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Abstract

Residual biomass is acknowledged as a key sustainable feedstock for the transition towards circular and low fossil carbon economies to supply whether energy, chemical, material and food products or services. The latter is receiving increasing attention, in particular in the perspective of decoupling nutrition from arable land demand.

In order to provide a comprehensive overview of the technical possibilities to convert residual biomasses into edible ingredients, we reviewed over 950 scientific and industrial records documenting existing and emerging waste-to-nutrition pathways, involving over 150 different feedstocks here grouped under 10 umbrella categories: (i) wood-related residual biomass, (ii) primary crop residues, (iii) manure, (iv) food waste, (v) sludge and wastewater, (vi) green residual biomass, (vii) slaughterhouse by-products, (viii) agrifood co-products, (ix) C_1 gases and (x) others. The review includes a detailed description of these pathways, as well as the processes they involve. As a result, we proposed four generic building blocks to systematize waste-to-nutrition conversion sequence patterns, namely enhancement, cracking, extraction and bioconversion. We further introduce a multidimensional representation of the biomasses suitability as potential as nutritional sources according to (i) their content in anti-nutritional compounds, (ii) their degree of structural complexity and (iii) their concentration of macro- and micronutrients. Finally, we suggest that the different pathways can be grouped into eight large families of approaches: (i) insect biorefinery, (ii) green biorefinery, (iii) lignocellulosic biorefinery, (iv) non-soluble protein recovery, (v) gas-intermediate biorefinery, (vi) liquid substrate alternative, (vii) solid-substrate fermentation and (viii) more-out-of-slaughterhouse by-products. The proposed framework aims to support future research in waste recovery and valorization within food systems, along with stimulating reflections on the improvement of resources' cascading use.

Abbreviations

DAC, Direct air capture; DHA, Docosahexaenoic acid; DM, Dry matter; EC, Electrochemical cell; HB, Haber-Bosch process; HOB, hydrogen-oxidizing bacteria; LCA: Life cycle assessment; LPC, Leaf protein concentrate; MOB, Methane-oxidizing bacteria; MPF, Macronutrient-poor feedstuff; MRC, Macronutrient-rich concentrate; SSF, Solid-substrate fermentation; TC, Targeted compound; TSE, Transmissible spongiform encephalopathies; VFA, Volatile fatty acids; WW, Wastewater.

Keywords

residual biomass, biorefinery, circular economy, microbial protein, insect, novel food, alternative feed, bioeconomy

1. Introduction

The urgency to rethink the food system is increasingly attracting attention (IPCC, 2019; Searchinger et al., 2018; Willett et al., 2019). The current agrifood system consumes about 70% of the world's freshwater (Sims et al., 2017), is responsible for at least 80% of deforestation (Ramankutty et al., 2018), 30% of the overall energy consumption, annually generates an estimated 20-30% of the anthropogenic greenhouse gas emissions (Rosenzweig et al., 2020) and is currently depleting non-renewable phosphorous ores (Schoumans et al., 2015). One underlying flaw of the current agrifood system is its overall inefficiency (Alexander et al., 2017b). For example, Schramski et al. (2020) showed that today, roughly six calories of input energy yield just one calorie of consumable food-based energy. Projected climate trends combined with forecasted demographic changes (including overall population growth and its dietary preferences) depict a challenging picture for food production capacities in 2050. For instance, the World Resources Institute estimates that food demand will grow by 56% compared to 2010 levels, leading to an additional agricultural land twice the size of India for food production to keep apace with demand (Searchinger et al., 2018). On the other hand, Gerten et al. (2020) calculated that if the current agrifood system was to operate within the safe zone of all planetary boundaries, it would only feed 3.4 billion people. Yet, because food is not a luxury, it is vital to identify solutions to sustain the future food demand of the world's population.

There is consensus that resolving the food conundrum requires simultaneous actions aimed at regulating food demand and consumption, improving production efficiency and diminishing food losses (Billen et al., 2021; Clark et al., 2020; van der Goot et al., 2016). To achieve these goals, it is possible to sustainably intensify agriculture, increasing production while lowering environmental impacts (Hamelin et al., 2021; Pretty, 2018; Rockström et al., 2017). Moreover, the emerging digitalization of agrifood systems is foreseen to boost outputs, increase nutritional quality and enhance environmental performance (Herrero et al., 2020; World Economic Forum, 2018). Finally, the adoption of advanced technologies, such as biotechnology, can procure novel foods and feed ingredients, providing nutritional services comparable to those of current food- and feedstuffs (Alexander et al., 2017a; Ercili-Cura and Barth, 2021; Parodi et al., 2018; Torres-Tiji et al., 2020). The present study focuses on the latter strategy, and particularly on solutions allowing to loop residual biomasses back into the food chain, thereby decoupling food production from the demand of additional arable land. In this work, such solutions are generically referred to using the term "waste-to-nutrition", and "residual biomass" denominates both unused and underused biogenic wastes, residues and co-products.

Residual biomass is a constrained resource (Hamelin et al., 2019), and many streams are already supplying energy (e.g. via the biogas from anaerobic digestion), materials (e.g. woodchips panel) and food-related services, either indirectly through agronomic valorization (e.g. manure and straws used as organic fertilizers) or direct use in animal diets (e.g. meals from vegetable oil extraction) when feed standards are met (Mottet et al., 2017). Given the foreseen importance of residual biomass in future development narratives such as bioeconomy (Muscat et al., 2021), competing value chains for these streams are emerging (e.g. fine chemicals for cosmetics and pharmaceutics), prompting the need to ensure the implementation of the most efficient and cascading uses of these resources (Baldoni et al., 2021; Duque-Acevedo et al., 2020; Venkata Mohan et al., 2016). Valorization hierarchies constitute a useful framework to tackle this challenge (EC Directive, 2008; Teigiserova et al., 2020). These suggest to privilege pathways where functional properties (e.g. proteins) are safeguarded and directly valorized (e.g. into ingredients) before the implementation of lower-value cascading recovery pathways (e.g. nutrients or energy) (Garcia-Bernet et al., 2020; Gómez-García et al., 2021).

The potential of residual biomass to directly (i.e. not through an agronomic valorization) produce food and feed ingredients has already been explored for specific cases such as space travels (Clauwaert et al., 2017), agricultural catastrophes (Denkenberger and Pearce, 2015) or through livestock recycling (i.e. direct inclusion in farmed animal diets) (Rajeh et al., 2021; Van Hal, 2020; Van Zanten et al., 2019). Yet, to our knowledge, no comprehensive attempts have been made to collate data and identify the multiple conversion pathways that allow this. In an endeavor to fill this gap, the aim of the present work is to provide an extensive overview of current and emerging waste-to-nutrition pathways. Overall, 660 scientific papers and 270 records from industrial literature, including patents, were reviewed (review methodology available in Supplementing information; SI). The approach developed does not allow to directly conclude on the environmental or economic relevance of the reviewed value chains. Indeed, those aspects are beyond the scope of the present work and are context-specific, requiring specialized assessment methodologies (e.g. life cycle or cost-benefit assessments). Nevertheless, as a stepping stone, this work is the first to detail, classify and systematize in a single framework the main waste-to-nutrition pathways, facilitating their further comparisons.

2. Scope: ingredients and biomasses considered

The umbrella categories of residual biomasses considered in this study are illustrated in figure 1. The terminology used (i.e. waste, residue, co-product and by-product) for these categories, as well as throughout this study, is carefully chosen and based on the EU legislation as further detailed in the SI. The scope of categories is an expansion and harmonization of the streams described in Hamelin et al. (2019), also described in the SI and briefly reported here. The category “Wood-related residual biomass” shown in figure 1 includes primary forestry residues (defined in Karan and Hamelin, 2020), pruning residues, wood-processing wastes (e.g. sawdust) and some packaging waste (e.g. cardboard). The “Primary crop residues” category only includes straws, stalks and corn stover; tuber’s top fractions (e.g. potato leaves) are included within the “Green residual biomass” category along with garden- and park wastes (e.g. mowed grass). “Food waste” (discarded food stemming from households or the service sector such as restaurants, etc.) and “Manure” (including all types of livestock excreta, whether managed as slurry, solid or deep litter) are stand-alone categories. “Sludge” and “Wastewater” (WW) are grouped in a single category that includes streams coming from both industrial (e.g. potato WW) and municipal (e.g. sewage sludge) origins. The “Agrifood co-products” category encompasses streams from primary transformation (e.g. bran, pulp, peels, spent grains, etc.) and secondary transformation (e.g. fruit canning, bakery, etc.) of agrifood industries. Despite their frequent valorization as feed (Chapoutot et al., 2019), these co-products host upgrading valorization potentials (Garcia-Bernet et al., 2020) and are therefore included in the scope of waste-to-nutrition pathways. Because of their specific composition and of the regulation they are subjected to, “Slaughterhouse by-products” (e.g. feather, carcass, bristle, etc.) are gathered in a distinct category. Additionally, bioeconomy-related wastes (e.g. insect frass, digestates, etc.) and specific wastes not stemming from the food sector (e.g. scrap newspapers) are added under the category “Others”. Finally, nutrient looping pathways building on C_1 gaseous feedstocks (CH_4, CO_2) are considered given their potential to decouple food production from land use (Pikaar et al., 2018), whether these stem from a biogenic (e.g. resulting from biomass processing) or fossil origin.

Three general categories of ingredients supplying nutritional services are distinguished. The first category encompasses macronutrient-rich concentrates (MRC) that include energy- and/or protein-rich products, considered as high nutritional quality ingredients. The macronutrient-poor feedstuff (MPF) category includes cellulose-rich agricultural biomass (e.g. straw, grass, etc.) commonly used in animal husbandry as fodder and roughage (Dale et al., 2009). The third category of ingredients, referred to as targeted compounds (TC), are simple molecules used as additives to balance diets. These include a wide variety of compounds from minerals and vitamins to amino acids. For the purpose of this review, the term TC describes compounds that confer direct nutritional benefits. Consequently, functional additives such as antioxidants or enzymes are excluded.

For animals, the specific nutritional characteristics of MRC, MPF and TC are combined in formulations to furnish balanced meals, often referred to as compound feed. Formulation is performed based on precise knowledge of the animal's gut physiology, nutritional requirements, health needs, legislative constraints, and an endeavor to minimize the overall cost (Saxe et al., 2018). In the case of animals farmed for human consumption, optimization also includes specific performance parameters (e.g., carcass lean meat, milk yield, feed conversion ratio, etc.). On the other hand, human food is mainly restricted to MRC and TC, even if the inclusion of ingredients in human diets also depends on cultural and social habits (Teigiserova et al., 2020), with consumer acceptability being a key factor in relation to the commercialization of novel food ingredients (Aschemann-Witzel and Peschel, 2019; Rumpold and Langen, 2020). This present review does not explicitly address consumer acceptability (figure 1), although it is reported when the issue is raised in the literature. Similarly, regulation aspects related to the entry of specific streams into food- and feed-related markets are not specifically covered in this work.

Figure 1. Scope of the literature review

Residual biomass categories, here illustrated by icons, are further detailed in the SI. Agronomic valorization (e.g. as fertilizer) is not part of the scope as this study focuses on the direct recovery of edible ingredients only.

3. Bridging the gap between waste and nutrition

From a physicochemical perspective, a resource is considered as a food or feed ingredient when its "composition-structure characteristics" (Axelos et al., 2020) enter the safety perimeter of the digestive tract, i.e. when the nutrients contained within the ingested ingredients are released and assimilated without adverse effects. This safety perimeter is determined by the inherent features of digestive tracts and thus varies across different species (Godon et al., 2013). The edibility, or nutritional quality of an ingredient is multidimensional, but is often characterized by three main factors: (i) the absence of anti-nutritional compounds, (ii) the degree of structural complexity (i.e., biodegradability) and (iii) the concentration of macro- and micronutrients. These determine to which extent an ingredient can be considered as food grade (figure 2).

The term anti-nutritional compound refers to a substance that may damage the organism or prevent (or severely diminish) proper nutrient absorption (Makkar, 1993). These are quite variable in nature, ranging from heavy metals to plants secondary metabolites and mycotoxins (Salami et al., 2019). Generally, (human) food regulations explicitly require exhaustive proof of the absence of anti-nutritional compounds in novel ingredients (EFSA Panel on Dietetic Products, Nutrition and Allergies (NDA), 2016).

Structural complexity is particularly prevalent in fibrous biomass, such as lignocellulose or keratin. These structures are highly robust and resist the chemical and enzymatic reactions of common digestive processes. Therefore, the ability of monogastric animals to degrade MPF is quite limited, while the multiple intestinal tracts of ruminants (and termites gut microbiomes) are adapted to the digestion of cellulose-based structures (Godon et al., 2013). However, even ruminants only display very limited ability to digest lignin (Chapoutot et al., 2010; Moore and Jung, 2001) which constitute a highly resistant, hydrophobic barrier that survives most biodegradation processes (Triolo, 2013).

Finally, the nutritional quality of an ingredient is shaped by the presence and quantity of digestible nutrients such as proteins, lipids and carbohydrates, often correlated with the absence of structurally complex macromolecules, anti-nutritional compounds, inorganic compounds (e.g., ashes) and moisture. The latter particularly affects the stability of the nutritional quality over time, given the interrelation between moisture levels, fermentable compounds and microbial growth (Teigiserova et al., 2019).

As illustrated in figure 2, most residual biomasses cannot be considered as food grade. Anti-nutritional factors often arise because of increased heterogeneity and/or biological activity (e.g. in food waste) when not intrinsically linked to the feedstock (e.g. activated sludge hosting toxic organic and inorganic substances, see section 5.3.2.). Moreover, streams from agricultural and forestry activities (primary crop residues, wood-related and to some extent green residual biomass) are rich in lignin, cellulose and hemicellulose, which together form composite, recalcitrant matrices that are incompatible with direct edibility. Accordingly, to bridge the gap between waste and nutrition, pathways require to implement a sequence of operations that breakdown structural barriers, remove noxious compounds and, if required, enrich the assimilable nutrient content. In other words, the initial composition-structure (i.e. position in figure 2) are defining properties that not only determine the direct nutritional value of waste, co-products and residues, but also determine their technical and economic potential as nutritional sources.

Fig. 2. Waste-to-nutrition gap

Ternary diagram representing food grade quality perimeter (gray right corner), and approximating relative location of the studied solid residual biomass streams (colored circles). Phenolic lignin acts as both structural complexity and anti-nutritional proxies, but the latter is here privileged to differentiate wood-related residual biomass from green residual biomass and primary crops residues. MPF ingredients perimeter is not represented for tractability reasons. For the same reason, agrifood co-products and slaughterhouse by-products are gathered within the same broad circle (dotted line).

*Albeit some slaughterhouse by-products (e.g. offal) are directly edible (within the gray right corner), others are mainly composed by keratin which is here considered as structural content (top corner), see section 5.2.2. Background data is available in the SI database and icons are as defined in figure 1.

