and Coe (1974)	Yes	No	No
Dougall (1963)	Yes	No	No
Edwards (1991)	Yes	No	No
Kamler et al. (2003)	Yes	No	No
Pacyna et al. (2019)	Yes	No	No
Blanchard et al. (2003)	Yes	No	No
van der Wal and Loonen (1998)	Yes	Yes	No
Kadamannaya and Sridhar (2009)	Yes	Yes	No
Barnes et al. (2019)	Yes	Yes	No
Wang et al. (2018b)	Yes	No	No
Sitters et al. (2017a)	Yes	No	No
Saastamoinen et al. (2020)	Yes	No	Yes
Joly et al. (2018)	Yes	Yes	No
Jia et al. (2015)	Yes	Yes	No
Mitlin et al. (1964)	Yes	Yes	No
Studier et al. (1994)	Yes	No	No
Subalusky et al. (2014)	Yes	Yes	No
Hansen and Jørgensen (1973)	Yes	Yes	Yes
Kamler and Homolka (2005)	Yes	No	No
Irwin et al. (1993)	Yes	No	No
Mould and Robbins (1981)	Yes	No	No
Howery and Pfister (1990)	Yes	No	No
Subalusky et al. (2017)	No	No	No

Table A.1 continued from previous page

Author (year)	Egesta	Excreta	Diet trial
Hodgman et al. (1996)	Yes	No	No
an Chen and Forschler (2016)	Yes	Yes	No
Kagata and Ohgushi (2010)	Yes	Yes	No
Kagata and Ohgushi (2011b)	Yes	Yes	No
de Swardt et al. (2018)	Yes	Yes	No
Kagata and Ohgushi (2012b)	Yes	Yes	No
Kagata and Ohgushi (2011a)	Yes	Yes	No
Grüning et al. (2018)	Yes	Yes	No
Hillstrom et al. (2010)	Yes	Yes	No
Cobb et al. (2010)	Yes	Yes	No
Mishra et al. (2013)	Yes	Yes	No
Zhang et al. (2014)	Yes	Yes	No
Gärttling et al. (2020)	Yes	Yes	No
Russell et al. (2004)	Yes	Yes	No
Lovett and Ruesink (1995)	Yes	Yes	No
Houben et al. (2020)	Yes	Yes	No
Poveda et al. (2019)	Yes	Yes	No
Fielding et al. (2012)	Yes	Yes	Yes
Frank et al. (2017)	Yes	No	No
Signa et al. (2013)	Yes	Yes	No
Wang et al. (2017)	Yes	Yes	No
Zdanowski et al. (2005)	Yes	Yes	No
Jauffrais et al. (2015)	Yes	Yes	No
Bancroft et al. (2005)	Yes	Yes	No
Liu et al. (2006)	Yes	Yes	No
Orłowski et al. (2015)	Yes	Yes	No

Table A.1 continued from previous page

Author (year)	Egesta	Excreta	Diet trial
Otero et al. (2015)	Yes	Yes	No
Finger et al. (2017)	Yes	Yes	No
Zhong et al. (2017)	Yes	Yes	No
Zhu et al. (2009)	Yes	Yes	No
Mizota et al. (2012)	Yes	Yes	No
Pérez (1998)	Yes	Yes	No
Sobey and Kenworthy (1979)	Yes	Yes	No
Smith and Johnson (1995)	Yes	Yes	No
Celis et al. (2014)	Yes	Yes	No
Klaassen et al. (2000)	Yes	Yes	No
Zhu et al. (2006)	Yes	Yes	No
Hayes and Caslick (1984)	Yes	Yes	No
Gwiazda (1996)	Yes	Yes	No
Fox and Kahlert (1999)	Yes	Yes	No
Wing et al. (2017)	Yes	Yes	No
Rial et al. (2016)	Yes	Yes	No
Marion et al. (1994)	Yes	Yes	No
Metcheva et al. (2011)	Yes	Yes	No
Dauwe et al. (2000)	Yes	Yes	No
Mizutani and Wada (1988)	Yes	Yes	No
Gwiazda et al. (2010)	Yes	Yes	No
Young et al. (2010)	Yes	Yes	No
Qin et al. (2014)	Yes	Yes	No
Portnoy (1990)	No	No	No
Ambarish and Sridhar (2016)	Yes	Yes	No
Wood et al. (2004)	Yes	Yes	Yes

Table A.1 continued from previous page

Author (year)	Egesta	Excreta	Diet trial
Abdouli et al. (1992)	Yes	No	Yes
Asada and Ochiai (1999)	Yes	No	No
Kucera (1997)	Yes	No	No
Dalmau et al. (2007)	Yes	No	No
Frost and Hunter (2008)	Yes	Yes	No
Klammsteiner et al. (2020)	Yes	Yes	No
Joly et al. (2020)	Yes	Yes	Yes
Watson et al. (2021)	Yes	Yes	Yes
Zaady et al. (2003)	Yes	Yes	No
Teuben and Verhoef (1992)	Yes	Yes	No
Goveas et al. (2006)	Yes	No	No
Palita et al. (2021)	Yes	No	No
Misra et al. (2019)	Yes	No	No
De Cuyper et al. (2020)	Yes	No	No
Whipple and Hoback (2012)	Yes	No	No
Burger et al. (1971)	Yes	Yes	No
Vega et al. (2020)	Yes	Yes	No

Table A.1: Literature sources for waste nutrient content described in chapter 1 and 2. Egesta, excreta, and diet trial describe respectively whether the study included chemical analysis on egesta (faeces), excreta (urine), and whether the study included food quality or quantity treatments (diet trial).

A.2 Body mass data sources

If body a species' body mass was not found in either Elton's traits (Wilman et al., 2014) or Amniote life history traits database (Myhrvold et al., 2015), we searched the literature. Here we list each species for which it was the case, the body mass found, along with the reference.

Species	Body mass (g)	Source
<i>Anthonomus grandis</i>	0.008	Silva et al. (2015)
<i>Dendrolimus pini</i>	2	Łukowski et al. (2021)
<i>Tenebrio molitor</i>	0.2	Zhang et al. (2019)
<i>Lymantria dispar</i>	0.6	Thompson et al. (2017)
<i>Apis mellifera</i>	0.15	Kaftanoglu et al. (2011)
<i>Oedaleus asiaticus</i>	0.52	Cease et al. (2010)
<i>Hermetia illucens</i>	0.15	Sheppard et al. (2002)
<i>Malacosoma americana</i>	0.05	Etilé and Despland (2007)
<i>Anacanthotermes ubachi</i>	0.003	Dahlsjö et al. (2015)
<i>Arthrospira dalyi</i>	8	Kadamannaya and Sridhar (2009)
<i>Arthrospira davisoni</i>	13	Kadamannaya and Sridhar (2009)
<i>Hogna carolinensis</i>	0.0028	Barnes et al. (2018)
<i>Glomeris marginata</i>	1.6	Ganault et al. (2022)
<i>Reticulitermes flavipes</i>	0.0022	McManamy et al. (2008)
<i>Reticulitermes virginicus</i>	0.021	Wagner et al. (2012)
<i>Zootermopsis nevadensis</i>	0.003	Dahlsjö et al. (2015)
<i>Incisitermes snyderi</i>	0.003	Dahlsjö et al. (2015)
<i>Mamestra brassicae</i>	0.75	Harvey and Gols (2011)
<i>Parasa consocia</i>	0.6	Murphy et al. (2011)
<i>Arthrospira disticta</i>	3	Dwarakanath et al. (1973)
<i>Arthrospira fumosa</i>	13	Kadamannaya and Sridhar (2009)
<i>Cepaea nemoralis</i>	1.3	Thomas et al. (1997)
<i>Porcellio scaber</i>	0.045	Abdel-Lateif et al. (1998)
<i>Tachypodoiulus niger</i>	0.02	Woodcock (2020)
<i>Gonimbrasia belina</i>	6	Gaston et al. (1997)
<i>Dendrolimus spectabilis</i>	2.25	Łukowski et al. (2021)
<i>Melanoplus borealis</i>	0.3	Branson (2004)

Species	Body mass (g)	Source
<i>Pseudochorthippus curtipennis</i>	0.1	Gutiérrez et al. (2020)
<i>Trachycephalus resinifictrix</i>	13	Bijma et al. (2016)
<i>Vipera berus</i>	80	(Olsson et al., 1997)
<i>Python regius</i>	1100	Aubret et al. (2005)
<i>Boa constrictor</i>	5000	Bertona and Chiaraviglio (2003)
<i>Natrix maura</i>	39.5	Santos et al. (2007)
<i>Salvator rufescens</i>	2300	Naretto et al. (2016)
<i>Centrochelys sulcata</i>	15000	Ardjima et al. (2020)

Table A.2: Literature source for body mass.