4. Describing waste-to-nutrition pathways using four building blocks

The systematic analysis of reviewed literature (see database in SI) revealed that the series of unit operations and processes implemented in waste-to-nutrition pathways vary according to two main considerations: (i) the degree to which the feedstock input composition-structure is altered, and (ii) the targeted nutrient recovery ratio (i.e., input versus desired output). These are represented as a scale gradient in the X-Y axis of figure 3. Along this scale, four generic processes are proposed as pathway building blocks: (i) enhancement, (ii) cracking, (iii) extraction and (iv) bioconversion. These are one key result arising from the transversal interpretation of the present review, and were defined with the aim to provide an interpretative framework highlighting common trends in waste-to-nutrition pathways. In fact, conversion pathways can be described as a sequential workflow of processes using these modular building blocks. Notably, the four building blocks proposed herein are in line with previous classification works (Colonna, 2020). Importantly, these blocks do not relate to specific technologies, but rather reflect the main macroscopic changes resulting from a set specific process when applied on a feedstock or product. Finally, the modular block representation (e.g. similarly used in Verstraete et al. 2016) reveals how different unit operations can be combined to generate varying degrees of nutritional quality and process intensity.

4.1. Enhancement: low composition-structure change, high nutrient recovery

Nutritional enhancement refers in this study to the application of one or several unit operations to augment the accessibility, preservation or quantity of nutrients, without the removal of any components. Accessibility is mostly increased by inducing structural changes that render the nutrient more attainable (i.e. macro-fractionation), whereas preservation is usually achieved through stabilization (e.g. water removal, homogenization, etc.). Nutrient enrichment can be realized using methods such as solid substrate fermentation (SSF). In this case, nutrient enrichment is mainly the result of either the partial degradation of fibers, the development of microbial proteins (e.g. mycelium colonization), or both.

Albeit minor losses might occur (typically ranging between 5-30% of the dry matter during ensiling (Borreani et al., 2018) or other SSF (Castoldi et al., 2014; Rajesh et al., 2010)), enhancement processes recover a major share of the initial nutrients in the final product, while safeguarding the global composition-structure characteristics. Indeed, modifications are generally limited to the macro- and mesoscopic scales (e.g. for comminution or drying), although some impacts at the microscopic scale are possible. The latter particularly applies for SSF as this process is based on microflora activities, hence generating microscopic changes (e.g. lignin mineralization). However, these induced changes remain partial and limited provided that the fermentation process is stopped before significant quantities of nutrients are converted. When this condition is fulfilled, the product displays compositional and structural properties that resemble that of the feedstock residue (e.g., ensiled grass versus raw grass), and therefore enters the enhancement building block.

4.2. Cracking: high composition-structure change, high nutrient recovery

Through the literature reviewed, the release of nutritional compounds entangled in extremely recalcitrant structures and/or locked chemically into macromolecules (e.g., glucose in cellulose) are only achieved through biomass deconstruction, hereafter referred to as cracking (Axelos et al., 2020). Cracking requires several process steps. It typically involves a first physico-mechanical pretreatment (e.g., hydrothermal, steam-explosion) which denatures organized macromolecular networks. Afterwards, macromolecules are subjected to some degree of lysis (e.g., enzymatic, hydrothermal, chemical), thus yielding smaller platform molecules (Farmer and Mascal, 2015) and unleashing chemical functions (Colonna, 2020; De Jong et al., 2020). Although the removal of nutrients is not a desired outcome of cracking processes, minor losses do occur. In recent examples, cracking led to the recovery of 73% of amino acids present in bristle keratin (Falco et al., 2019), while commonly more than 90% of sugars are recovered from wood-based cellulose (Wyman et al., 2009).

4.3. Extraction: low composition-structure change, low nutrient recovery

Extraction includes all unit operations and processes that selectively solubilize and/or separate a target fraction from a matrix, while safeguarding its initial functional properties (Jimenez et al., 2015). Some extraction processes are hybrid, combining the features of both extraction and cracking processes (e.g., alkaline extraction). However, extraction processes differ from cracking in as much that the targeted compound or fraction is not necessarily a structural component of the feedstock and is generally a minor fraction (e.g., proteins in tomato seeds). Unlike cracking, extraction does not induce generalized molecular-scale disruptions (Gençdağ et al., 2020; Rodriguez-Lopez et al., 2020). Extraction often involves a sequence of separation processes (e.g., precipitation and filtration) and isolation processes, all included within the extraction building block.

According to the literature reviewed, the recovery potential of an extraction step is limited by (i) the amount of the targeted TC available in the feedstock and (ii) the maximum achievable yield using the extraction technique. The latter is heavily dependent on the compound-structure interactions and inversely correlated to the desired purity (Colonna, 2020; Tamayo Tenorio et al., 2018). For example, considering proteins present in green residual biomasses (<20%DM), only a fraction (5-45% of total) is recovered using the extraction techniques described in section 5.3.3. (Santamaría-Fernández and Lübeck, 2020). Similarly, all common downstream separation and purification processes used to obtain TC such as valuable fatty acids (e.g. docosahexaenoic acid: DHA) compliant with market specifications imply mass and nutrient losses. For example, in weight terms, 1 to 15 units of DHA is obtained per 100 units of microalgae or aquatic protists (Russo et al., 2021; Xiangping et al., 2019). The reviewed literature often highlighted this particular point: extraction processes typically generate significant quantities of side streams whose synergetic valorization is key to ensure economic sustainability (Teekens et al., 2016).

4.4 Bioconversion: high composition-structure change, low nutrient recovery

Both microorganisms and animals retain and concentrate the nutrients they ingest, integrating them into a variety of products, including their own cellular or body mass. This is achieved through bioconversion, which refers in this study to the conversion of feedstocks into nutritional ingredients using the metabolic processes of living organisms. Bioconversion yields a relatively low nutrient recovery, intrinsic to the fact that part of the feedstock is converted to non-edible biomass or oxidized to gases instead of being recovered in the edible product (i.e., meat, mushroom, etc.). Major losses are due to respiration (carbon-rich gases), nitrogen-rich excretions and heat (El Abbadi and Criddle, 2019; Parodi et al., 2020; Wirsenius, 2000). To provide concrete examples, a benchmark of bioconversion efficiency figures was derived from the literature review, including both livestock, insects and microorganisms-related products (background data in SI). It indicates that even for optimized species and farming conditions, hardly more than 50% and 30% of respectively proteins and calories invested as feedstuff are recovered within animal-based food products. Reported values are slightly higher for insect farming in ideal conditions, yielding up to 70% of proteins recovery and 30% for calories recovery into insect biomass. Finally, benchmarked values for edible microorganisms, despite being highly dependent on specific strain, culture conditions and metabolic pathway, suggest that their energy conversion into edible calories ratio is generally below 30-40%. The aforementioned values illustrate the highest bioconversion efficiencies encountered; however, it should be highlighted that these efficiencies are closely tight to the nutritional quality of input feedstock. Bioconversion efficiencies shrink rapidly as the input feedstock's nutritional quality (or nutrient availability) decreases (details in SI).

For convenience, microbial and farmed animal bioconversion sub-groups are further distinguished. Microbial bioconversion encompasses the use of microorganisms both as biocatalysts that produce enzymes and nutritional TC such as vitamins, amino acids or flavor compounds (Specht and Crosser, 2020; Sun et al., 2021; Yang and Xu, 2016), and as final standalone nutritional MRC themselves. Currently, this latter function is encountering renewed interest, especially regarding so-called “single cell proteins” i.e., microbial proteins and fungal proteins (Ciani et al., 2021; Hüttner et al., 2020; Linder, 2019; Singh et al., 2020; Tubb and Seba, 2019) which cover organisms that generate high protein (up to 70-75%DM) content (Pikaar et al., 2018). Similarly, single cell oils (Ochsenreither et al., 2016) and all microbial-based fermentation and cell-culturing aiming at substituting common food products (Crosser et al., 2019; Lv et al., 2021; Specht and Crosser, 2020) are also considered within this bioconversion building block.

Farmed animal bioconversion refers to the use of livestock to produce food from non-edible biomass (Boland et al., 2013; Smith et al., 2013). This includes ruminants (e.g., that convert lignocellulosic biomass into milk), but also monogastric livestock (e.g., swine) whose potential role in upcycling residual biomass into foodstuff is also highlighted in the literature reviewed (ten Caat et al., 2021; Van Zanten et al., 2019). The use of insect (entomo-) farming as waste-to-nutrition bioconversion strategies is also part of this sub-category.

Fig. 3. Waste-to-nutrition pathways in four building blocks

Four generic families of conversion processes, illustrated with examples from the literature. Icons represent residual biomass categories as defined in figure 1 From top-down and left-right: (i) Fermented olive press-cake as fodder. (ii) Brewer’ spent grains milled into bakery flour. (iii) Extraction of proteins from grass. (iv) Carbohydrates recovery from organic wastewater. (v) Recovery of cellulosic sugars. (vi) Feather processed with keratinases releasing amino acids. (vii) Insects farming on food waste and (viii) Microalgae cultured on aquaculture wastewater.

5. Waste-to-nutrition pathways debunked

Each waste-to-nutrition pathway derived from the literature review is expressed as a combination of building blocks, representing the different process steps. Advantageously, this provides a means to detect common patterns among the different waste-to-nutrition pathways, while also representing their diversity. Most pathways are built upon a core conversion unit, with accessory units being usually referred to as pre- and post-treatments. The choice of these accessory units varies depending on the exact nature of the initial feedstock and the target nutritional market i.e., the waste-to-nutrition gap as defined in figure 2. Accordingly, in this section, waste-to-nutrition pathways are grouped on the basis of the common core building block. Each sub-section is illustrated with (i) a table reporting a selection of related examples from the literature and (ii) a figure representing the unit operations sequence pattern (table 1-3 and figure 5; other figures and tables available in SI).

5.1. Direct upgrading: nutritional enhancement pathways

Nutritional enhancement pathways upgrade residual biomass into food and feed ingredients using a single, or multiple enhancement steps, as illustrated in figure S1 of the SI. Concrete examples are provided in table 1.

For animal feed, enhancement pathways typically increase the digestibility of fibrous materials by disrupting the complex plant cell wall matrix and releasing macromolecular structures, such as polysaccharides in lignocellulosic feedstocks. In addition to breaking down structural barriers, enhancement strategies sometimes achieve a net nutritional enrichment of the feedstock. This is the case for ammonia-fiber expansion treatments increasing the total nitrogen content of ruminant forage (MPF), but also for SSF treatments provoking protein and/or lipid enrichment. SSF treatments are often applied after a first mechanical enhancement step. Used on lignocellulosic residual biomass, SSF allows to selectively degrade lignin while avoiding microbial polysaccharide consumption (e.g., using white rot fungi) (van Kuijk et al., 2015; Villas-Boas et al., 2002), and thus provides access to a wider range of lignocellulosic biomass for use as MPF. In the case of monogastrics, enhancement pathways are employed to substitute MRC, using residual biomass with low lignin content as feedstock for SSF aiming to convert part of the polysaccharide fibers into assimilable nutrients (e.g., free sugars and proteins) (Patil et al., 2020; Villas-Boas et al., 2002; Wongputtisin et al., 2014). Consequently, the product is characterized by higher nutrient availability and content and displays improved palatability. As conventional aquaculture uses high quality feed products (high protein and lipid digestibility), the inclusion of mildly treated fibrous materials is often avoided (Leduc, 2018). Nevertheless, SSF transformation units are used to generate alternative feed products for aquaculture, by improving digestibility of non-lignocellulosic feedstocks such as feather meal and isolated plant-based proteins (Dawood and Koshio, 2020; Hamidoghli et al., 2020).

For food markets, nutritional enhancement can be used to tailor organoleptic properties (e.g., texture, taste) of streams that are edible, but unappealing to consumers. These feedstocks mainly enter the agrifood co-products category (e.g., apple pomace, bakery surplus) (Gmoser, 2021; Sabater et al., 2020; Souza Filho, 2018). The combination of mechanical and/or SSF enhancement steps render these co-products suitable for direct consumption or for inclusion in processed food products (e.g., as flour) in bakeries, drinks or meat-alternatives (Torres-León et al., 2018), often with unlocked bioactivity properties (Leonard et al., 2021).

Table 1. Selection of inventoried nutritional enhancement pathways – reported with wording used by original references

Residual biomass	Barriers to direct edibility	Transformation units	Results	Final use	Status and references
Sunflower shell	High lignin content (50%DM)	Drying, milling, mixing	Unlock carbohydrates, added directly in pellets	Ruminant forage	Lab-experiment: (Osman et al., 2018)
Almond hulls	Total phenolics content (106g/kgDM)	3-5% urea solution moisturizing, covering for several weeks	Can substitute alfalfa in diets without adverse effects	Ruminant forage	Feeding trial: (Rad et al., 2016)
Sugarcane crop residues	Recalcitrance to digestion due to lignocellulose	Ammonia-fiber expansion (ammonia and steam, 100-130°C)	Digestibility improved for ruminant (true digestibility, metabolizable energy, total nitrogen content)	Ruminant forage	Lab-experiment: (Mokomele et al., 2018)
Olive cake	Anti-nutritional content: phenols	1. Ground, sieved 5mm, sterilized 20min, 121°C, moistened 2. SSF: *Fusarium flocciferum* fungal strain: 2 weeks, 25°C	Increase of protein content up to 94%, decrease of phenolic content by 70%	Ruminant feed	Lab-experiment: (Chebaibi et al., 2019)
Groundnut shells, pigeon pea husk, wheat bran	Anti-nutritional content and lignin structure	1. Pre-washed, sundried and pulverized residues 2. Supplementation with 2% ammonium nitrate and glucose and SSF with fungal strain *Colletotrichum spp,* 21 days, 30°C	Cellulose, hemicellulose, lignin, tanins and phytates contents were reduced and carbohydrates and proteins increased. Successfully added in poultry diets.	Monogastric feed	Lab-experiment: (Patil et al., 2020)
Cheese whey, molasse, fruits pulp, spent grains and rootlets	Mixed biowaste (heterogeneity)	1. Solid substrate autoclaved 15min, 120°C 2. SSF with *Kluyveromyces marxianus* for 4 days, 30°C 3. Optional lipids extraction	Protein and lipid content doubled. Extraction of lipids and press-cake as protein-rich animal feed ingredients	Animal feed	Lab-experiment: (Aggelopoulos et al., 2014)
Feather meal	Keratin content: low digestibility	1. Autoclaved 100°C, 15min 2. SSF with *Bacillus subtilis* bacterial strain 50°C, pH8, 72h	Can substitute fish meal up to 20% in silver pompano diets	Aquaculture feed	Lab-experiment: (Adelina et al., 2020)
Fish by-products	Acceptability	Cleaning, drying, milling	Increased acceptance of edibility, and enhancement of conservation	Human food	Lab-experiment: (Abbey et al., 2017)
Apple pomace	High perishability and moisture	Cleaning, drying, milling	Can substitute flour in bakery with dietary improvements	Human food	Lab-experiment: (Lyu et al., 2020; Zlatanović et al., 2019)
Brewer's spent grain	Organoleptic properties: bitter taste and unpleasant mouthfeel	Cleaning, drying, milling	Can substitute flour in snacking and pasta formulation	Human food	Lab-experiment: (Nocente et al., 2019), patent: (McHugh et al., 2020) with early commercial use (ReGrained, 2020)
Fruits bagasse and peels	Acceptability	1. Sanitized, dried 55°C and ground 2. SSF: *Saccharomyces cerevisiae* strain, 30°C, 70% moisture 3. Homogenization and dried 55°C.	Protein content increased 11 times. Can be included in cereal bars with improved censorial attributes and purchase intention	Human food	Lab-experiment: (Muniz et al., 2020), Similar process of (Villas-Boas and Granucci, 2018) under commercial development (Green Spot, 2020)

SSF: Solid Substrate Fermentation

5.2. Cracking pathways: Unlocking nutrients in structural biomass

To supply nutritional services, the literature reveals that cracking processes form the core of two conversion pathway categories: (i) the recovery of edible sugars and fibers from lignocellulosic streams and (ii) the recovery of amino acids and bioactive peptides from slaughterhouse by-products. The proposed unit operation pattern and a selection of relevant examples of cracking pathways are illustrated in the SI (figure S2 and table S1).

5.2.1. Lignocellulosic feedstock to sugars and dietary fibers

Lignocellulosic feedstocks are characterized by three interlinked macromolecules: (i) cellulose, (ii) hemicellulose and (iii) lignin representing 38-52%, 15-30% and 10-40% of the dry matter, respectively (Kapu and Trajano, 2014). Cellulose is a homopolymer composed of glucose, while hemicellulose is a generic term for β-1,4-linked non-cellulosic plant-based polymers (Scheller and Ulvskov, 2010). The most abundant class of hemicelluloses are xylans that are mainly composed of pentoses (i.e., C_5 sugars like xylose and arabinose).

Prior to cracking, lignocellulosic materials must be pretreated, using comminution methods to reduce particle size, partially disintegrate the plant cell wall matrix and promote lignin removal. Afterwards, within the cracking process hemicelluloses and cellulose are hydrolyzed, procuring “wood molasses”. These products were originally used as nutritional ingredients (Harris, 1947), but more recently have been driven towards chemical and energy markets (Reese et al., 1972). When cracking is coupled to downstream separation and purification, exploiting the different solubilities of cellulose and hemicellulose, it is possible to isolate pure sugar streams (Ingle et al., 2020). Purified cellulose can be used to supply the glucose or starch markets (You et al., 2013). However, wood-based glucose is currently uncompetitive compared to sugar-beet or sugarcane, regarding both economic and environmental aspects (Bello et al., 2021; Denkenberger et al., 2019). Finding markets for pentose sugars is less straight-forward, because their nutritional and fermentable value is lower than that of hexose sugars (Huntley and Patience, 2018; Rolston and Mathan, 1989). However, partial hydrolysis of hemicelluloses procures pentooligosaccharides (e.g. xylooligosaccharides) that can be used as prebiotic food ingredients (Poletto et al., 2020). Moreover, further functionalization of monomeric pentoses yields molecules such as the low-calorie sweetener, xylitol (Chandel et al., 2018; Franceschin et al., 2011). Finally, although the nutritional value of polyphenolic lignin is rather marginal, it has limited use in food industry as a texturizer or emulsifier (Bhat et al., 2020; Tenlep, 2020).

For food applications, product purity is of prime importance, because high severity (e.g. high temperature, pH changes) cracking processes often generate undesirable products and neoformed chemical species, such as furfural or acetic acid (Venkateswar Rao et al., 2016). The hydrolysates detoxification stage (i.e., removal of anti-nutritional compounds) is thus often a prerequisite for commercialization (Domingos et al., 2020; Dupoiron et al., 2017). In this regard, the use of alternative strategies, such as preventive pretreatment and/or enzyme-mediated hydrolysis might be advantageous and provide economically more viable routes to target food ingredients from lignocellulose (Paës et al., 2019; You et al., 2013). Enzymes act as highly selective catalysts that operate in mild (e.g., low temperature and near neutral pH) conditions and do not generate neoformed compounds, thus potentially positively influencing costs (Ingle et al., 2020; Roth et al., 2020). Consolidated bioprocesses involving the *in-situ* production of enzymes are often preferred for economic reasons, albeit requiring an additional stage of bioconversion to produce them.

5.2.2. Amino acids recovery from slaughterhouse by-products

Slaughterhouse by-products are here defined as low value animal body parts (offal, carcass, bristle, etc.) generated during meat production, which are included in the category 3 of the EU Animal By-products Regulation (see SI). These represent 35-50% of the animal body in weight (Alao et al., 2017; Ferraro, 2020). Aquaculture trimmings (30-75% of the fish in weight) are also included in this category (Leduc, 2018). These by-products share the fact that they are protein and/or lipid-rich, despite their quite different physical and chemical properties.

Meat scraps, offal, blood, bones and assimilates group into a single category of mostly edible (albeit unappealing to certain populations) slaughterhouse by-products that can be consumed directly or after organoleptic enhancement (Said, 2019; Toldrá et al., 2016). Being mostly devoid of structural barriers, this category of slaughterhouse by-products is commonly transformed using rendering processes into protein-rich meal for livestock and pets (e.g., bone meal, meat meal), fats and oils, while recovering functional compounds such as gelatin and collagens (Paul et al., 1962). Rendering mostly involves heat and mechanical treatments, like the processes used to generate fish meal and oil (Aspevik et al., 2017). Therefore, rendering is an enhancement technology. Unfortunately, health and safety concerns related to the use of slaughterhouse by-products (e.g., the risk of transmissible spongiform encephalopathies or TSE diseases) mean that these protein-rich co-products are currently forbidden for use as animal feed in several countries. For this reason, cracking processes are appropriate to treat slaughterhouse waste, because these can mitigate risk and satisfy regulatory bodies. For example, protein hydrolysate produced from slaughterhouse by-products is authorized for the feed market under specific conditions (Aspevik et al., 2017; European Commission, 2020). The second category of slaughterhouse by-products consists of inedible fibrous residues (e.g., animal horn and bristle) mainly composed by keratin (Ferraro et al., 2016; Perța-Crișan et al., 2021). When mildly processed, keratin-based residues provides low grade feed ingredients (e.g., feather meal), providing that it is not banned by TSE-derived regulations (Heuzé V. et al., 2020).

Because the direct use of animal by-products proteins is hampered by safety, health concerns and/or low digestibility, cracking processes are often used to obtain amino acids. For edible slaughterhouse by-products, enzymatic proteolysis is the preferred method to achieve this, because enzyme selectivity provides the means to generate not only amino acids, but also peptides displaying specific biological activities (Ferraro et al., 2016; Martínez-Alvarez et al., 2015), without the risk of generating unwanted substances. However, releasing amino acids contained in keratinous slaughterhouse by-products requires higher severity methods (e.g. higher temperatures) to breakdown the keratin polymer network (Chaitanya Reddy et al., 2021; Holkar et al., 2018). Such cracking processes are both energy demanding and poorly selective, leading to the denaturation of certain amino acids/peptides and reduction of the potential nutritional value (Falco, 2018; Tasaki, 2020). Fortunately, recent research on enzymes has revealed keratin-specific proteases that can convert keratin into highly digestible nutrients for animals (Chaudhary et al., 2021; de Menezes et al., 2021; Prajapati et al., 2021). The addition of a specific bioconversion stage to produce the enzymes is not necessarily required, as illustrated by a recent experience which performed a simultaneous *in-situ* keratinase production and keratin hydrolysis using the filamentous fungi *Amycolatopsis keratiniphila* on bristle (Falco et al., 2019). Irrespective of the slaughterhouse starting material, the generation of protein hydrolysates generally requires a subsequent purification step to produce the final, marketable product that meets food and feed standards (Martínez-Alvarez et al., 2015; Tasaki, 2020).

5.3. Extraction of nutritional compounds from residual biomass: pathways

Several waste-to-nutrition pathways reviewed are based on the extraction of TC or MRC ingredients trapped within residual biomass. Reported TC extractions from residual biomass are mainly targeting secondary metabolites additives (e.g. tannins, polyphenols or bioactive fibers) (Ben-Othman et al., 2020; Hussain et al., 2020; Rodríguez García and Raghavan, 2021; Saha and Basak, 2020; Tlais et al., 2020) and thus are not included in the scope of this work. Regarding MRC, the extraction pathways reviewed mainly target protein recovery (Pojić et al., 2018; Sari et al., 2015b; Tamayo Tenorio et al., 2018). Indeed, from both economic and energetic standpoints proteins are the costliest macronutrients obtained from photosynthesis (Bentsen and Møller, 2017). Considering that they generate underused protein-rich streams, three residual biomass categories are the focus of growing attention: (i) agrifood co-products, (ii) (activated) sludge and (iii) green residual biomass. The waste-to-nutrition pathways required to upgrade these different streams are similar in as much that they all involve a series of extraction unit operations and are devoid of bioconversion and cracking steps (proposed unit operation patterns and relevant examples are displayed in the SI, figure S3 and table S2).

5.3.1. Protein recovery from agrifood co-products

Some agrifood co-products, mostly from cereal (e.g., wheat bran, 13% DM proteins) and oilseed co-products (e.g., canola press-cake, 40% DM proteins) contain proteins enmeshed in lignocellulosic matrices (Contreras et al., 2019). While these co-products are already widely used as animal feed (section 5.5.), the application of extraction technologies can extend their nutritional potential up to food-grade markets. The first extraction step is employed to release the proteins from the residual matrix, for example through alkaline or enzyme-based extraction (Baker and Charlton, 2020; Kamal et al., 2021; Sari et al., 2015a). Afterwards, target purity is often achieved using a sequence of precipitation and membrane filtration. In the case of co-products already under a liquid form (e.g., dairy industry), recovery pathways mainly involve membrane-based extraction sequences (Lakra et al., 2021; Shahid et al., 2021). Overall, the reviewed literature reveals two main extraction strategies:

(i) A stepwise method providing the means to recover proteins from specific single protein-rich feedstocks, such as canola, sunflower (Subaşı et al., 2021; Tan et al., 2011), distiller's grains (Roth et al., 2019) and lupine meal (Prolupin GmbH, 2020). This approach is already close to the commercial scale (Mupondwa et al., 2018).

(ii) Cascade methods that allow the recovery of a single protein extract from several feedstock streams within a process that simultaneously isolates a variety of products. These methods can be applied to low-protein content materials such as primary crop residues (e.g., wheat straw with a protein content around 4%DM). This is advantageous because the low protein content of such feedstocks is offset by their high availability (Contreras et al., 2019; Hamelin et al., 2019).

Current extraction methods need further environmental and cost optimization to allow effective recovery (Baker and Charlton, 2020) and lead to competitive production. One solution highlighted in the literature lies in pairing conventional extraction processes with microwave and ultrasound technologies: besides often increasing protein extraction yields, these technics can also reduce operational expenditure (Franca-Oliveira et al., 2021).

5.3.2. Protein recovery from activated sludge

Activated sludge is the solid fraction remaining after the biological treatment of WW. Activated sludge is mainly composed of microbial biomass and is rich in proteins (up to 60%DM). Albeit sometimes directly reused for example in “sewage fish farms” (Verstraete et al., 2016), the presence of noxious compounds (e.g., pathogenic bacteria or detergent) usually prevent its direct use as animal feed (Vriens et al., 1989). Therefore, several studies have investigated the means to extract proteins implementing “sludge-to-proteins route” (Xiao and Zhou, 2020). In addition to the high moisture content of sludge, another disadvantage is that sludge proteins are contained within microbial cells. Therefore, it is necessary to use a first stage, such as hydrothermal and ultrasound treatments, to disintegrate microbial cells and release proteins. Afterwards, the recovery stage yields up to 90% of the proteins and the removal of most noxious compounds, such as heavy metals (Gao et al., 2020; Liang et al., 2020; Zhang et al., 2018). The resulting sludge protein concentrates display a complete amino acids profile and are investigated to supply the animal feed markets (Belyaev et al., 1978; Hwang et al., 2008; Markham and Reid, 1988). However, to drive sludge proteins into the food sector, it is necessary to implement more intensive, cost prohibitive purification methods (Xiao and Zhou, 2020). Nevertheless, to obtain food-grade proteins, it might be more reasonable to focus on sludge derived exclusively from WW treatment facilities associated with food transformations units (e.g., brewer effluent, bakery effluent), with the drawback of limited available volumes (Vriens et al., 1989).

5.3.3. Protein recovery from green residual biomass

Green biomass refers to all photosynthetic organs of plants, such as grass, vegetable tops and leaves. Those all harbor significant quantities of Rubisco, which is the key CO_2-fixing enzyme in plants. Although crude protein levels vary among species and as function of pedoclimatic conditions, they nevertheless represent 10-25% DM of green biomass, of which up to 50% is soluble (Solati et al., 2018). A specificity of green biomass compared to general plant-based biomass, is their low lignin content (<10%DM) coupled to high moisture, typically well above 70% of total weight (Tamayo Tenorio et al., 2018; Triolo, 2013). These characteristics are compatible with the mechanical separation of the freshly harvested green biomass into two fractions: a nutrient-rich juice and a fiber-rich cake, each harboring around 50% of the initial proteins (Kromus et al., 2008). This first mechanical extraction process is the starting point of most protein recovery in green residual biomass conversion pathways.

To maximize protein recovery, common extraction units such as thermal coagulation followed by centrifugation and drying are commonly performed on the green juice. The resulting leaf protein concentrate (LPC) (Davys et al., 2011; Pirie, 1971) targets monogastric livestock market, as a substitute for soy meal (Stødkilde et al., 2019). The implementation of additional refining steps can lead to food-grade extracts (Di Stefano et al., 2018; Martin et al., 2019). The fiber-rich cake mostly contains non-soluble proteins, hence preventing their direct recovery. However, this cake can be used as a substitute for raw grass in ruminant diets, while additionally providing the means to reduce nitrogen excretions (Damborg et al., 2020; Lucci et al., 2019). Advantageously for this fraction, the initial mechanical fractionation of e.g., grass increases the overall accessibility of grass proteins and thus offsets the absence of soluble proteins present in the green juice fraction (Damborg et al., 2018).

While a wide panel of residual biomass for LPC production had been historically screened (Pirie, 1971; Rosas Romero and Diaz, 1983), to-date commercial-stage developments are only based on premium green crops such as alfalfa. Monogastric-grade alfalfa LPC is already commercialized (Andurand et al., 2010) while alfalfa food-grade extracts are recently entering markets (Luzixine, 2020; Tereos, 2020). However, numerous European-based consortia attach to widen the panel of LPC production feedstocks, such as LPC production from raw grasses (Agroväst, 2020; Go Grass, 2020), green cuttings (GrasGoed, 2020) and vegetable tops such as sugar-beet (Green Protein Project, 2020; Tamayo Tenorio, 2017). The seasonality, heterogeneity and perishability of green biomass, coupled to energy-intensive technologies that procure insufficiently high protein yields are increasingly driving LPC production towards green biorefinery schemes in which LPC is just one of several added-value products (Corona et al., 2018b; Djomo et al., 2020; Santamaría-Fernández et al., 2020). Depending on local contexts, diverse green biorefinery setups and schemes exist, each aiming to supply energy, material and chemicals (e.g. lactic acids) from the LPC co-products (i.e. fiber-rich cake and supernatant “brown” juice) (Corona et al., 2018a; Kamm et al., 2016; Kiskini, 2017; Parajuli et al., 2018). Similarly, focus has also been put on the recovery of proteins in cellulosic bioethanol biorefineries (Bayat et al., 2021), using for this purpose non-residual biomass streams, such as switchgrass (Bals and Dale, 2011; Kammes et al., 2011; Laser et al., 2009).