A.3 Complementary measurements

In complement to the literature data synthesis, wastes were sampled in various structures housing animals and analysed. In table A.3 is the list of these structures along with the number of samples retrieved from each one of them.

Structure	Number of waste sample
ZooSafari de Thoiry	138
Zoo African Safari	62
Zoodyssée	48
Zoo de La Flèche	33
Réserve africaine de Sigean	31
Parc animalier d’Auvergne	31
Parc zoologique de Paris	31
Ménagerie du MNHN	27
Domaine de Pescheray	15
Institut d’écologie et des sciences de l’environnement de Paris	6
La Ferme Tropicale	4
Palais de la Découverte	3
Total	429

Table A.3: List of facilities keeping animals which provided samples for the study.

A.4 Absorption efficiencies data sources

Here, we provide the data sources for the data synthesis on absorption efficiency on P, Ca, K, Mg and Na of Chapter 2.

Source	Number of observations
Allen et al. (1990)	5
Beynen and Yu (2003)	6
Beynen et al. (2001)	3
Beynen et al. (2002)	9
Buraczewska et al. (1996)	2
Callegaro et al. (2010)	15
Cargo-Froom et al. (2019)	20
Childs Sanford and Angel (2006)	16
Clauss et al. (2005)	38
Clauss et al. (2011)	8
Clauss et al. (2003)	64
Crozier et al. (1997)	12
Cymbaluk (1990)	32
Cymbaluk et al. (1989)	10
Den Hartog et al. (1988)	20
Frommelt et al. (2014)	16
Grandhi (1994)	48
Grandi et al. (2018)	5
Grela et al. (2011)	12
Groenendyk et al. (1988)	10
Hagen et al. (2015)	50
Hellgren and Pitts (1997)	12
Hintz and Schryver (1972)	8

Source	Number of observations
Hintz and Schryver (1973)	9
Hintz and Schryver (1976)	8
Kienzle et al. (1995)	10
Kies et al. (2005)	10
Landes et al. (1997)	35
Leon and Belonje (1979)	6
Levrat-Verny et al. (1999)	4
Lohakare et al. (2010)	6
Mroz et al. (1994)	2
Schauf et al. (2021)	16
Schryver et al. (1970)	11
Schryver et al. (1971)	8
Staaland et al. (1988)	25
Sullivan et al. (2011)	12
Tebbe et al. (2018)	10
Teshima et al. (2010)	7
Valaja et al. (1998)	6
van der Klis et al. (1995)	20
Wolf et al. (1998)	20

Table A.4: Sources for the data synthesis on absorption efficiencies of P, Ca, K, Mg and Na from Chapter 2.

A.5 Data base structure

In this section, we describe each of the database columns, with the column name, its purpose, and the possible values (table A.5).

[H]

Variable	Description	Possible values/examples
reference_ID	reference of the paper	1234_001
first_author	family name of the first author of the reference	einstein, tilman
reference_year	year of the reference	1905
data_source	the reference or other source in the reference	1234_001
data_digitizer	family name of who entered the data	einstein
data_checker	family name of who checked the data	schrodinger
sample_type	nature of the sample	food, feces, urine, body
body_part	part of the body on which the analysis was done	muscle, hair, leaf, root, whole
food_ref	food consumed in the reference	fruits
egestion_age	time since egestion	1
egestion_age_unit	time unit of egestion_age	hour, day, week, month, year
bodymass_mean	average bodymass value	115
bodymass_min	minimum value	90
bodymass_max	maximum value	150
bodymass_value_error	raw error of the value	50
bodymass_error_type	type of error	variance (v), coefficient of variation (cv), mean absolute error (mae)

Variable	Description	Possible values/examples
bodymass_n_samples	number of samples used to estimate the value	42
bodymass_unit	unit in which the bodymass is given	g, kg, t, lb
bodymass_weight_type	wet weight or dry weight	ww (wet weight), dw (dry weight)
age_mean	average age	115
age_min	minimum value	90
age_max	maximum value	150
age_value_error	raw error of the value	50
age_error_type	type of error	variance (v), coefficient of variation (cv), mean absolute error (mae)
age_n_samples	number of samples used to estimate the value	42
age_unit	unit in which the bodymass is given	hour, day, week, month, year
male_prop	proportion of males in the group	0.5
sampling_year	year the sample was produced	1904
sampling_month	month the sample was produced	12
sampling_day	day in the month the sample was produced	25
sampling_season	season the sample was produced	winter, spring, summer, fall, dry, wet
sampling_location	name of the place of sampling	russia, ile de France, lourdes
sampling_latitude	latitude in decimal degrees	48.6494
sampling_longitude	longitude in decimal degrees	7.2454
location_in_reference	where the data were taken from	table 17, figure 2.1, SI (supplementary information)

Variable	Description	Possible values/examples
organism_name_ref	species common name in the reference	rose_chafer
species_latin_name_ref	species latin name in the reference	cetonia_aurata
species_latin_name_gbif	accepted species latin name in the gbif	cetonia_aurata
gbif_id	gbif ID of the organism at species level	1077829
gbif_id2	modified GBIF for subspecies	1077829
organism_stage	stage of the organism	larvae, nymph, pupa, imago, juvenile, adult
environment	environment in which the animal was living	lab, farm, zoo, aquarium, wild
temperature	average daily air temperature (C°)	25
food_ID	ID of the food observation	X a number from 1 to n, with n the number of observation of food
body_ID	ID of the body observation.	X a number from 1 to n, with n the number of observation of body
feces_ID	ID of the feces observation.	X a number from 1 to n, with n the number of observation of feces
urine_ID	ID of the urine observation.	X a number from 1 to n, with n the number of observation of urine
nb_items_per_sample	the number of items that were put in the tube	1
nb_individuals_per_sample	the number of individuals represented in the tube	2
individual_known	whether the individual can be identified	0 (not known), 1 (known)

Variable	Description	Possible values/examples
observation_resolution	resolution of the observation in the following list	individual (intra, inter), population (intra, inter), food, intra_food, inter_food
observation_ID	unique ID for this observation	1, 2, 3
animal_group_ID	unique ID for organism	1, 2, 3
times_series_ID	unique ID for the times series	1, 2, 3
time_point	time point in time unit	1, 2, 3, 48, 72
time_unit	time unit of time_point	h, day, week, month, year
repetition_ID	unique ID for the repetition in the time point	1, 2, 3
component_name	chemical component or fraction of the component	C, N, P
component_mean	average value	115
component_min	minimum value	90
component_max	maximum value	150
component_value_error	raw error of the value	50
component_error_type	type of error	variance (v), coefficient of variation (cv), mean absolute error (mae)
component_n_samples	number of samples used to estimate the value	42
component_unit	unit in which the component is given	g/g, g/kg, kg/ind/day, kg/kgind/day, L/day, g, kg, t, lb
component_weight_type	wet weight or dry weight	ww (wet weight), dw (dry weight)

Variable	Description	Possible values/examples
component_data_type	unit dimension	stock (mass), flux (mass/time) or rate (mass/time/body mass or individual)
component_detail	fraction or nature of component	total, assimilable, dissolvable, Olsen-P
component_extraction_method	details or the name of the extraction method	olsen, combustion, kjeldahl
component_measure_method	details or the name of the measure method	icp-oes, CHN, pH in water, pH in KCl
freezing	whether freezing occurred or not	0,1
autoclaving	whether autoclaving occurred or not	0,1
drying	whether the sample was dried or not	0,1
oven	whether the sample was dried in an oven or not	0,1
drying_time	drying duration	14
drying_time_unit	drying duration unit	minute, hour, day
drying_temp	drying temperature	60
drying_temp_unit	drying temperature unit	°C, °F
grinding	whether the sample was ground or not	0,1
grinding_fineness	diameter of the grinding sieving	10
grinding_fineness_unit	unit of the diameter	m, mm

Table A.5: Description of the database entries. Each entry is described by its definition and the possible values associated.