5.4. Microbial bioconversion pathways

The literature survey revealed that the use microorganisms to recover and concentrate nutritional products from residual biomass is a well-studied route. Obviously, the term “microorganism” embraces an extraordinarily large number of species. Therefore, waste-to-nutrition pathways reviewed herein are classified according to the main metabolic processes involved, consistent with previous works (Jones et al., 2020; Spalvins et al., 2018). Resulting sub-categories are displayed in figure 4, and mainly differ regarding the preferred carbon and energy sources of the microbes. The categories are indicative, because some microorganisms are mixotrophs, being capable of several metabolic processes (e.g., purple bacteria), while other conversion pathways involve simultaneously more than one microbial culture (Alloul et al., 2021a; Rasouli et al., 2018; Yang et al., 2019; Zhu et al., 2020).

Overall, two main trends are apparent for microbial bioconversion pathways. The first (direct) approach involves direct microbial bioconversion of raw or mildly processed residual biomass, while the second (indirect approach) involves a preliminary sequence of enhancement, cracking and extraction units. These processes convert the feedstock into a form assimilable by the targeted microorganism.

Fig. 4. Waste-to-nutrition microbial bioconversion pathways

Metabolic pathways are adapted from (Alloul et al., 2021b; Choi et al., 2021; Linder, 2019) and complemented to capture the diversity of inventoried waste-to-nutrition microbial bioconversions. Key nutrients such as nitrogen and phosphorus are not represented to ensure visual tractability. Chemo(auto)trophic carbon-monoxide-oxidizing bacteria pathways are not represented here due to the scarcity of reported information on these.

5.4.1. Direct microbial bioconversion pathways

Direct microbial bioconversion pathways are heavily dependent on the characteristics of the feedstock. Accordingly, two main approaches are distinguished, in which the substrate is either under a solid or a liquid (i.e., wastewater) form. The proposed unit operation pattern is displayed in SI (figure S4) and corresponding examples are presented in table 2.

5.4.1.1. Fungiculture

In the review, SSF processes to generate harvestable nutritional metabolites targeting both TC and MRC ingredients were reported. Regarding TC production, identified pathways mainly focus on enzymes and flavors (Aggelopoulos et al., 2014; Sharma et al., 2020; Teigiserova, 2020) which are not the purpose of the present study. On the other hand, the production of MRC is principally achieved through fungiculture, as further detailed. The fruiting bodies of fungi (i.e., mushrooms) are commonly cultivated on moisturized lignocellulosic materials, meaning that food grade foodstuff (e.g., *Pleurotus spp.* ranging 15-45%DM protein content) is obtained in a single unit operation from non-food feedstock (Bellettini et al., 2019; Chanakya et al., 2015; Ritota and Manzi, 2019). The fungiculture unit operation can be decomposed into two main sub-stages corresponding to mycelium colonization of the substrate, followed by fructification (cf., table 2). The spent mushroom substrate displays a reduced lignin content, and is enriched in proteins and lipids (Khan et al., 2015; Wang et al., 2001). Therefore, depending on the initial feedstock, it is possible to use the spent substrate in animal feed regimes (Mhlongo et al., 2021; Wanzenböck et al., 2017), mix it with fresh feedstock to generate new SSF substrate (Hamed et al., 2020), or implement subsequent transformation steps. In this case fungiculture acts as a pretreatment for cellulosic sugar recovery for example (Chen et al., 2021). The time period required to convert residual biomass into mushrooms is generally at least three to four weeks when using optimized strains and culture conditions, but this often extends to several months, especially when it is necessary to first compost the feedstock (i.e., a prolonged bioconversion process).

5.4.1.2. Wastewater to nutrition

WW has been successfully used as microbial bioconversion medium, mostly using WW from: (i) food (e.g., vegetable oil) and beverage (e.g., brewing) processing (Amenorfenyo et al., 2019; Marchão et al., 2018; Patsios et al., 2020), (ii) animal effluents from farms and slaughterhouses (Li et al., 2019) and (iii) certain non-food industries, such as fertilizer manufacture (Chavan and Mutnuri, 2020) or paper pulp mills (Romantschuk, 1975). These WW have in common to host rich organic loads and a low carbon-to-nitrogen ratio (Spalvins et al., 2018; Vethathirri et al., 2021). However, the presence of toxic compounds can vary greatly depending on their specific origin. The services supplied by microbial bioconversion on such residual liquid substrate are thus two-fold: (i) production of microbial biomass from WW and (ii) removal of the nutrient charge (i.e., WW treatment) (Muys et al., 2020; Tomlinson, 1976). Mixed-culture mixotrophic microalgae and purple bacteria are particularly adapted to such diluted media (Cao et al., 2020; Capson-Tojo et al., 2020; Solovchenko et al., 2020). They combine atmospheric carbon capture with the use of soluble organics and nutrients, reducing the need for additional inputs (Hülsen et al., 2018; Shahid et al., 2020).

The aquaculture market is a prime target for wastewater-to-nutrition pathways, because microorganisms are already part of the fish trophic chain (Glencross et al., 2020; Milhazes-Cunha and Otero, 2017). However, if not deployed *in-situ* (e.g., through activated sludge-derived biofloc technologies) (Alloul et al., 2018; Bossier and Ekasari, 2017), the requisite harvesting and dewatering of low concentration microbial biomass using a series of energy-intensive extraction steps rapidly becomes cost ineffective. Furthermore, the final market is currently dependent on the quality of the initial WW, because technical specifications (e.g., fecal contamination) drive the requirements of additional intensive prior/post purification treatment steps (Verstraete et al., 2016). In this respect, food-grade applications are mainly limited to high quality food-processing WW (e.g., from starch production, table 2), which is only available in limited volumes.

Table 2. Selection of inventoried direct microbial bioconversion pathways – reported with wording used by original references

Residual biomass	Transformation units	Results	Potential	Status and references
Wastewater				
Piggery wastewater	1. Digestion and sterilization with ozone 30min 2. Microalgae *Chlorella pyrenoidosa* and yeast *Rhodotorula glutinis* cultured at 28°C for 5-7 days. Addition of glucose and yeast extract, pH7-7.5. 3. Decantation, centrifugation and washing (sodium hydroxide, 47°C) 4. Ultrasonic processing (25min at 47°C), then centrifugated washed and lyophilized	Recovery of a microbial protein concentrate	Feed protein additive	Lab-pilot-experiment : (Li et al., 2019)
Alcoholic beverage wastewater	1. Direct aerobic submerged fermentation with microalgae (undisclosed strain)	Omega-3 rich biomass	Aquaculture feed	Commercial development: (MiAlgae, 2020)
Fishpond wastewater	1. Direct aerobic submerged fermentation with microalgae (undisclosed strain)	Microalgae rich stream recirculated back	Aquaculture feed	Commercial pilot: (Microterra, 2020)
Fishpond wastewater	1. Add C source to equilibrate C:N ratio in wastewater 2. Aerobic heterotrophic bacteria growth in the form of bioflocs in-situ or in dedicated reactor 3. Direct recirculation of bioflocs in fishpond, or pelletizing.	Microbial protein rich stream recirculated back	Aquaculture feed	Lab experiments (Crab et al., 2012)
Spent sulphite liquor and permeate	1. Steam treatment to remove SO_2 and sterilization 2. Cooling, aerobic fermentation by *Paecilomyces varioti* fungi 3-4h, pH4.5-4.7, 38-39°C with addition of NPK. 3. Filtering and washed, dried and ground mechanically	Recovery of a microbial protein concentrate (55-60%DM)	Animal feed	Discontinued commercial Pekilo process (Halme et al., 1977) with renewed interests[1]
Starch processing wastewater	1. Anaerobic fermentation (formation of fatty acids, sugars and oligosaccharides) 2. Aerobic fermentation with edible strains (undisclosed) 3. Dewatering and drying (various technologies)	Recovery of protein concentrates (60-80%DM)	Human food and animal feed	Patents: (Logan et al., 2011; Verstraete et al., 2020), commercial developments (Avecom, 2020; iCell Sustainable Nutrition Co., 2020)
Liquid fraction of anaerobically digested organic wastes	1. Microfiltration (0,2 µm) to concentrate P, coupled with ultra- and nano-filtration to concentrate N 2. Culture of heterotrophic microalgae (here *Chlorella vulgaris*, 28 days) 3. Harvesting with microfiltration 4. Wet biomass metabolite extraction	Algal biomass derived bioproducts	To assess	Conceptual formulation by (Stiles et al., 2018) with pilot test (Fernandes et al., 2020)
Solid biomass				
Sawdust and small wood residues, bran, husks	1. Addition of carbohydrates (e.g corn, seeds) and steam sterilization 2. SSF with fungal strains (*Shiitake, Pleurotus sp…*) in bags for 3-20 weeks until filaments colonized the whole substrate 3. Harvesting of fruiting bodies few days after transfer in culture room	Recovery of mushrooms (diverse)	Human food	Commercial production: (Biopilz, 2020)
Horse manure (75%) and straws (25%)	1. Composting for 20 days, then pasteurization 5-6 days, at 50-60°C 2. When T°<25°C, SSF with *Agaricus bisporus* strain for 2-3 weeks (22-25°C, high moisture) until the mycelium develop 3. Mycelium block tapped with soil mixture to keep humidity. 4. Harvesting cycles through a 4-6 weeks period	Recovery of common white mushrooms	Human food	Commercial production: (Roulleau, 2020)
Coffee ground and wood wastes	1. Homogenization and SSF with *Pleurotus*: 2 weeks without light, 20-24°C until white foam appears. 2. Position substrate outside air-exposed, high moisture (85-95%) until fruiting bodies reaches 4-7cm diameter.	Home-made mushroom culture	Human food	Commercial production : (La Boîte à Champignons, 2020)

[1]: (Eniferbio, 2020) ; C : Carbon; K : Potassium; N : Nitrogen; P : Phosphorous; SSF : Solid Substrate Fermentation

5.4.2. Indirect microbial bioconversion pathways

In the field of nutritional services, direct microbial bioconversion is restricted to small number of microorganisms and the use of quality feedstocks (cf., 5.4.1. and 5.1.). The delivery of nutritional services from residual biomass through microorganisms can be extended by adapting the feedstock to the specific requirements of the fermentative microbial cultures. The common objective of these indirect bioconversion pathways is the substitution of high-grade nutrients (commonly used to formulate fermentation medium) with lower grade materials. However, the scientific literature mainly focuses on the use of mixed feedstocks where only a part of the nutrient requirement is furnished from lower grade materials and completed with quality ingredients. Nonetheless, the conversion pathways included in this section all share the feature of at least partially supplying the energy, carbon and nutrients required for microbial bioconversion from residual biomass or C_1 gases.

Indirect microbial bioconversion pathways can be subdivided into two categories. The first group relates to bioconversion of C_1 gases, while the second group targets the elaboration and bioconversion of alternative soluble fermentable compounds (C_1 to C_6).

5.4.2.1. Gas-to-nutrition conversion pathways

The gas-to-nutrition pathways employ C_1 gases (mainly CH_4 or CO_2) as carbon source for microbial biomass production. The generic unit operation pattern is illustrated in SI (figure S5). The energy source defines the exact nature of the pathway: phototrophic bioconversion fixes carbon dioxide using light (representative examples in SI, table S3), while chemotrophic bioconversion converts high-energy gases such as dihydrogen into biomass (table 3).

Phototrophic pathways are similar to wastewater-to-nutrition pathways (section 5.4.1.2.), especially regarding post-treatment. However, phototrophic pathways usually focus on the capture of concentrated CO_2 streams (figure 4). Accordingly, phototrophic organisms (mainly microalgae and cyanobacteria) are operated in reactors optimized for light penetration and gas transfer and fed with essential nutrients (e.g., N, P, K, etc.) in order to produce proteins and omega-3 fatty acids. According to the literature, these nutrients are often sourced from high grade products (e.g., glutamate, peptone, fertilizers) instead of being upcycled from residual biomass streams. However, in addition to the use of waste C_1 gases, some gas-to-nutrition pathways also harness nutrients from underused streams (e.g., predominant N leakages such as animal and human effluents) to satisfy the nutritional requirements of the microorganism (Matassa et al., 2015; Yang et al., 2021). The versatility of bacterial strains, which can use different forms of nitrogen such as NH_3, NH_4^+ (Dou et al., 2019) and N_2 (Hu et al., 2020; Pfluger et al., 2011) provide the basis for a whole range of pathway variants.

Chemotrophic pathways mainly rely on either hydrogen-oxidizing bacteria (HOB) or methane-oxidizing bacteria (MOB), both of which use gases as their carbon and energy sources and hence provide the basis for “full-gas” pathways (Matassa et al., 2020). Importantly, chemotrophic processes are characterized by high conversion efficiencies (Claassens et al., 2016; Liu et al., 2016; Pander et al., 2020) in large part because, unlike phototrophic processes, they are not limited by energy availability. Additionally, chemotrophic bacteria can fix between 80% and 100% of their N supply (Pikaar et al., 2017) into microbial biomass, which yields a protein content of approximately 70%-80% and an amino acids profile analogous to that of fish meal (Matassa et al., 2015; Øverland et al., 2010). For these reasons, HOB and MOB strains have been arousing interest for some time, with their proteins being studied for human nutrition, especially in the context of space travel (Alvarado et al., 2021; Foster and Litchfield, 1964; Steinberg et al., 2017). The suitability of MOB meals as a substitute for conventional high-protein ingredients in monogastric animal diets has been demonstrated (Øverland et al., 2011, 2010) and these are already close to commercialization unlike HOB routes. However, one cause for concern is the significant presence of anti-nutritional RNA/DNA and endotoxins in bacterial biomass. Therefore, if not mitigated through genetic engineering, this often must be eliminated before the microbial biomass is considered fit for consumption. Nucleic acids removal can be achieved through heat treatments, as already performed during the industrial production of *F. venenatum* (RNA content reduced from 8-9% down to 1% in weight) (Whittaker et al., 2020).

The origin of C_1 gases is key to the economy of chemotrophic pathways (García Martínez et al., 2021; Huizing, 2005; Verbeeck et al., 2020). While scaling projects currently focus on the use of fossil-based methane and electrolysis-based hydrogen, syngas and biogas are also investigated (cf., table 3). The inherent variability and heterogeneity of these biogenic gases are attenuated through scrubbing, removing undesirable gas components, such as carbon monoxide and hydrogen sulfide (Tsapekos et al., 2019; Xu et al., 2020). Accordingly, gases for chemotrophic pathways can be derived from residual biomass through a sequence of cracking and/or bioconversion units (e.g., anaerobic digestion, gasification) followed by refining units.

The low solubility of H_2 (De Vrieze et al., 2020) and the safety issues related to the simultaneous presence of H_2 and O_2 for aerobic HOB production (Molitor et al., 2019) are also questions that are addressed by current research work. Often, to meet these challenges, additional processes are envisaged for chemotrophic pathways (Sakarika et al., 2020). For example, gases are first converted into organic compounds (e.g., acetic acid or methanol) using either biocatalysis (e.g., fermentation using an acetogenic bacteria) or physico-chemistry (e.g., hydrogenation) (Linder, 2019; Mishra et al., 2020). The resulting organic compound is then used as substrate to support the growth of a common heterotrophic organisms such as yeast. Alternatively, the overall process can be achieved in a single step using the co-culture of several microorganisms (Du et al., 2020). An emerging route is the use of volatile fatty acids (VFAs) as platform intermediates instead of end-gases. This novel approach, described in Alloul et al. (2018) targets acidogenic fermentation on dissolved carbon sources (obtained through prior cracking or conversion of residual biomass) to recover VFAs. These are further converted into edible biomass through flexible microorganisms such as purple bacteria (Capson-Tojo et al., 2020; Lu et al., 2021) or filamentous fungi (Uwineza et al., 2021).

5.4.2.2. Alternatives to common microbial bioconversion medium

The previous section describes processes that require the use of novel substrate-microbe associations regarding nutrition. However, axenic microbial bioconversion is already a core technology of the feed and food industries, being widely used to produce amino acids, lipids or mycoproteins from well-defined substrates such as raw glucose or methanol. Nevertheless, with increasing pressure to deliver cost-competitive carbohydrates in a framework of environmental sustainability and food/feed security, analysis of the literature reveals that considerable focus is put on the investigation of alternative carbon sources (Siben et al., 2018; Specht, 2020; Specht and Crosser, 2020). Accordingly, this section provides a description of attempts to drive low-cost residual biomass into common microbial bioconversion pathways, using a series of conversion processes to ensure that nutrient and end-product quality and safety are maintained, as represented in figure 5. A selection of examples from the literature is available in SI, table S4.

The use of sugar- and lipid-rich streams has been previously reviewed (Spalvins et al., 2018). These pathways rely on quite homogeneous agrifood co-products, such as whey or molasses (Caporusso et al., 2021), and are used to upgrade their current animal feed value to food quality TC and MRC ingredients production. Considering the quantities available, certain biofuel co-products (e.g., glycerol) are also included because these can be used, for example, to implement *in-situ* microbial protein production (Fazenda et al., 2017; Tracy et al., 2020).

Cracking and/or extraction processes have been developed to breakdown structural complexity and deal with feedstock heterogeneity characteristic of (for example) urban food waste. Common cracking operations, such as hydrolysis and saccharification, are deployed either in stand-alone single product processes (Kwan et al., 2018; Pleissner et al., 2014) or in multi-production platforms to solubilize compounds that serve as nutritional feedstock for microbial bioconversion. In multi-production platforms, co-products (e.g., arising from protein extraction pathways) such as supernatants and residual fibers are used as sources of sugars to sustain bioconversion (Øverland et al., 2019; Thomsen et al., 2008). Lignocellulosic biomass is also a source of fermentable sugars (cf., section 5.2.1.) and can sustain for example straw- or wood-to-protein pathways (Upcraft et al., 2021). This type of strategy has already been implemented at industrial scale (e.g., Tornesch plant producing 20,000 tons of yeast per year in the 1930's) in response to wartime (Harris, 1951). However, renewed interest in this route has been prompted by recent advances in selective and food-grade lignocellulose cracking (Asim et al., 2021; Tenlep, 2020; Voutilainen et al., 2021).

Finally, synthetic pathways to produce fermentable TC are reported in the literature. Also called power-to-food or power-to-protein (Mishra et al., 2020; Sillman et al., 2020), these approaches use electricity to produce the reducing power further converted by a target microorganism. A first application is to extend the possibilities of gas-to-nutrition pathways, for example through the "CO_2-to-CH_4-to-protein" route (Xu, 2021) or converting hydrogen into methanol and acetic acid as mentioned in section 5.4.2.1.. Similarly, synthetic pathways are also engineered to fix CO_2 through "biological-inorganic" (Nangle et al., 2017) or "microbial electrosynthesis" (Dessì et al., 2020) processes into non-gaseous fermentable TC such as formate or methanol (Mishra et al., 2020; Sakarika et al., 2020).

Fig. 5. Producing alternative fermentation mediums from residual biomass: unit operations pattern

The indicative ranking of residual biomass families in the nutritional quality scale is derived from figure 2., and allows to visualize the estimated chain of unit processes required to bridge the gap between the initial composition-structure of a feedstock and the composition-structure which is adequate to deliver a nutritional service. Icons are as defined in figure 1. The identified conversion pathways are rather straightforward when starting from sugar- or lipid-rich residual biomass, but can be more complex, involving prior cracking and extraction operations to release fermentable compounds. Albeit limited by economic considerations (Kwan et al., 2019), purification technologies are often required to detoxify feedstocks and bring them up to nutritional specifications. C_1 gases can either have a fossil or biogenic origin, as represented in figure S5.

Table 3: Inventoried examples of biomass recovery into food and feed through chemotrophic gas-to-proteins pathways – reported with wording used by original references

Residual stream targeted	Technological requirements for the carbon source	Technological requirements for the nitrogen source	Bioconversion conditions (incl. energy source)	Results (incl. potential)	Status and references
Atmospheric CO_2	Direct air capture (DAC) to concentrate CO_2	Haber-Bosch process to fix N_2 into NH_3	1. Renewable electricity allows DAC, Haber-Bosch process, and water electrolysis 2. Submerged fermentation of *Curpiavidus necator* HOB bacterial strain 3. Centrifugation and evaporation	Protein-rich biomass for humans and animals	Concept: (Givirovskiy et al., 2019; Sillman et al., 2019), lab-pilot-experiment by (Solar Foods, 2020) with patent (Pitkänen, 2020)
Industrial combustion flue gases (e.g. power plant)	Cooling and direct pumping of flue gases in the bioreactor if reduced impurities	Direct use of raw materials	1. Electrolysis to supply H_2 to the bioreactor 2. Submerged anaerobic fermentation of HOB strain 3. Centrifuging and drying.	Aquaculture feed and human food	Commercial development: (Deep Branch Biotechnology, 2020; Kiverdi, Inc., 2020; NovoNutrients, 2020), patent: (Reed, 2019)
Anaerobically digested sewage sludge	Raw biogas upgraded to separate CO_2 (here carbon source) from CH_4	Air stripping to capture ammoniacal nitrogen from the digestate and direct pumping into bioreactor	1. Electrolysis or CH_4 reforming to produce H_2 2. Submerged fermentation of HOB strain with recovered CO_2 3. Transformation to edible products	Protein-rich ingredients and prebiotics	Concept: (Matassa et al., 2016), Demo-pilot-plant: (Power-to-Protein, 2020)
Undiluted source-separated urine	Electrochemical NH_3 recovery to accumulate CO_2 at the electrochemical cell (EC) anode	1. Autohydrolysis of urine (28°C) 2. Hydrolysate supplied to the EC: recovery of NH_3 at the cathode. 2. NH_3 recovered through air stripping and absorption	1. H_2 and O_2 are produced in the EC (respectively cathode and anode) 2. All gases are supplied to a bubble column reactor for HOB production	Microbial protein production (no specified market)	Lab-experiment: (Christiaens et al., 2017)
Fecal WW	1.COD capture in sludge (aeration) 2. Anaerobic digestion to get CH_4 and CO_2	NH_3 stripping of liquid fraction of digestate	Axenic submerged fermentation of edible MOB and microalgae (aerobic) with recovered gases and nutrients	Microbial protein (no specified market)	Concept: (Verstraete et al., 2016)
Lignocellulosic, biowaste, digestate	Pyrolysis/Gasification to produce syngas with proportions of CO and CO_2	Direct use of NH_3 present in syngas	Submerged fermentation of edible HOB or CO-oxidizing bacteria (aerobic)	Microbial protein (no specified market)	Concept: (Matassa et al., 2020)
Human solid and liquid waste	1.Homogenezation 2. Fixed-film, flow-through anaerobic digester 3. Inorganic removal, and remaining effluents treated with strong base to remove CO_2	Release of NH_3 from digestate as a result of the strong base treatment	1.Both NH_3 and CH_4 sterilized and fed to *M.Capsulatus* MOB (and conversion of excess NH_3 into NO_2) 2. Effluents from MOB reactors and treated digestate are sent to denitrifying bioreactor (*Halomonas desiderata* strain at high pH)	MOB proteins: astronaut's foodstuff and denitrifying biomass as feed	Lab-experiment: (Steinberg et al., 2017)
Urban biowaste	1. Biopulp pretreatment[1] 2. Anaerobic digestion to produce biogas, directly used 3. Removal of H_2S	1. Centrifugation and filtration (0,2 µm) of liquid digestate 2. Pasteurization (70°C 1h) and dilution	Submerged fermentation with a mixed-MOB culture of *Methylophilus sp,* or *Methylococcales* and *Methylophilales*	Microbial protein (presumably for animal feed markets)	Proof-of-concept experiences: (Khoshnevisan et al., 2019; Tsapekos et al., 2019)
Pumpkin and pig manure	1. Anaerobic digestion 2. Biogas upgraded with EC: resulting cathode off-gases are CH_4, O_2 and H_2, anode off-gases are O_2, CO_2, H_2	Direct use of raw materials (ammonium mineral salts)	Simultaneous fermentation of HOB and MOB in a single reactor to use all gases. Synergy of MOB fermentation releasing CO_2 used by HOB	Microbial protein (presumably for animal feed markets)	Proof-of-concept experiment: (Acosta et al., 2020)

N-rich effluents (urine, sewage sludge)	CO_2 concentrated from flue gases, gasification exhaust or biogas upgrading	Not detailed	Two stages bioprocess: 1. Electrolysis to produce H_2 2. Submerged fermentation of *Clostridium ljungdahlii* HOB acetogenic strain (35°C, pH 6, anaerobic) 3. Fermentation of edible *Saccharomyces cerevisiae* on the acetate media (30°C, pH 5,5, aerobic)	Microbial protein concentrate (presumably for human food markets)	Proof-of-concept-experiment: (Molitor et al., 2019), concept: (Mishra et al., 2020)

[1]: As in Khoshnevisan et al. (2018), includes pulper, separator and dewatering; COD: Chemical Oxygen Demand; DAC: Direct Air Capture; EC: Electrochemical cell; HOB: Hydrogen-Oxidizing Bacteria; MOB: Methane-Oxidizing Bacteria; WW: Wastewater

5.5. Farmed animal bioconversion pathways

A wide range of residual biomass has already been tested as direct animal feed, ranging from fruit wastes (Wadhwa and Bakshi, 2013) to manure (Mueller, 1980). Not only limited to circumstances of extreme necessity (De Groot and Bogdanski, 2013; Makkar et al., 2018), the wide adoption of residual biomass to sustain animal husbandry has been explored in recent literature (te Pas et al., 2021). Animal farming, or rather the farmed animal themselves can then be considered as a bioconversion process in waste-to-food pathways.

5.5.1. Waste-to-meat, milk and eggs

Two recent studies revealed that supplying all food waste, agricultural residues and grasslands available in Europe to a combination of swine, laying hens and dairy cattle could provide 9 to 31g of proteins per person per day for the continent (Van Hal et al., 2019; Van Zanten et al., 2018). This is significant if one considers that the daily recommended protein intake for an adult is 50-60g (EFSA Panel on Dietetic Products, Nutrition and Allergies (NDA), 2012).

Provided that the use of residues and co-products does not affect performance and food safety, and that it does not require intensive pretreatments, the use of livestock as direct bioconverters is a viable option and indeed is already widely implemented (Mottet et al., 2017; Wilfart et al., 2019). Residual feedstocks still need to meet feed standards, and therefore mainly consist of agrifood industry co-products, which on average represent 10% and 20% of compound feeds used in France for monogastric and ruminants respectively (Agreste, 2019, 2017). Monogastric animals are restricted to low-lignin feedstocks (Chapoutot et al., 2019), but ruminants can also convert green biomass and pretreated crop residues. Direct bioconversion of slaughterhouse by-products is also reported, especially for aquaculture in some regions, but in others this is considered unacceptable (Leduc, 2018; Meeker, 2006). Besides direct enhancement techniques such as grass ensiling (cf., section 5.1.), a common strategy involves the inclusion of specific enzymes in diets. These degrade anti-nutritional compounds (e.g., mycotoxins) and increase the digestibility of fibrous components (Nunes, 2018).

Less homogeneous residual biomass, such as food waste, are already used in livestock diets, not only in small-holder farming or periurban systems (Cesaro et al., 2019), but also in industrial production after enhancement-like pretreatments (e.g., heat-treated urban food waste in Eastern-Asia) (Dou et al., 2018; Georganas et al., 2020; Zu Ermgassen et al., 2016). Such practices are banned in other parts of the world, mainly because of TSE-related risks (Castrica et al., 2018). An option to ensure safety and acceptance lies in only considering pre-consumer food losses (e.g., surplus vegetables) (Luyckx et al., 2019; Pinotti et al., 2021; San Martin et al., 2016). In addition to animal health concerns, livestock industries are quite risk-adverse and take precautions to preserve meat/milk/egg quality (Research and Innovation, 2017; Salami et al., 2019). An example of the risk/benefit analysis of novel feed is the inclusion of some plant-based residues in animal diets which would positively furnish functionally valuable phytochemicals (e.g., antibiotic substitute) but will negatively alter organoleptic properties of meat (Achilonu et al., 2018; Valenzuela-Grijalva et al., 2017). Further issues also include human health problems arising from imbalances in animal diets such as the omega-6/omega-3 fatty acids ratio correlated with the prevalence of chronic diseases in humans (Duru and Magrini, 2017).

The main challenge of using livestock as residual biomass bioconverters is the fact that the current key determinant of stakeholder practices and choices is performance, mainly measured as a feed-to-food ratio (Shepon et al., 2016; Wirsenius et al., 2010). Including biomass of lower nutritional value into diets is detrimental to livestock's bioconversion efficiency (details and benchmark in SI), and less-productive animals, better adapted for the direct digestion of residual biomass, are not included in current farming strategies (Van Zanten et al., 2019). Therefore, the extension of livestock bioconversion to a wider range of residual biomass will involve reconsidering the choice of animal breeds and/or the development of strategies to deal with the anti-nutritional and fibrous components of low-grade feed ingredients (Peyraud et al., 2020; te Pas et al., 2021). For the latter, this can be dealt with using different waste-to-feed pathways yielding MPF, MCR and TC ingredients, as those inventoried through the past sections. Regarding human nutrition, the consumption of animal-based food (i.e., meat, milk, etc.) involves the addition of a livestock bioconversion building block at the end of the biomass conversion pathway. In this respect, in the representation scheme proposed in this work, the slaughterhouse should be considered as a combination of enhancement and extraction blocks that intervene before human consumption.