B

Data synthesis supplementary figures

This section provides supplementary figures related to the dataset used in Chapters 1 and 2.

B.1 Influence of bodymass and diet on waste nutrient content: supplementary figures

We performed an analysis of the waste nutrient content according to body mass, combining all diets. Body mass and diet have co-evolved in mammals because being large increases gut passage time and protects from predation, thus, herbivores are, on average larger than carnivores ([Price and Hopkins, 2015](#)). This co-evolution between body mass and diet was thus hypothesized to influence the overall relationship between body mass and waste nutrient content. This co-evolution indeed seems to play a role for N faeces content in mammals, where large animals are rather herbivores, and thus have lower faeces N. Smaller animals are rather omnivores and carnivores, with higher faeces N (fig.B.2.b and d). However, it was the contrary in non-mammals, where we observe larger animals being rather carnivores. This may be due to another evolutionary trend which favours predators to become larger than their prey ([Van De Walle et al., 2023](#)). However, the statistical power of this analysis was

limited (fig.B.3.b).

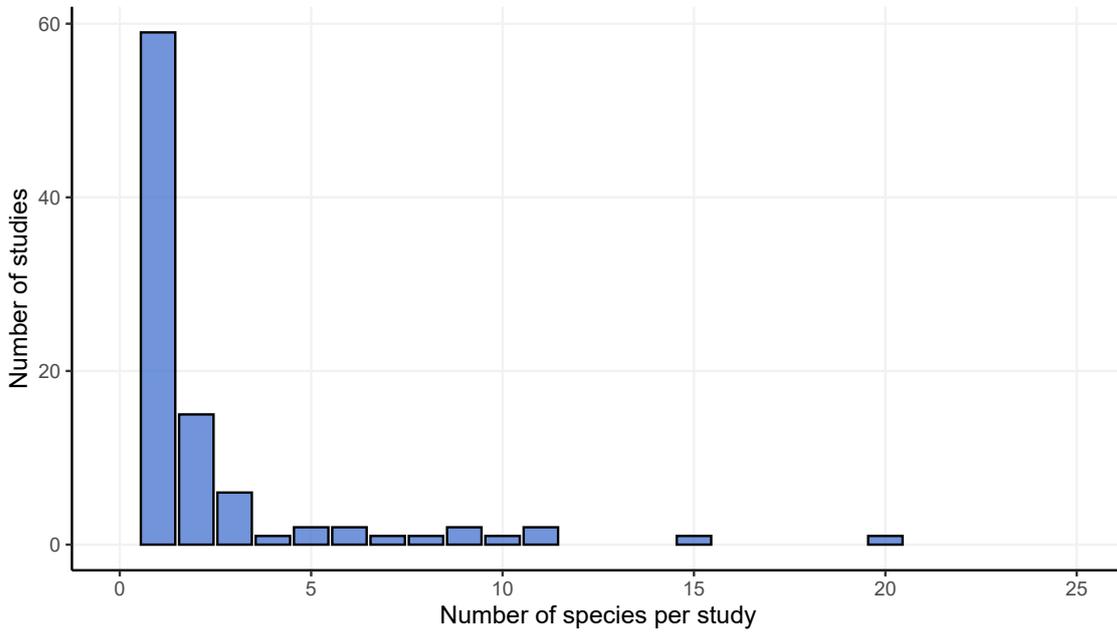


Figure B.1: Number of studies with n species.

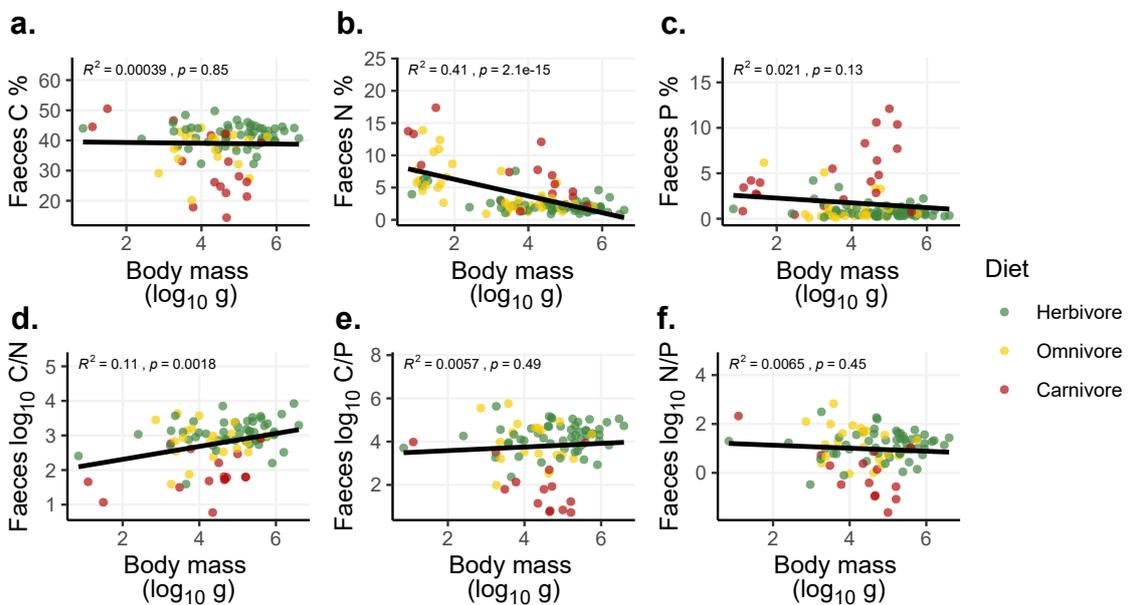


Figure B.2: Effect of body mass on CNP absolute concentration and ratio on mammals faeces, all diets combined. Each point represents the mean value for one species. Only significant relationships are shown

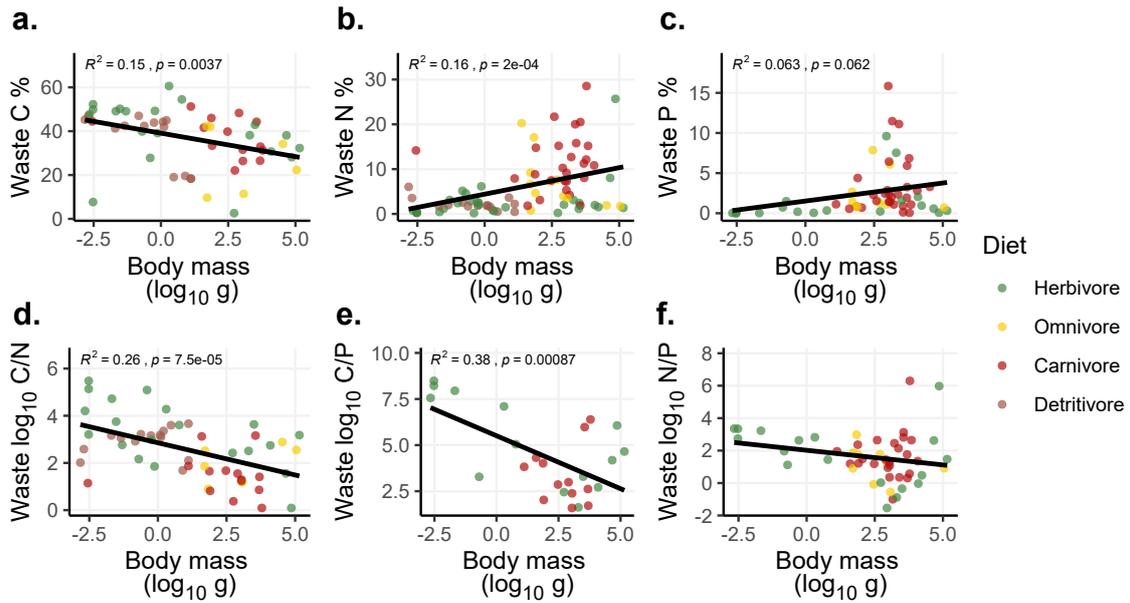


Figure B.3: Effect of body mass on CNP absolute concentration and ratio on non-mammals total waste, all diets combined. Each point represents the mean value for one species. Only significant relationships are shown