5.5.2. Insect bioconversion pathways

The use of insects to convert residual biomass into nutritional ingredients for both animals and humans has been extensively reviewed in the literature (FAO, 2020; Rumokoy et al., 2019; Van Huis, 2020). Among the numerous known species, focus is given herein to those that are the subject of commercial projects for nutrition in Europe, especially *Hermetia Illucens* (black soldier fly), *Musca domestica* (common housefly) and *Tenebrio molitor* (yellow mealworm) (Cadinu et al., 2020). Depending on their diets and stage of life (e.g., larvae), these insects accumulate proteins and transform sugars into lipids (Colonna, 2020) to achieve contents in the range 40-70%DM and 10-40%DM respectively (Makkar et al., 2014).

The "waste-to-protein" insect pathway (Zurbrugg et al., 2018) follows a pattern that is almost identical to that of livestock bioconversion (illustrated in SI figure S6, S7 and table S5). First, common enhancement processes such as grinding, mixing, moisturizing are used to improve nutrient uptake by the insects. The intensity of such pretreatment depend on insects specific characteristics, flies requiring an almost liquefied substrate while termites directly degrade lignocellulose (Hubert and Berezina, 2020). The bioconversion itself takes place in either fully automated or low-tech facilities, depending on the context (Cortes Ortiz et al., 2016; Dortmans et al., 2017; Kröncke et al., 2020; Melgar-Lalanne et al., 2019). Once the insects reach maturity (i.e., bioconversion culminates), they are harvested, sanitized and usually dried when not directly fed fresh. The final MRC is either the whole insect or a fraction of it (Pippinato et al., 2020). Fractionation often targets the generation of a protein-rich meal and thus involves lipid extraction (i.e., generation of insect oil). Once missing nutrients (e.g., methionine) have been added, insect meals are good candidates to substitute soya meal or fish meal (Azagoh et al., 2016; Pleissner and Smetana, 2020) in compound feed formulations. Initially only permitted for use in aquaculture and petfood, the inclusion of insect protein meal in animal diets has been recently extended to swine and poultry in Europe (IPIFF, 2021). Regarding waste-to-nutrition conversion pathways, the inclusion of insect-based products in livestock feed corresponds to a successive sequence of bioconversion (i.e., insect followed by livestock).

Additionally, insects (or corresponding meal) are also ground and used as protein-rich ingredients for ready-to-eat products for humans (e.g., snacks) through common enhancement processes (García-Segovia et al., 2020; Lamsal et al., 2019), this strategy being preferential for many populations that are so far reluctant to consume whole insects

(Orsi et al., 2019; Poortvliet et al., 2019). Like other common protein-rich ingredients, insect proteins can further enter a series of extraction units to refine and isolate precise functionalities (Gravel and Doyen, 2020; Smetana et al., 2018). The main co-product, insect oil, also has the potential to directly enter food and feed markets (Phan Van PhI et al., 2020; Smetana et al., 2020). However, nutritional composition of the insects was found to be variable, being correlated to diet quality (Gold et al., 2020; Oonincx et al., 2015), and relatively few background data are available regarding biological and chemical risks associated with such residual substrates (ANSES, 2015; Bessa et al., 2020; EFSA Scientific Committee, 2015). Consequently, European authorities have so far only authorized commercial insect farming fed with "feed grade materials", thus creating potential competition with conventional animal feeds (Gasco et al., 2020). Entomofarming facilities currently operating in Europe mainly use industrial agrifood co-products (e.g. bran, peels) or homogeneous surplus food (e.g. unprocessed expired food) (IPIFF, 2019). Mainly intended for feed markets, the latest legislation recognizes *Tenebrio Molitor* larvae, *Locusta Migratoria* and whole house crickets *Acheta Domesticus* as the first safe insect foodstuffs in Europe, under the condition that these are fed with feed-grade materials (EFSA Panel on Nutrition, Novel Foods and Food Allergens (NDA) et al., 2021c, 2021a, 2021b). Of particular interest for stakeholders is the expansion of the authorized rearing substrates for insects and the wider development of substrate-enhancement techniques (Raksasat et al., 2020). Food waste is particularly mentioned in the literature because this represents significant volumes besides its nutritional potential (Jensen et al., 2021; Ojha et al., 2020; Varelas, 2019).

6. A comprehensive overview of waste-to-nutrition pathways

6.1. Building block framework: implications and limits

Overall, waste-to-nutrition pathways involve diverse technologies and different degree of nutrients and energy circularity, using different schemes of unit operations of increasing intensity and complexity. In general, the less edible the feedstock (as defined in section 3), the more processing is required to derive an edible foodstuff from it, as it can be visualized in figures 5 and S1-S7. Bioconversion can sometimes be used to circumvent this, providing foodstuff in a reduced number of steps (e.g. figures S4, S6 and S7). This is because living organisms can be considered as complex reactors performing a series of unit operations (Godon et al., 2013). However, in the case of highly structured and chemically complex plant-based feedstock, most organisms display only limited direct conversion capabilities. As a result, a pretreatment sequence to render the feedstock suitable for subsequent bioconversion is often needed (e.g. figures 5 and S7). One notable exception to this rule are fungi, as these secrete complex arsenals of biomass-degrading enzymes (Kuyper et al., 2021; Souza Filho, 2018). Mushrooms cultivated on wood residues (figure S4) exemplify such shortened bioconversion pathways that bridge the gap between an inedible feedstock and edible nutrient production.

Often, the production of edible nutrients is the result of sequential bioconversions. In this case, animal-animal bioconversions are rather inefficient (e.g., 4-5 pelagic fishes bioconverted in 1 salmon) (Tacon and Metian, 2008), while microorganism-animal (e.g., microbial proteins to animals) or microorganism-microorganism (e.g., first strain freeing a TC in turn processed by a second strain of interest as in figure 5) sequences are more efficient. This is because the inherent losses associated with bioconversion may to some extent be compensated by two aspects. First, microorganisms are able to convert non-carbohydrates energy (including light) into carbohydrates and convert non-protein nitrogen into proteins. Particularly, some bacteria and microalgae report nitrogen fixation ratio higher than 70%

(details in SI). Second, animals are able to autonomously capture and concentrate diluted nutrients. For example, some insects efficiently concentrate residual biomass proteins (<50-60% recovery efficiency, see SI) and are themselves easily harvestable. As a second example, farming fishes within microalgae production systems is an indirect way of collecting microalgae biomass (as fish) otherwise diluted in production pond/reactor (Verstraete et al., 2016). In this case, conventional energy-intensive microalgae harvesting and drying techniques are replaced by fishing techniques, yet at the expense of a significantly lower overall nutritional output yield. It is also important to point out the ability of some edible microorganisms to grow in biomats at the liquid-air interface, removing the need of energy-intensive extraction stage (Kozubal et al., 2020).

Besides initial feedstock composition-structure considerations, the target market also strongly defines the intensity of conversion process strategies. Indeed, most conversion pathways involve extensive post-treatment (extraction and enhancement of nutritional/organoleptic properties) to polish the final product’s functionalities (e.g. microalgae-based meat-analogs) (Bernaerts et al., 2019; Fu et al., 2021). Currently, these steps are mostly implemented to concentrate/purify nutrients (up to TC) and attenuate anti-nutritional and safety issues.

As the effects and drawbacks of each unit operation are cumulative, it is still unclear to what extent the foreseen advantages associated with waste-to-nutrition strategies would offset their drawbacks if massively implemented (Guthman and Biltekoff, 2020; Helliwell and Burton, 2021; Van Eenennaam and Werth, 2021). The building blocks framework proposed herein is intended to simplify the representation of processes involved in waste-to-nutrition pathways, systematizing their transformation sequence patterns and grouping these into large categories. Accordingly, this framework is a stepping stone to further assessments, providing a convenient way to visualize available options when comparing different feedstocks. However, as key aspects such as energy demand or greenhouse gas emissions are technology- and operation-specific, further state-of-the-art life cycle assessments (LCA) accounting for all inputs, outputs including wastes and co-products generated during a process are required to quantitatively estimate their full environmental performance. Accounting for services provided by co-products in waste-to-nutrition pathways is key, because these are potential sources of energy, chemicals, materials and even feed. When feedstock give rise to multiple pathways and multiple products and services it is appropriate to use the term biorefinery.

6.2. Waste-to-nutrition pathways into eight large families

Earlier (cf., section 5) waste-to-nutrition pathways were grouped based on their core building block. To refine the analysis, the classification is here extended by grouping pathways into large families on the basis of belonging to the same biorefinery scheme or addressing the same challenge (figure 6). These families are not defined based on the use of specific feedstocks, nor do they deliver specific services. Moreover, livestock-based bioconversion was not considered as a waste-to-nutrition family, being rather a plug-in often present at the end of the other families.

Value chains built on the extraction of rubisco, or the cracking of plant fibers are well-studied, constituting respectively the green and lignocellulosic biorefinery families. Similarly, insect farming is increasingly studied from the angle of biorefining, because use of the co-products will form part of the business model (da Costa Rocha et al., 2021; Hubert and Berezina, 2020; Ravi et al., 2020), hence the insect biorefinery proposed herein. Likewise, we propose a "gas-intermediate biorefinery" family, as gas-based proteins can be part of larger anaerobic digestion and gasification platforms (Matassa et al., 2020), but also because it positions C_1 gases as key basic bricks for nutrition. Besides proteins and fats, slaughterhouse by-products already constitute a source of ingredients for cosmetics and medical products. However, a "more-out-of-slaughterhouse by-products" family is defined with the aim to convey the idea of valorizing such hitherto underused streams (cf., 5.2.2.). The remaining categories are not related to specific value chains, but are rather challenge-oriented. These include the development of (i) non-soluble protein extraction from diverse residual biomass feedstocks, (ii) solid substrate fermentation for nutrition and (iii) alternative liquid substrates for fermentation. Importantly, the eight families proposed herein can interact and are likely complementary to achieve a better use of resources from a circular economy standpoint. For example, cellulosic sugars, or organics remaining in the liquid fraction of anaerobic digestion, can be used as alternative fermentation substrates. Furthermore, because the families are not defined by specific technologies, they should be amenable to future technology innovations, for example biotechnology-based processes.

Fig. 6. Identified waste-to-nutrition conversion pathway categories and current status

[*] Technology Readiness Level (1-9): based on information available to date (SI).

[**] Valid for all pathways involving microorganisms.

7. Criteria for waste-to-nutrition pathways assessments

Obviously, the waste-to-nutrition pathways reviewed herein do not hold the same potential to supply novel food and feed resources and further studies are required to ascertain their true relevance and feasibility. To perform a quantitative prospective assessment, common criteria are required.

First, a clear hierarchy of residual biomass valorization must be established and respected. From a sustainability standpoint it is unacceptable to use avoidable wastes and residues as feedstock, especially when these are directly derived from food (Leipold et al., 2021; Mourad, 2016; Redlingshöfer et al., 2020). Similarly, residual biomass prioritization is essential to prevent the risk of rebound effects (i.e. encouraging additional waste and residues generation to ensure feedstock availability for biorefineries) (Teigiserova et al., 2020).

A second criterion must consider potential drawbacks and disruptions of diverting biomass streams from their current value chain (Abel and Blanc, 2017; Hedegaard et al., 2008). In this respect, a sensitive point is related to biomass that already sustain the food production system either directly (e.g. co-products as animal feed) or indirectly through agronomic valorization (e.g., composting, ploughing, fertilizing). The latter, not dealt with in this review, echoes the numerous incentives to close nutrient cycles through the promotion of organic fertilizers, among others those widening the scope of streams able to enter agronomic valorization pathways (European Union, 2019). Examples of their uses in urban farming are increasingly put forward (Billen et al., 2021; Stoknes et al., 2016; Van Zanten et al., 2019). Therefore, not only is it necessary to carefully compare waste-to-nutrition pathways between themselves, but also with conventional scenarios, also referred to as counterfactuals in LCA involving constrained resources (Pehme et al., 2017). Another trade-off of waste-to-nutrition pathways is the burden shifting between resource efficiency and utilities requirements. Indeed, previous analyses revealed that, depending on the scenario, novel ingredients do not necessarily always perform better (environmentally) than conventional ones, mainly because of higher requirements in energy, water, chemical and material (Bohnes and Laurent, 2021; de Boer et al., 2014; Sillman et al., 2020; Smetana et al., 2015; Spiller et al., 2020).

A third criterion must capture the spatio-temporal and context-dependent dimension (Dries et al., 2020). The demand for alternative practices that reduce pressure on arable land use is urgent and cannot be delayed for an indefinite period. However, different waste-to-nutrition pathways are characterized by different technology readiness and feasibility levels (Tuomisto, 2019). Some technologies are immature, while other are perhaps quite mature, but face major regulatory hurdles, stakeholder risk aversion or consumer rejection (Cameron et al., 2019; Specht et al., 2019; Tubb and Seba, 2019). In this regard, while synthetic “cultured” animal products (e.g. cultured meat) are still far from widespread commercialization (Post et al., 2020; Zhang et al., 2020), rapidly evolving socio-cultural considerations are likely to push innovation and accelerate development in the area (Crosser et al., 2019). Similarly, novel waste-to-nutrition pathways will not be deployable everywhere in the same way, either because of local availability of feedstock (see below) and technical skills, and/or because of socio-cultural trends. It is generally recognized that neophobia, cultural values and disgust are the major barriers for the widespread consumer acceptance of novel food (Fischer and Van Loo, 2021; Siegrist and Hartmann, 2020; Tuorila and Hartmann, 2020). These barriers make market uptake projections quite challenging, particularly when genetic engineering is involved (Boccia et al., 2018; Lähteenmäki-Uutela et al., 2021). Therefore, the challenge is to motivate change in people’s perception so that they can progressively accept such novel ingredients at their tables. For example, the inclusion of bacterial meal in astronauts’ diets could trigger a wider acceptance of microbial-based food (Verstraete et al., 2016). Similarly, many initiatives investigate the organoleptic enhancements of novel food such as plant-based proteins and upcycled agrifood co-products (cf. table 1 and SI database), aiming to increase their attractiveness. Safety considerations (see below) will also condition market uptake, especially in the case of ingredients stemming from feedstocks currently covered by waste regulations. About 75% of the pathways reviewed in this study target inclusion of novel ingredients in animal diets, suggesting a foreseen trend of waste-to-nutrition approaches development preferentially towards feed rather than food markets.

Another spatially related criterion concerns the potential impact and development pattern of a given waste-to-nutrition pathway. The feasibility of a pathway is intrinsically linked to the availability and processability of an appropriate residual feedstock. Many biomass feedstocks are characterized by high moisture content, which limits transport and increases perishability (e.g., sugar beet leaves). For these reasons, it is often preferable to process biomass close to the site of production. In the case of industrial streams, it might be even preferable to process them onsite. When waste-to-nutrition pathways are implemented in stand-alone facilities, it is necessary to carefully balance biomass availability and storage constraints with considerations related to the economy of scale, either opting for small-scale decentralized facilities or large-scale centralized ones (Maity, 2015). In this regard, although technology considerations partially dictate which option is most appropriate, this is not always the case. For example, insect biorefineries are economically feasible at both scale (Chia et al., 2019; Kröncke et al., 2020). Moreover, biotechnology-based processes also offer scope for downscaling and decentralization, with microbial bioconversion being feasible in transportable containers (Kernel.bio, 2020) and even domestic scales (Shojinmeat Project, 2020). Therefore, it is crucial to understand the ways in which waste-to-nutrition pathways are likely to be deployed, because evidence-based future narratives and scenarios on food transition are essentials to the proper context-dependent prospective comparison of different pathways (Antonsen and McGowan, 2021). Finally, one important future narrative to consider is the degree to which meat will still be produced and will coexist with its alternatives (plant-based, microbe-based). Change in meat production will have implications both on the feedstock side of waste-to-nutrition pathways, but also on the market side, eventually reducing the relevance of producing feed ingredients.

The final criterion relates to safety and the way this affects the substitution potential of novel nutritional services. Safety is a complex issue because it covers potential and real risks and needs to be addressed using technical and regulatory means. The application of the principle of precaution means that the introduction of any novel nutritional services will be confronted by strict institutional barriers (Lähteenmäki-Uutela et al., 2021; Tzachor et al., 2021). Overcoming these requires the compilation of large amounts of background data on risk assessment, so the "Generally recognized as safe" or "Novel food" labels can be granted (EFSA Panel on Dietetic Products, Nutrition and Allergies (NDA), 2016). In cases where the risk is patent (e.g., use of sludge or other feedstocks under the Waste Regulation), the hurdles will be higher and advanced technical solutions (e.g., sequence of cracking, refining and conversion units) will likely be required to attenuate the presence of noxious substances, viruses and microorganisms (Alloul et al., 2018; Verstraete et al., 2016). Therefore, safety-related barriers to implementation of novel waste-to-nutrition pathways must be assessed to properly compare these, establishing the plausible timeline to implementation and the likely technology cost involved. Additionally, because safety often involve purity and intense refining, it is necessary to assess a collateral risk, which is that of the market product being part of a cracking-building food chemistry pattern, likely leading to ultra-processed food ingredients (Fardet, 2018; van der Goot et al., 2016).

8. Conclusion

To enhance food system resilience and limit its environmental impacts, pathways transforming residual biomasses and C_1 gases into food and feed ingredients are gaining increasing attention. As a first step to assess their potential, this study classifies the main waste-to-nutrition pathways through the review of 950 literature records. The analysis reveals that most nutritional services can be provided through pathways built on different residual feedstocks, and reversely, one residual biomass can lead to a variety of nutritional outputs. Identified waste-to-nutrition pathways employ a sequence of unit operations workflow to adapt the initial composition-structure (i.e. nutritional, anti-nutritional and structural contents triangle) of the input to the end-market requirements while ensuring safety and regulations compliance. This study proposes a qualitative four-quadrant building block framework, composed by bioconversion, cracking, extraction and enhancement processes to systematically compare value chains, and classifies the reviewed waste-to-nutrition approaches into eight generic families.

Waste-to-nutrition pathways directly target the reduction, closing and shortcutting of nutrients flows loops, and should therefore be integrated within the broader context of transition towards low fossil carbon and planetary boundaries-compliant economies. In this regard, this comprehensive review highlights the wide span of the basket of solutions, where traditional residual biomass recycling approaches (e.g. livestock, compost) are likely complemented with emerging biotechnologies and extraction processes. Yet, further work remains necessary to capture the economic- and environmental relevance of a wide deployment of waste-to-nutrition strategies, considering context-dependencies.

CRediT authorship contribution statement

U. Javourez: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – Original Draft.

M. O'Donohue: Validation, Writing – Review & Editing.

L. Hamelin: Conceptualization, Funding acquisition, Resources, Supervision, Validation, Writing – Review & Editing.

Declaration of competing interests

The authors declare no conflict of interest.

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Credits

Figures of the present manuscript have been designed using free icons resources from Flaticon.com (authors: Surang, Linector, Good Ware, Monkik, Smashicons, Smalllikeart, Itim2101, DinosoftLabs, Roundicons, Vector markets, Darius Dan) and Wikipedia commons.

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Fig. 1. Scope of the literature review

Residual biomass categories, here illustrated by icons, are further detailed in the SI. Agronomic valorization (e.g. as fertilizer) is not part of the scope as this study focuses on the direct recovery of edible ingredients only.

Fig. 2. Waste-to-nutrition gap

Ternary diagram representing food grade quality perimeter (gray right corner), and approximating relative location of the studied solid residual biomass streams (colored circles). Phenolic lignin acts as both structural complexity and anti-nutritional proxies, but the latter is here privileged to differentiate wood-related residual biomass from green residual biomass and primary crops residues. MPF ingredients perimeter is not represented for tractability reasons. For the same reason, agrifood co-products and slaughterhouse by-products are gathered within the same broad circle (dotted line). Background data is available in the SI database and icons are as defined in figure 1.

*Albeit some slaughterhouse by-products (e.g. offal) are directly edible (within the gray right corner), others are mainly composed by keratin which is here considered as structural content (top corner), see section 5.2.2.

Fig. 3. Waste-to-nutrition pathways in four building blocks

Four generic families of conversion processes, illustrated with examples from the literature. Icons represent residual biomass categories as defined in figure 1 From top-down and left-right: (i) Fermented olive press-cake as fodder. (ii) Brewer' spent grains milled into bakery flour. (iii) Extraction of proteins from grass. (iv) Carbohydrates recovery from organic wastewater. (v) Recovery of cellulosic sugars. (vi) Feather processed with keratinases releasing amino acids. (vii) Insects farming on food waste and (viii) Microalgae cultured on aquaculture wastewater.

Fig. 4. Waste-to-nutrition microbial bioconversion pathways

Metabolic pathways are adapted from (Alloul et al., 2021; Choi et al., 2021; Linder, 2019) and complemented to capture the diversity of inventoried waste-to-nutrition microbial bioconversions. Key nutrients such as nitrogen and phosphorus are not represented to ensure visual tractability. Chemo(auto)trophic carbon-monoxide-oxidizing bacteria pathways are not represented here due to the scarcity of reported information on these.

Fig. 5. Producing alternative fermentation mediums from residual biomass: unit operations pattern

The indicative ranking of residual biomass families in the nutritional quality scale is derived from figure 2., and allows to visualize the estimated chain of unit processes required to bridge the gap between the initial composition-structure of a feedstock and the composition-structure which is adequate to deliver a nutritional service. Icons are as defined in figure 1. The identified conversion pathways are rather straightforward when starting from sugar- or lipid-rich residual biomass, but can be more complex, involving prior cracking and extraction operations to release fermentable compounds. Albeit limited by economic considerations (Kwan et al., 2019), purification technologies are often required to detoxify feedstocks and bring them up to nutritional specifications. C_1 gases can either have a fossil or biogenic origin, as represented in figure S5.

Fig. 6. Identified waste-to-nutrition conversion pathway categories and current status

[*] Technology Readiness Level (1-9): based on information available to date (SI).

[**] Valid for all pathways involving microorganisms.