B.2 ANCOVA of nutrient contents with body mass and diet

Variable	Term	Estimate	Standard error	Statistic	p-value
C	(Intercept)	41.7	0.816	51.1	4.72E-65
	Body mass	-0.0861	0.312	-0.276	0.783
	Carnivore	-15.2	2.07	-7.34	1.26E-10
	Omnivore	-3.54	2.22	-1.59	0.115
	Body mass:Carnivore	-2.03	0.585	-3.47	0.000812
	Body mass:Omnivore	0.427	0.762	0.561	0.576
N	(Intercept)	2.01	0.279	7.19	6.96E-11
	Body mass	-0.277	0.0825	-3.36	0.00105
	Carnivore	1.3	0.719	1.8	0.0742
	Omnivore	-0.748	0.62	-1.21	0.23

Variable	Term	Estimate	Standard error	Statistic	p-value
	Body mass:Carnivore	-0.679	0.157	-4.32	3.36E-05
	Body mass:Omnivore	-0.373	0.126	-2.95	0.0038
	(Intercept)	0.742	0.21	3.54	0.000599
P	Body mass	-0.1	0.0794	-1.26	0.21
	Carnivore	5.98	0.564	10.6	3.14E-18
	Omnivore	-0.121	0.582	-0.207	0.836
	Body mass:Carnivore	0.581	0.125	4.66	9.59E-06
	Body mass:Omnivore	-0.11	0.171	-0.647	0.519
log C/N	(Intercept)	3.09	0.0666	46.4	4.20E-61
	Body mass	0.0451	0.0257	1.75	0.083
	Carnivore	-1.03	0.168	-6.13	2.82E-08
	Omnivore	-0.251	0.181	-1.39	0.169
	Body mass:Carnivore	0.0176	0.0478	0.367	0.715
	Body mass:Omnivore	-0.047	0.0621	-0.756	0.452
log C/P	(Intercept)	4.26	0.117	36.3	4.90E-51
	Body mass	0.0466	0.0449	1.04	0.302
	Carnivore	-2.81	0.308	-9.12	5.65E-14
	Omnivore	-0.451	0.342	-1.32	0.191
	Body mass:Carnivore	-0.274	0.0967	-2.83	0.00582
	Body mass:Omnivore	-0.133	0.118	-1.13	0.264
log N/P	(Intercept)	1.14	0.092	12.4	1.01E-20
	Body mass	0.0163	0.0354	0.46	0.647
	Carnivore	-1.72	0.248	-6.94	7.23E-10
	Omnivore	-0.23	0.265	-0.869	0.387
	Body mass:Carnivore	-0.273	0.0776	-3.52	0.000688
	Body mass:Omnivore	-0.142	0.0917	-1.54	0.126

Variable	Term	Estimate	Standard error	Statistic	p-value
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Table B.1: ANCOVA model components with C, N, P and stoichiometric ratio as the response variable and body mass and diet as explanatory variable in mammals. The reference diet is herbivore. Body mass were log-transformed and centered

Variable	Term	Estimate	Standard error	Statistic	p-value
C	(Intercept)	34	4.12	8.26	1.24E-10
	Body mass	-0.756	0.432	-1.75	0.0866
	Carnivore	-0.61	5.99	-0.102	0.919
	Detritivore	-24.8	12.1	-2.06	0.0454
	Omnivore	-8.12	7.04	-1.15	0.255
	Body mass:Carnivore	-0.353	0.978	-0.361	0.72
	Body mass:Detritivore	-2.07	1.19	-1.73	0.0897
	Body mass:Omnivore	0.177	1.61	0.11	0.913
N	(Intercept)	5.12	1.49	3.43	0.001
	Body mass	0.31	0.164	1.88	0.0636
	Carnivore	6.86	1.96	3.49	0.000818
	Detritivore	-5.7	5.03	-1.13	0.261
	Omnivore	-1.65	2.64	-0.624	0.534
	Body mass:Carnivore	-0.052	0.371	-0.14	0.889
	Body mass:Detritivore	-0.598	0.498	-1.2	0.234
	Body mass:Omnivore	-1.57	0.59	-2.66	0.00965
P	(Intercept)	2.12	1.02	2.07	0.0432
	Body mass	0.124	0.122	1.02	0.313
	Carnivore	1.8	1.32	1.36	0.179
	Detritivore	-1.54	18.3	-0.0843	0.933
	Omnivore	0.309	1.99	0.155	0.877
	Body mass:Carnivore	0.186	0.364	0.512	0.611
	Body mass:Detritivore	-0.0686	2.73	-0.0252	0.98

Variable	Term	Estimate	Standard error	Statistic	p-value
log C/N	Body mass:Omnivore	-0.161	0.486	-0.331	0.742
	(Intercept)	2.32	0.312	7.43	2.09E-09
	Body mass	-0.131	0.0327	-4.02	0.000215
	Carnivore	-0.93	0.454	-2.05	0.0462
	Detritivore	0.958	0.914	1.05	0.3
	Omnivore	-0.0976	0.533	-0.183	0.856
	Body mass:Carnivore	0.114	0.074	1.54	0.131
	Body mass:Detritivore	0.168	0.0903	1.86	0.0691
	Body mass:Omnivore	0.256	0.122	2.1	0.0414
log C/P	(Intercept)	3.85	0.576	6.67	4.44E-07
	Body mass	-0.24	0.0664	-3.61	0.00128
	Carnivore	-0.34	0.951	-0.358	0.724
	Detritivore	-1.55	9.27	-0.167	0.869
	Omnivore	-1.17	1.15	-1.02	0.317
	Body mass:Carnivore	0.285	0.245	1.17	0.254
	Body mass:Detritivore	-0.103	1.38	-0.075	0.941
	Body mass:Omnivore	0.236	0.275	0.858	0.399
log N/P	(Intercept)	1.13	0.467	2.42	0.0197
	Body mass	-0.102	0.0557	-1.83	0.074
	Carnivore	0.712	0.643	1.11	0.274
	Detritivore	1.67	8.37	0.2	0.842
	Omnivore	-0.373	0.909	-0.41	0.684
	Body mass:Carnivore	0.193	0.179	1.08	0.287
	Body mass:Detritivore	0.247	1.24	0.198	0.844
	Body mass:Omnivore	-0.0597	0.222	-0.269	0.789

Table B.2: ANCOVA model components with C, N, P and stoichiometric ratio as the response variable and body mass and diet as explanatory variable in non-mammals. The reference diet is herbivore. Body mass were log-transformed and centered

B.3 Mammals absorption efficiency and diet nutrient content: model comparison

We checked that the model fitted on fig.2.5 indeed improved variance explained compared to a linear model. For both N and P, these non-linear fits had lower AIC than the linear approaches, showing that this relationship was non-linear.

Element	Model	N	sigma	log likelihood	AIC	BIC	Deviance	df residual
N	linear	2487	19.0682355	-10859.6351	21725.2703	21742.7268	903540.046	2485
	non-linear	2487	18.8374397	-10829.3496	21664.6993	21682.1558	881800.098	2485
P	linear	193	28.9566758	-922.449469	1850.89894	1860.68701	160151.413	191
	non-linear	193	26.4738915	-905.14861	1816.29722	1826.08529	133865.583	191

Table B.3: Goodness of fit of the non-linear regression given in fig.2.5. The linear model estimates intercepts and slope, non-linear models estimate E, the constant of egestion, and k, the maximal absorption efficiency. For both N and P, the non-linear models have lower Akaike information criteria (AIC).

C

Details on the relationship between intake and chemical balance

The following figures and graphs provide details of the methods (table C.1 and fig.C.2) and some supplementary results (fig. C.9 - C.7). You will find the ingredients (table C.1) and the measured elemental composition (fig. C.7) of food. The fresh body mass of larvae at the onset of the treatment period is given for each week of the experiment in fig.C.2. As growth rate is dependent on initial body mass, it was essential to make sure that starting body mass was overall similar among temporal blocks. Despite small variations, all larvae were in the same larval stage (L6), ensuring an overall similar growth pattern. The absorption of elements provided in the main text fig.3.4 are shown in separate panels in fig.C.4 showing for all elements, an increase of absorption at lower intake. The details of body and frass elemental compositions are shown in fig.C.5 and C.6, respectively. Larvae C content is increased at higher intake, whereas all other nutrient contents are decreased. All measured nutrient contents are decreased at lower intake in the frass, suggesting an increase of either O or H at low intake (not measured). The relative content of each element in food, body and frass is shown in fig.C.7. Body is richer in all elements but Ca at low intake. We also highlight the decrease in relative fluxes devoted to maintenance as intake decreases (fig.C.9) which, as said in the model box in chapter 2, might motivate

some changes in the model.

C.1 Experimental controls

Ingredient	Mass fraction % m/m
Deionized water	76.7
Soja meal	6.79
Corn flour	6.79
Germalyne	3.40
Yeast	2.55
Agar	1.20
Casein	7.19E-01
D-Glucose	6.01E-01
Ascorbic acid	5.10E-01
Benzoic acid	2.69E-01
Linseed oil	1.92E-01
Nipagin	1.16E-01
Choline chloride	5.41E-02
Formaldehyde	3.60E-02
Alpha-Tocopheryl acetate	1.59E-02
Actitetra (Oxytetracycline 50%)	9.59E-03
Ampicillin sodium salt	7.19E-03
Myo-inositol	3.61E-03
Nicotinic acid	3.21E-03
Menadione	1.62E-03
Retinyl acetate	1.30E-03
Riboflavin	7.21E-04
Pyridoxine	7.21E-04
Thiamine hydrochloride	7.21E-04
Ergocalciferol	9.02E-05
Folic acid	6.49E-05
Biotin	1.44E-05
Cobalamin	9.74E-07

Table C.1: Composition of food distributed to larvae in mass fraction. Ascorbic acid is vitamin C, Nipagin™ is a broad-spectrum antimicrobial agent. Alpha-tocopheryl acetate is a vitamin E acetate. Oxytetracycline is a broad-spectrum tetracycline antibiotic. Nicotinic acid is a vitamer of vitamin B₃. Menadione is a vitamin K₂ precursor. Retinyl acetate is a form of vitamin A. Riboflavin is vitamin B₂. Pyridoxine is a form of vitamin B₆. Thiamine is vitamin B₁. Ergocalciferol is vitamin D₂. Folic acid is vitamin B₉. Biotin is vitamin B₇ or vitamin H. Cobalamin is vitamin B₁₂.

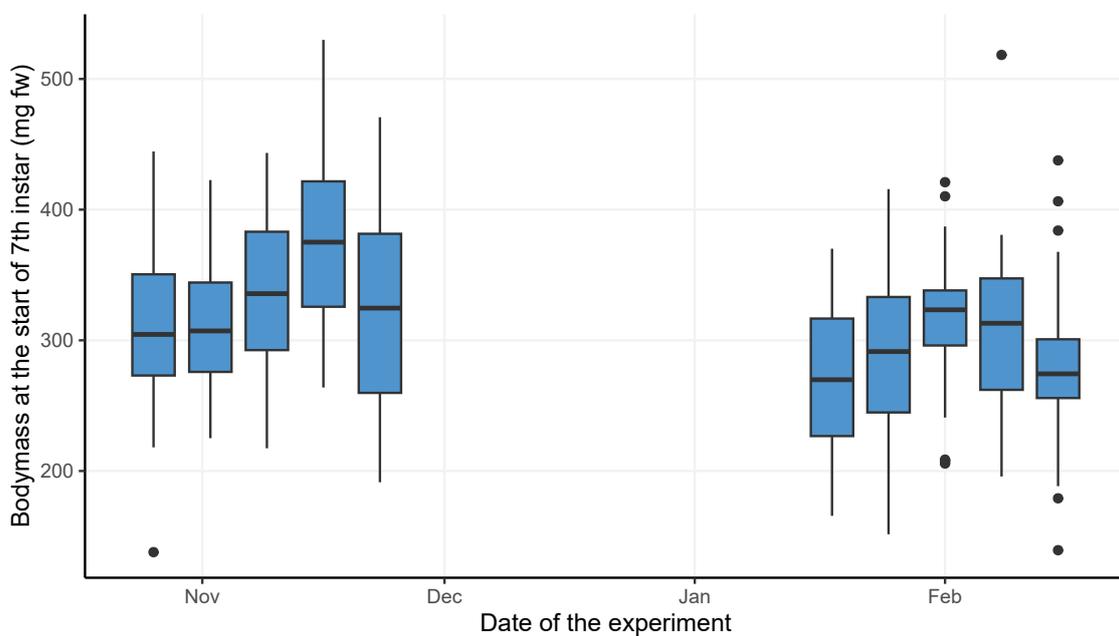


Figure C.1: Variation of larvae fresh body mass at the start of the experiment among the ten weeks of work. Each point represents an individual. At the start, larvae are at the very beginning of their seventh larval stage. Only one week (4) shows a slightly higher body mass than the expected 300 mg.

C.2 Nutrients dynamics during growth under constrained intake: supplementary figures

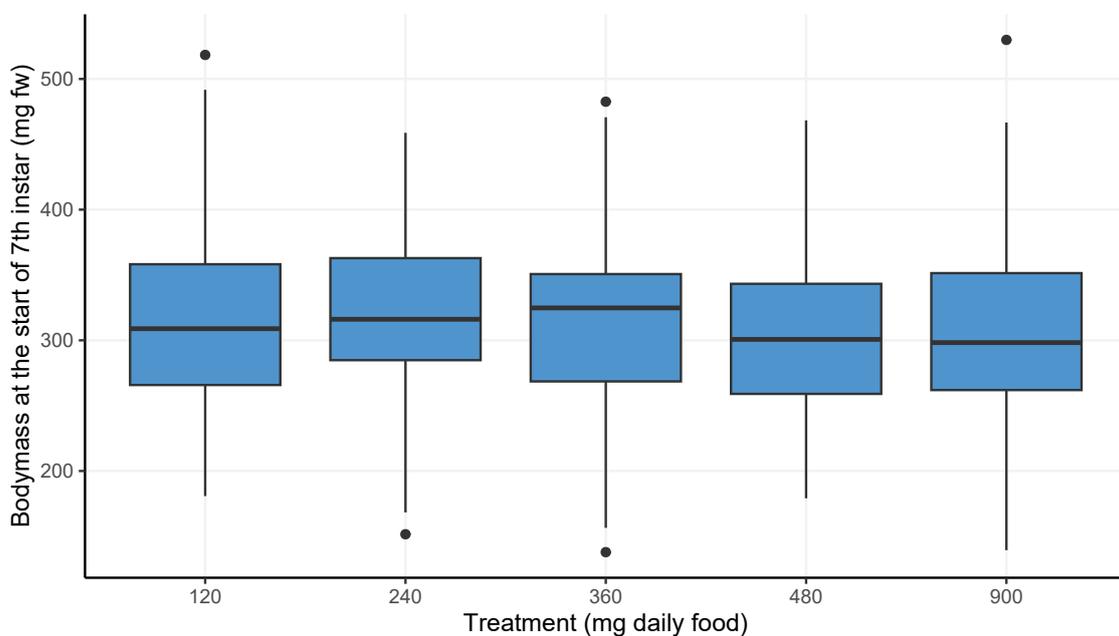


Figure C.2: Variation of larvae fresh body mass at the start of the experiment among the five treatments. Each point represents an individual. At the start, larvae are at the very beginning of their seventh larval stage. F-test shows that there was bodymasses did not differ between treatment (p-value = 0.3022).

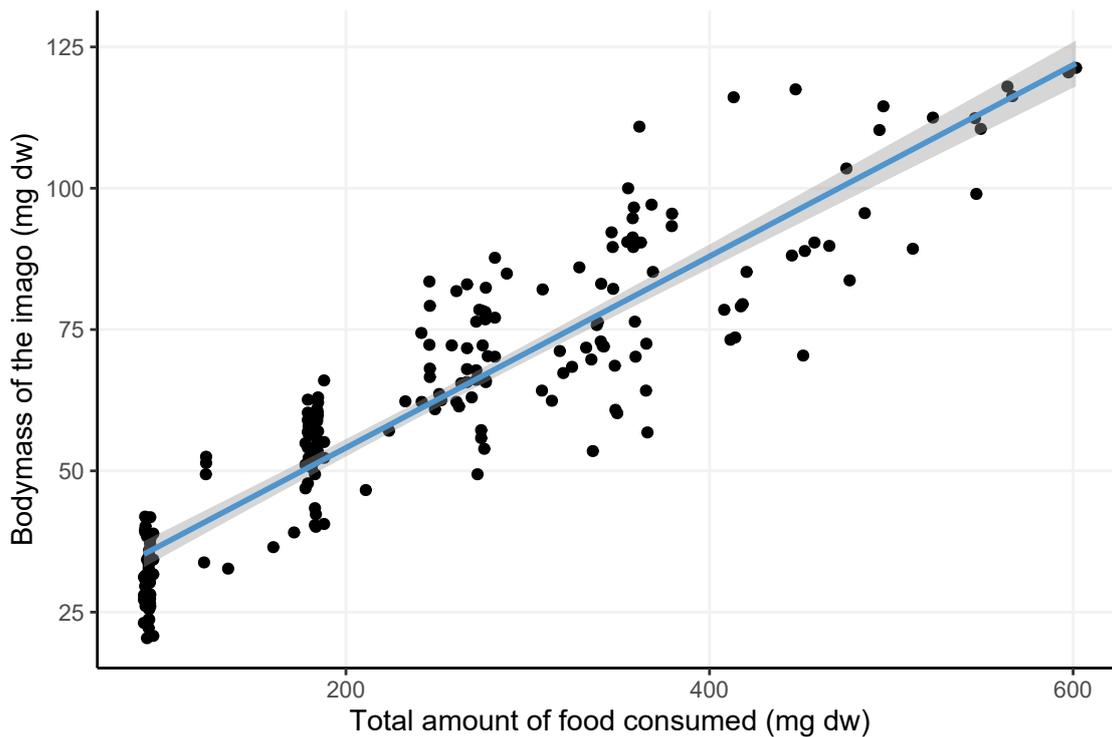


Figure C.3: Variation of adult body mass according to food consumed during the experiment. Each point represents an individual.

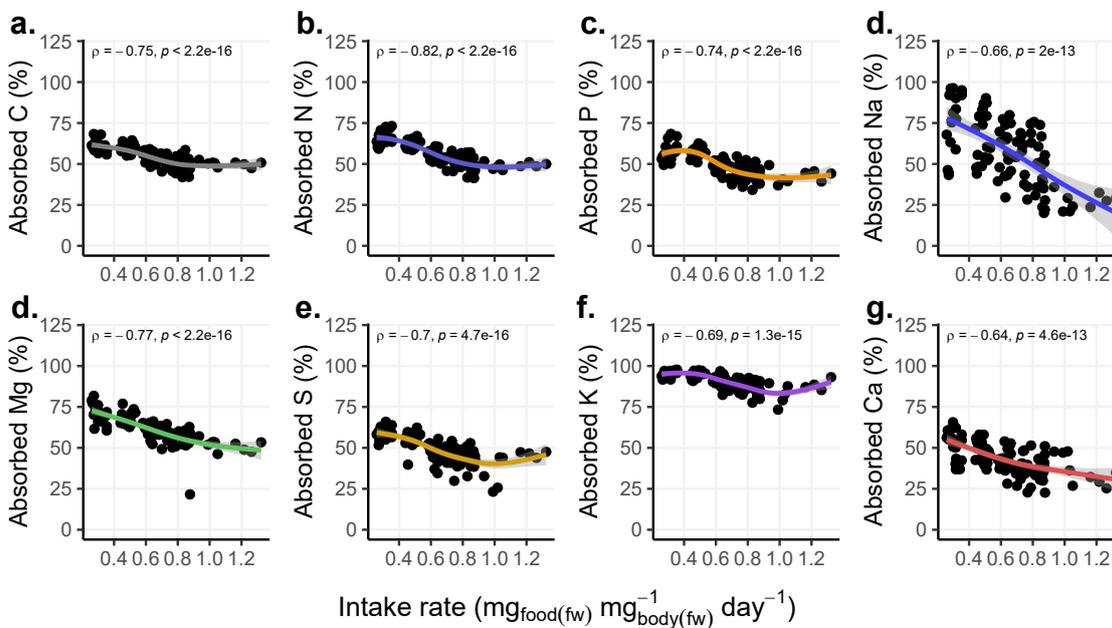


Figure C.4: Absorption efficiencies of the eight tested elements as a function of mass-specific intake rate. Each point is a measurement done on four larvae. Lines are linear models, ρ are correlation coefficients and the p-value associated with the correlation test is shown.

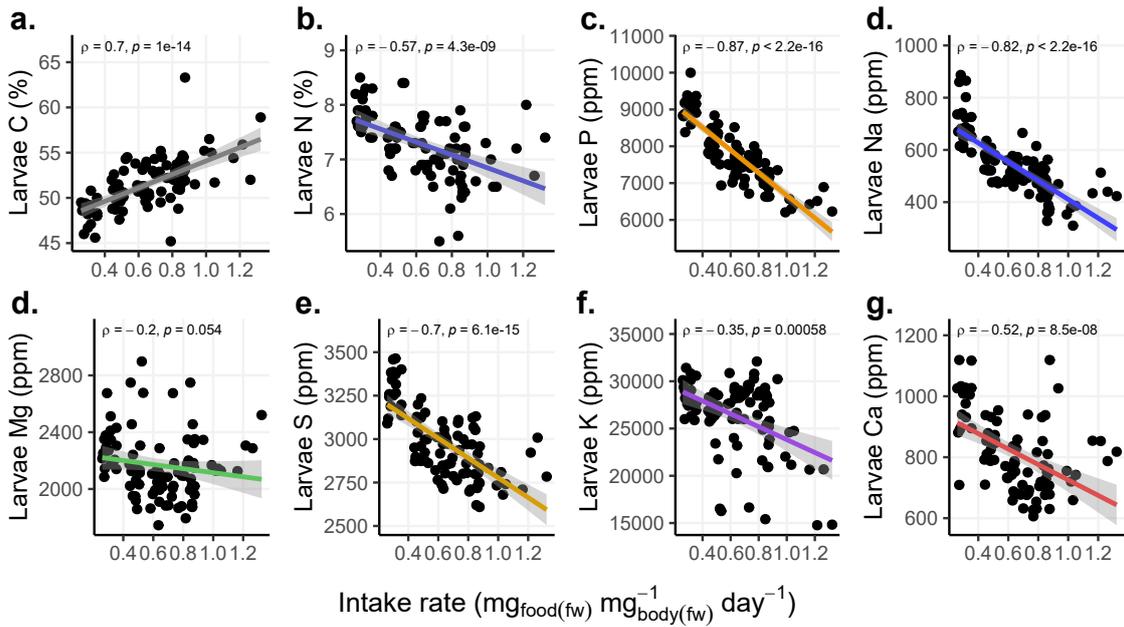


Figure C.5: Body content in the eight tested elements as a function of mass-specific intake rate. Each point is a measurement done on four larvae. Lines are linear models, ρ are correlation coefficients and the p-value associated with the correlation test is shown.

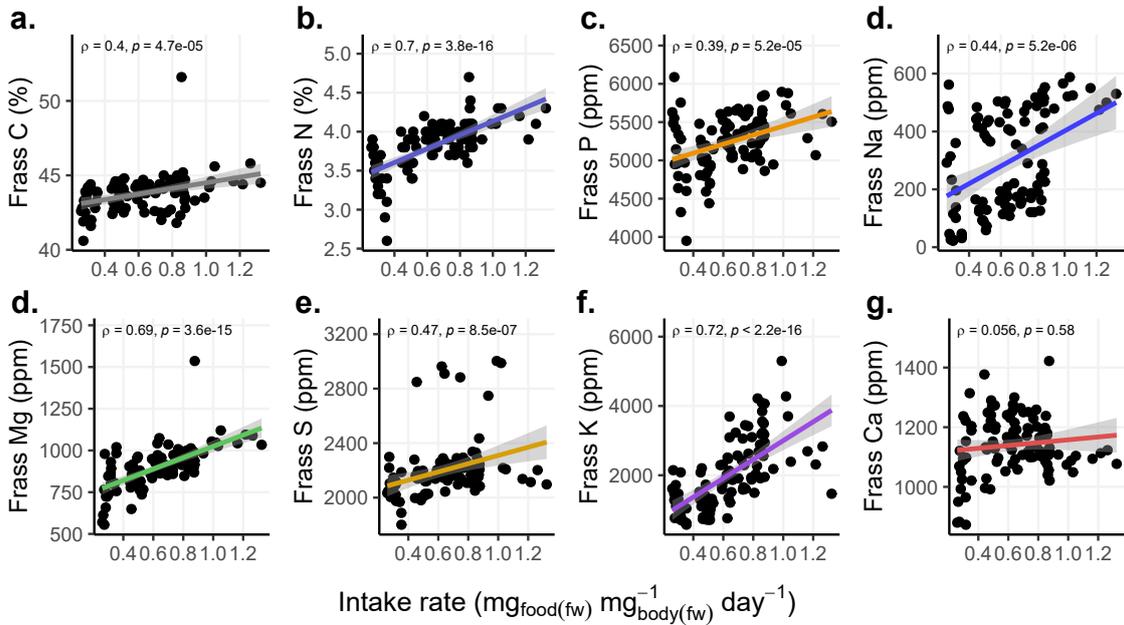


Figure C.6: Frass (egestion) content in the eight tested elements according to the mass-specific intake rate. Each point is a measurement done on four larvae. Lines are linear models, ρ are correlation coefficients and the p-value associated with the correlation test is shown.

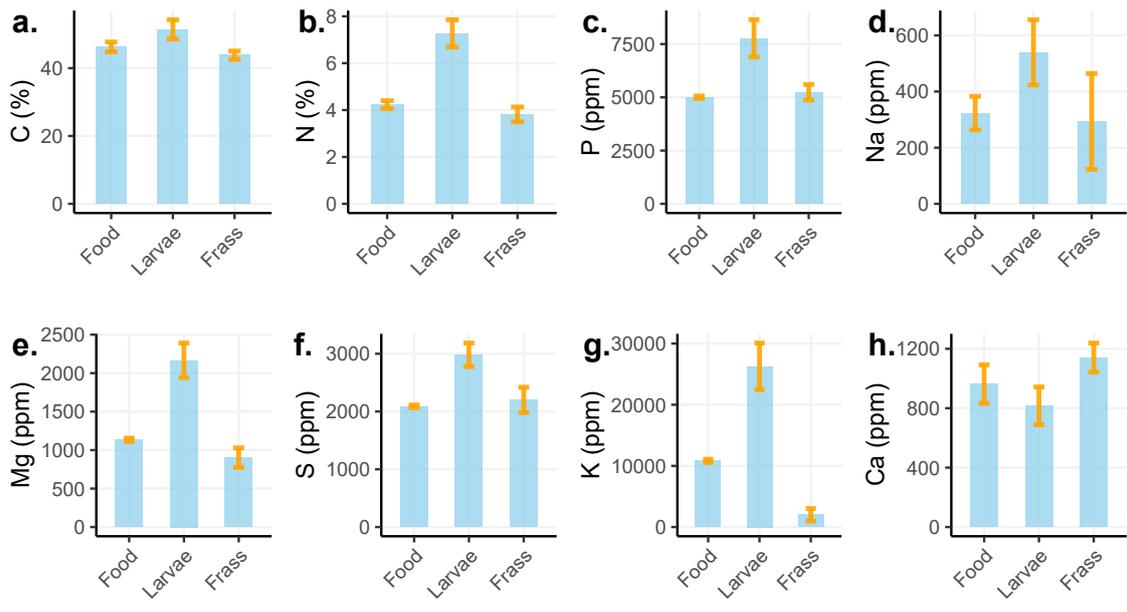


Figure C.7: Differences in content between food, larvae (all conditions) and frass in the eight elements.

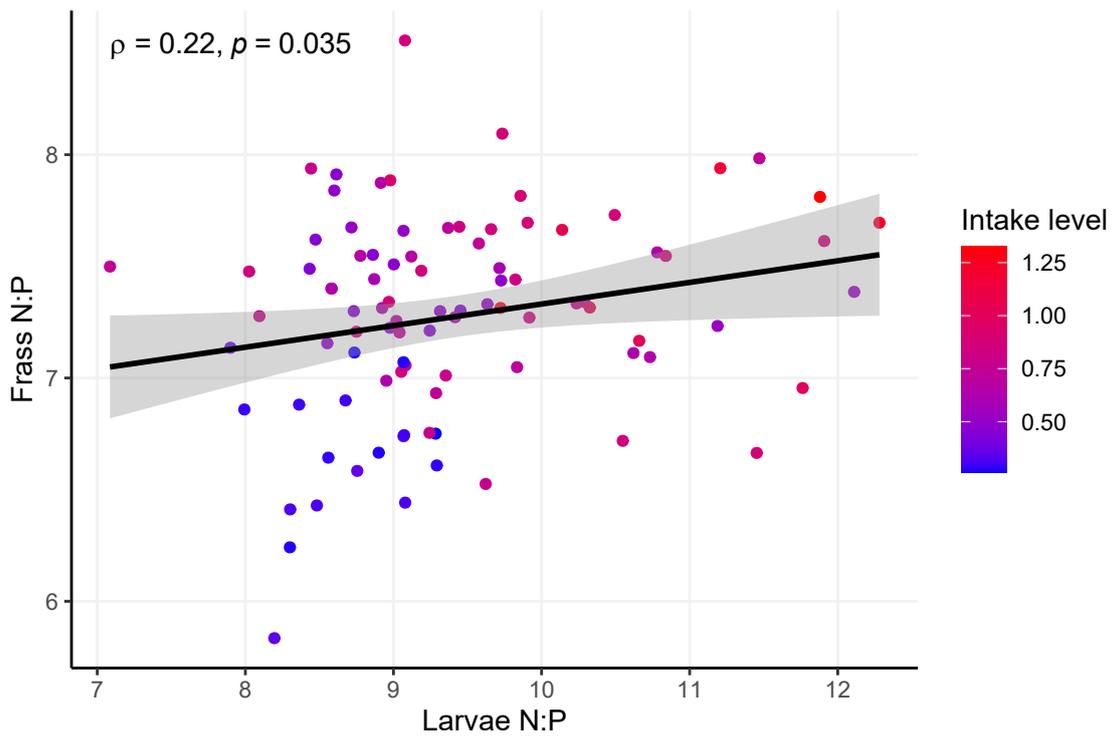


Figure C.8: Relationship between larvae and frass N/P. Each point represents a group of four larvae. The regression line represents a linear model, ρ is the correlation coefficient and the p-value associated with the correlation test is shown. In colour is shown intake level measured as mass-specific intake rate ($\text{mg} \times \text{mg}^{-1} \times \text{day}^{-1}$ in fresh weight).

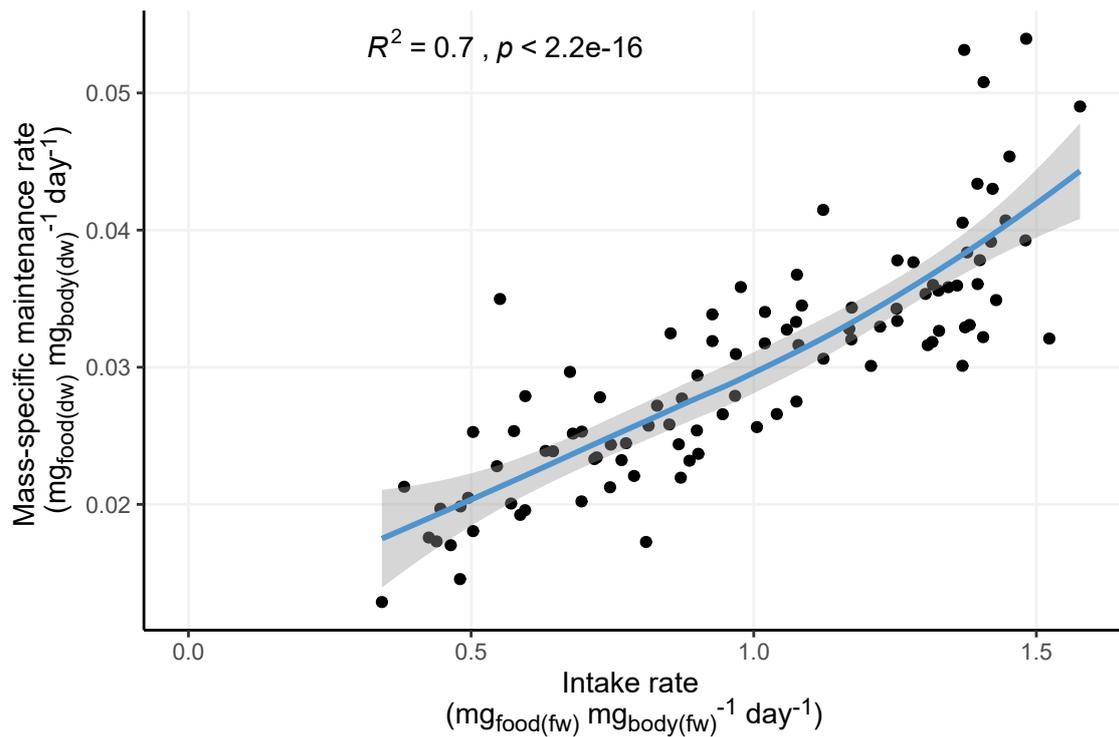


Figure C.9: Mass-specific maintenance rate according to mass-specific intake rate. Each point represents an individual. Note that the maintenance flux is calculated as the difference between absorption and growth. It can occur that we measure absorption over a slightly shorter period of time than the growth process. However, in this particular situation, the larvae had entered the pre-pupal stage, and as a result, their growth had halted since the measurements of absorption ceased.

D

Model derivation: relationships between mass fluxes during absorption and growth

Assumptions

To survive, the organism requires the maintenance flux M to be met. To meet this minimal requirement, the organism intakes resources at the flux I , the absorption at the flux A , and egest with the rate E .

We have that:

$$I = A + E$$

I , A and E are expressed as $\frac{[M]}{[T]}$

We hypothesize that the absorption rate A increases with intake rate I but adapts to low intake rates imposed by resource scarcity by increasing. We want a positive, decreasing function of I with a y -intercept of A_0 and a sensitivity to I of k , we obtain the following function:

$$\frac{dA}{dI} = A_0 \frac{k}{k + I}$$

with $0 < A_0$ an absorption rate sensitive to starvation. We have the following:

$$\frac{dA}{dI}(I = 0) = A_0$$

$$\lim_{I \rightarrow +\infty} \frac{dA}{dI} = 0$$

Integration

Upon integration, we obtain

$$A(I) = A_0 k \ln(I + k) + C$$

We have:

$$A(I = 0) = 0 = A_0 k \ln(k) + C$$

$$C = -A_0 k \ln(k)$$

We obtain:

$$A(I) = A_0 k \ln \frac{I + k}{k}$$

Conditions analysis

An important condition is that $A < I$ because absorption can not be greater than ingestion. There is, therefore, a constraint on A_0

$$A_0 k \ln \frac{I + k}{k} < I$$

To investigate this condition, let us have $k = I$. The condition becomes:

$$A_0 < \frac{1}{\ln 2}$$

For $k = 2I$

$$A_0 < \frac{1}{2 \ln \frac{3}{2}}$$

As we increase n in $k = nI$, we approach 1, since

$$\lim_{n \rightarrow +\infty} n \ln \frac{n+1}{n} = 1$$

Therefore, we have $0 < A_0 < 1$.

Absorption efficiency depends on intake rate

Absorption efficiency is defined as $A_e = \frac{A}{I}$ and depends on I :

$$\frac{A}{I} = \frac{A_0 k}{I} \ln \frac{I+k}{k}$$

When $I = 0$, we determine the limit of the function using l'Hopital's rule.

$$\lim_{I \rightarrow 0} A_e = A_0$$

We therefore have $0 < A_e < 1$

Growth efficiency depends on intake rate

Growth efficiency is defined as $G_e = \frac{A-M}{I}$ and depends on I by. Let us have the maintenance cost also depend on I :

$$M(I) = aI + M_0$$

$$G_e = \frac{A-M}{I} = \frac{A_0 k}{I} \ln \frac{I+k}{k} - \frac{aI + M_0}{I}$$

$$G_e = \frac{A-M}{I} = \frac{A_0 k}{I} \ln \frac{I+k}{k} - a - \frac{M_0}{I}$$

$$G_e = \frac{1}{I} (A_0 k \ln \frac{I+k}{k} - M_0) - a$$

This last equation is used in chapter 2 in the fit of growth efficiency.

E

Supplmentary material for the isotopic analyses

E.1 Isotope absorption efficiencies ratio (IAER) and C_{Ejk} / C_{Ijk} calculation

Mass spectrometer usually directly gives isotopes ratio rather than isotopic content because usually, one of the isotopes has a low concentration. Still, it is possible to compute the isotope content of egestion C_{Ejk} and intake C_{Ijk} . For carbon, ignoring the very low concentration in unstable isotopes, we have that the total carbon content is equal to the sum of the content of each stable isotope. So that, for sample s :

$$C_s = {}^{13}C_s + {}^{12}C_s$$

On the other hand the isotopic data are usually given in delta notation:

$$\delta^{13}C_s = 1000 \left[\frac{^{13}C_s/^{12}C_s}{^{13}C_{PDB}/^{12}C_{PDB}} - 1 \right]$$

We have thus two unknowns, $^{13}C_s$ and $^{12}C_s$, as well as two equations, enabling us to solve for the two isotopes content:

$$\begin{aligned} \frac{^{13}C_{PDB}}{^{12}C_{PDB}} \left(\frac{\delta^{13}C_s}{1000} + 1 \right) &= \frac{^{13}C_s}{^{12}C_s} \\ \frac{^{13}C_{PDB}}{^{12}C_{PDB}} \left(\frac{\delta^{13}C_s}{1000} + 1 \right) (C_s - ^{13}C_s) &= ^{13}C_s \\ ^{13}C_s &= C_s \frac{\frac{^{13}C_{PDB}}{^{12}C_{PDB}} \left(\frac{\delta^{13}C_s}{1000} + 1 \right)}{1 + \frac{^{13}C_{PDB}}{^{12}C_{PDB}} \left(\frac{\delta^{13}C_s}{1000} + 1 \right)} \\ ^{12}C_s &= \frac{C_s}{1 + \frac{^{13}C_{PDB}}{^{12}C_{PDB}} \left(\frac{\delta^{13}C_s}{1000} + 1 \right)} \end{aligned}$$

We have that $\frac{^{13}C_{PDB}}{^{12}C_{PDB}} \approx 0.0112372$, so, finally:

$$^{12}C_s = \frac{C_s}{1 + 0.0112372 \left(\frac{\delta^{13}C_s}{1000} + 1 \right)}$$

Using the isotopic content, we can compute the absorption efficiency of each isotope.

E.2 Justification of the choice of linear models

We predicted that growth experienced during a given period at a certain rate would affect the isotopic content of the organism, that is, taking the example of carbon, which also holds for nitrogen:

$$^{13}C_l = a.R + b$$

with $^{13}C_l$ the ^{13}C content in the larva, R the growth rate, a and b some constant, we should have $\delta^{13}C$ expressed as a function of growth rate R as follows:

$$\delta^{13}C_l = 1000 \left(\frac{c.a.R + b}{1 - a.R - b} - 1 \right)$$

which is a hyperbolic function of R (c here is the standard isotopes ratio constant). We should thus expect non-linearity. However, as $^{13}C_l$ is very low, and making the approximation that for $x \ll 1$, $\frac{x}{x-1} \approx x$ we can model this relation using a linear approach. We nevertheless tested for non-linearity by performing generalized additive models and examining the effective degree of freedom (edf). For the two trophic fractionations and C IAER, the EDF indicate a linear dependence, with EDF roughly between 1 and 2 (table E.1). We therefore chose to use linear models.

GAM formula	n	EDF	p-value	R^2
$\Delta^{13}C \sim s(\text{GR})$	92	2.03	<2e-16	0.368
$\Delta^{15}N \sim s(\text{GR})$	92	1	<2e-16	0.524
C IAER $\sim s(\text{MSIR})$	100	1	<2e-16	0.27

Table E.1: Generalized additive models results, with the sample size n , the effective degree of freedom (edf), p-value of the smooth term and the R^2 .

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