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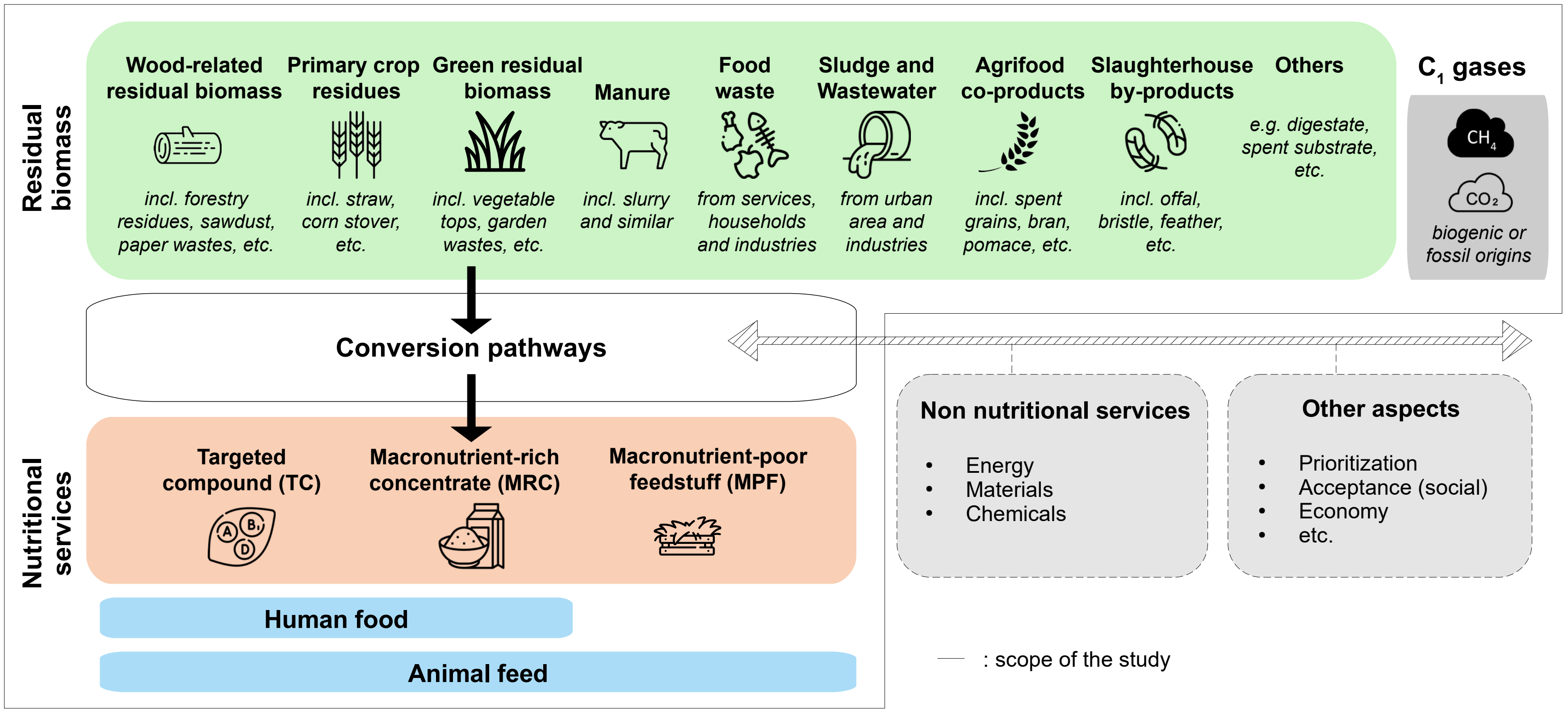
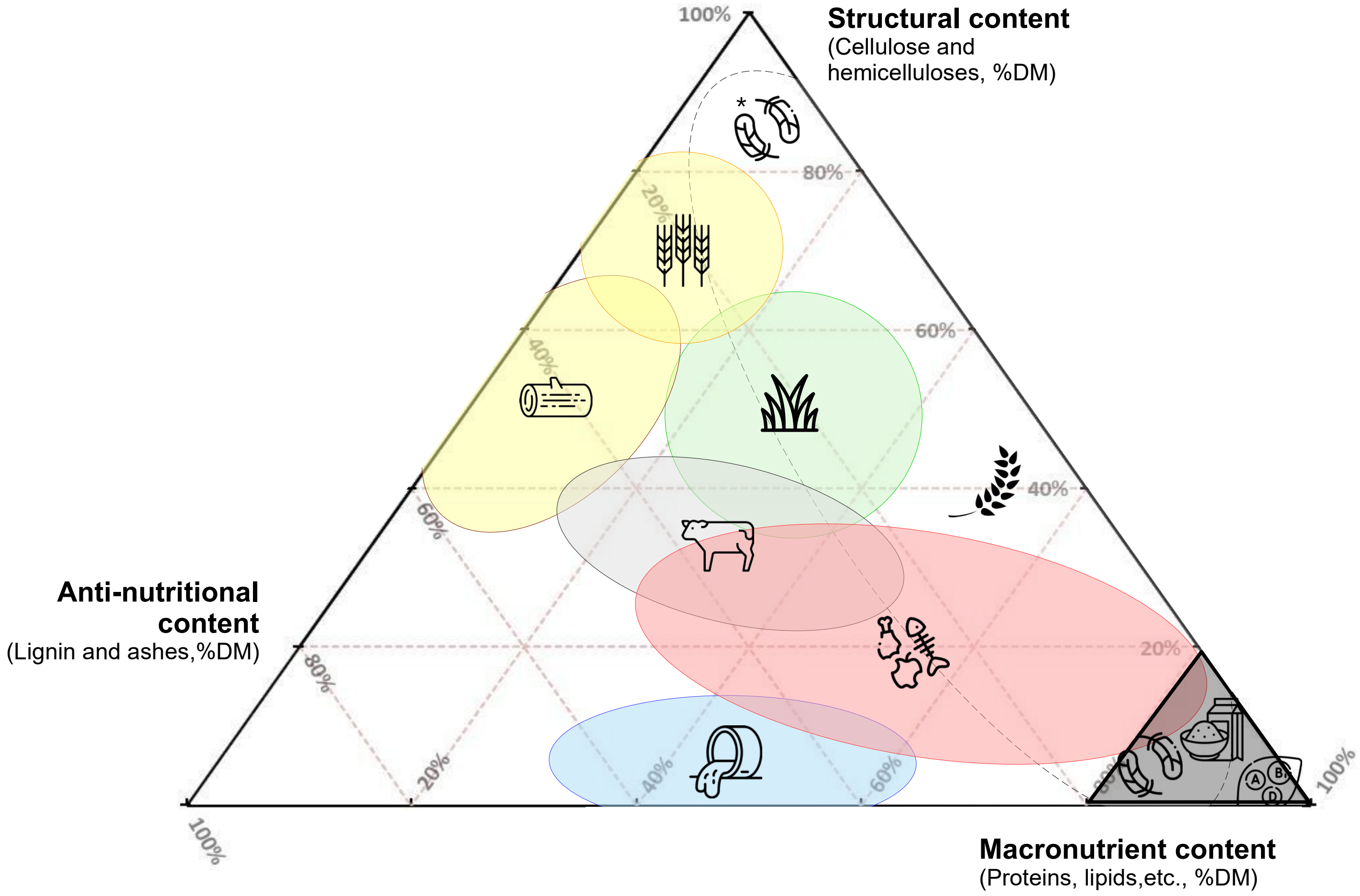
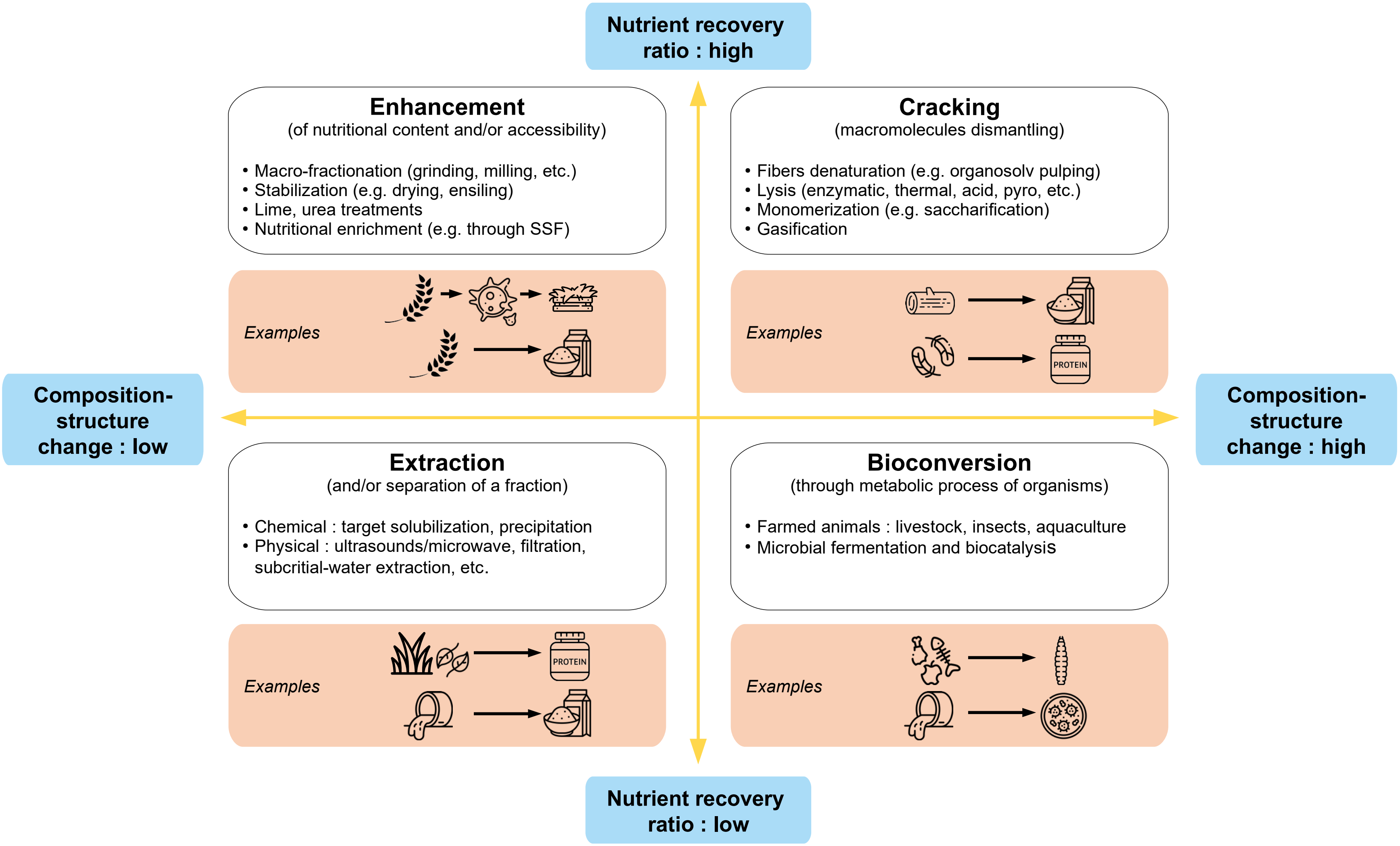
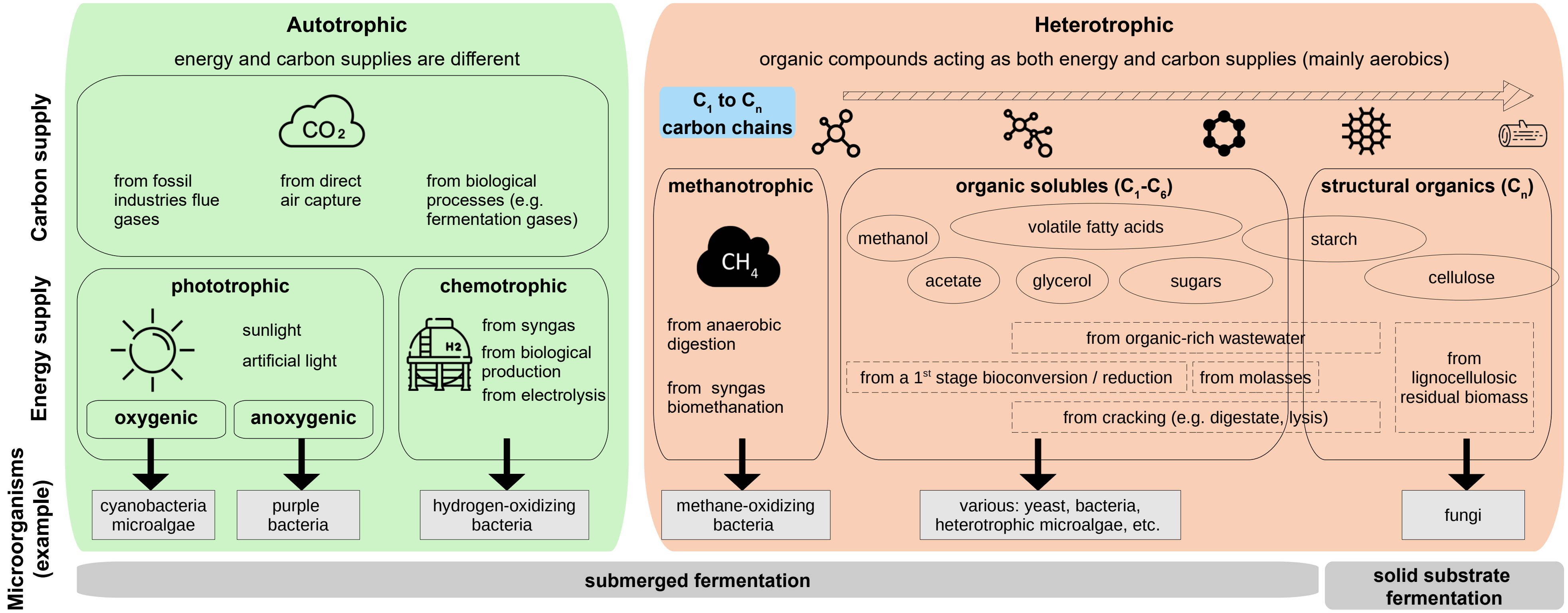
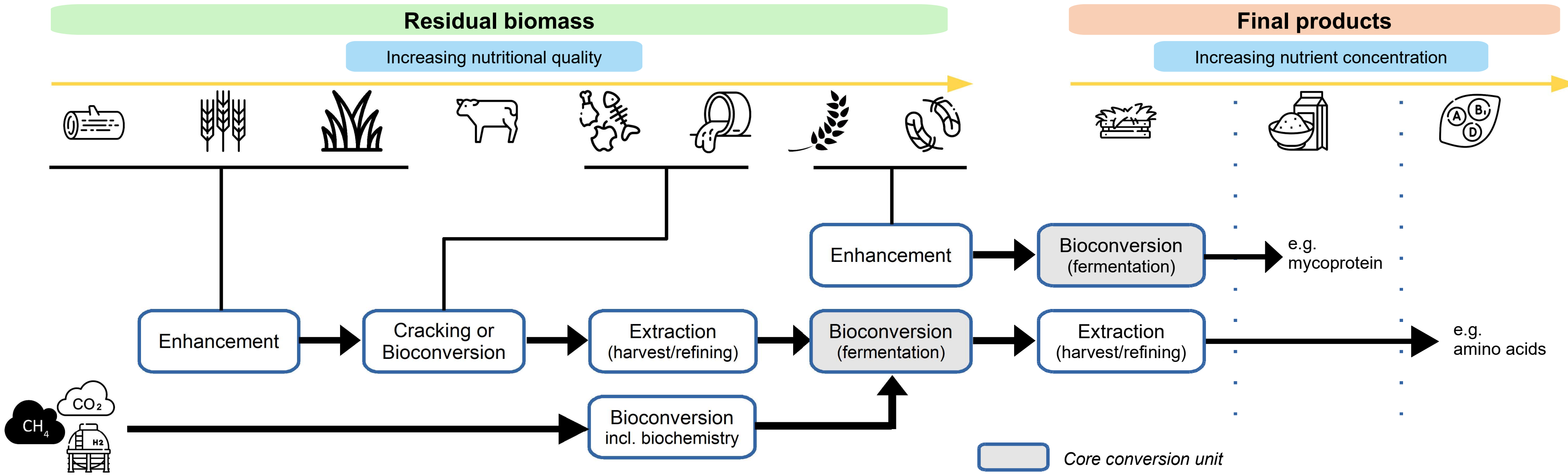

Residual biomass
Wood-related residual biomass
incl. forestry residues, sawdust, paper wastes, etc.
Primary crop residues
incl. straw, corn stover, etc.
Green residual biomass
incl. vegetable tops, garden wastes, etc.
Manure
incl. slurry and similar
Food waste
from services, households and industries
Sludge and Wastewater
from urban area and industries
Agrifood co-products
incl. spent grains, bran, pomace, etc.
Slaughterhouse by-products
incl. offal, bristle, feather, etc.
Others
e.g. digestate, spent substrate, etc.
C_1 gases
CH_4
CO_2
biogenic or fossil origins
Conversion pathways
Nutritional services
Targeted compound (TC)
Macronutrient-rich concentrate (MRC)
Macronutrient-poor feedstuff (MPF)
Human food
Animal feed
Non nutritional services
• Energy
• Materials
• Chemicals
Other aspects
• Prioritization
• Acceptance (social)
• Economy
• etc.
: scope of the study

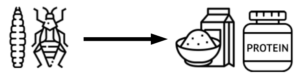
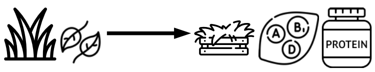
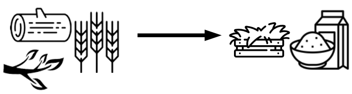
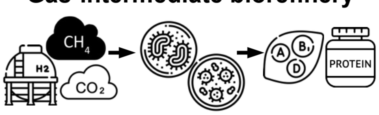
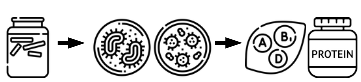
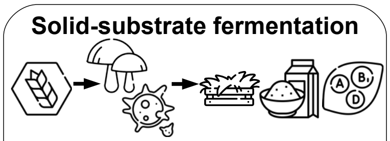
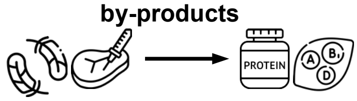

Structural content
(Cellulose and hemicelluloses, %DM)
Anti-nutritional content
(Lignin and ashes,%DM)
Macronutrient content
(Proteins, lipids,etc., %DM)
100%
80%
60%
40%
20%
*
A
B
D



Nutrient recovery ratio : high
Enhancement
(of nutritional content and/or accessibility)
• Macro-fractionation (grinding, milling, etc.)
• Stabilization (e.g. drying, ensiling)
• Lime, urea treatments
• Nutritional enrichment (e.g. through SSF)
Examples
Cracking
(macromolecules dismantling)
• Fibers denaturation (e.g. organosolv pulping)
• Lysis (enzymatic, thermal, acid, pyro, etc.)
• Monomerization (e.g. saccharification)
• Gasification
Examples
PROTEIN
Composition-structure change : low
Composition-structure change : high
Extraction
(and/or separation of a fraction)
• Chemical : target solubilization, precipitation
• Physical : ultrasounds/microwave, filtration, subcritial-water extraction, etc.
Examples
PROTEIN
Bioconversion
(through metabolic process of organisms)
• Farmed animals : livestock, insects, aquaculture
• Microbial fermentation and biocatalysis
Examples
Nutrient recovery ratio : low


Autotrophic
energy and carbon supplies are different
Heterotrophic
organic compounds acting as both energy and carbon supplies (mainly aerobics)
Carbon supply
CO_2
from fossil industries flue gases
from direct air capture
from biological processes (e.g. fermentation gases)
C_1 to C_n carbon chains
Energy supply
phototrophic
sunlight
artificial light
oxygenic
anoxygenic
chemotrophic
H2
from syngas
from biological production
from electrolysis
methanotrophic
CH_4
from anaerobic digestion
from syngas biomethanation
organic solubles (C_1-C_6)
methanol
volatile fatty acids
acetate
glycerol
sugars
structural organics (C_n)
starch
cellulose
from organic-rich wastewater
from a 1st stage bioconversion / reduction
from molasses
from cracking (e.g. digestate, lysis)
from lignocellulosic residual biomass
Microorganisms (example)
cyanobacteria microalgae
purple bacteria
hydrogen-oxidizing bacteria
methane-oxidizing bacteria
various: yeast, bacteria, heterotrophic microalgae, etc.
fungi
submerged fermentation
solid substrate fermentation


Residual biomass
Increasing nutritional quality
Final products
Increasing nutrient concentration
Enhancement
Bioconversion (fermentation)
e.g. mycoprotein
Enhancement
Cracking or Bioconversion
Extraction (harvest/refining)
Bioconversion (fermentation)
Extraction (harvest/refining)
e.g. amino acids
CO2
CH4
H2
Bioconversion incl. biochemistry
Core conversion unit
Pre- / Post-treatment units

Waste-to-nutrition families	Arguments	Challenges	TRL*
Insect biorefinery  Residual biomass digested by insects, further fractionated or used as a whole	• Animal proteins with reduced impacts • Markets for co-products (e.g. chitin and frass) • Insect proteins approved for swine and poultry markets, three species approved as novel food in EU to date	• Influence of feed on insect characteristics, risk of bio-accumulation • Acceptance as food limited • Risk of livestock-competing feed use	8-9
Green biorefinery  Separation of juice and fibers from green residual biomass	• Rubisco is the most abundant protein • Opportunity to directly grow it (if land is made available) • Markets for co-products (e.g. press-cake)	• Seasonality, heterogeneity and short shelf-life • Polyphenols interaction with proteins: trade-off between purity and yield	6-8
Lignocellulosic biorefinery  Cracking of lignin-based biomass into its basic compounds	• Highly available and no current direct use in nutrition • Integration potential within biofuel and biomaterial production platforms	• Utilities-intensive processes • Under-developed use of C_5-derived products	6-8
Non-soluble protein recovery  Techniques to extract structure-tied proteins (e.g. sludge and press-cake)	• Widely available streams • Under-efficient current use (if not hazardous) • Rapeseed meal protein extract approved as novel food in EU	• Low protein recovery efficiency • Costs of purification / refining • Legal barriers for streams not currently used as feed	5-9
Gas-intermediate biorefinery  Biogenic- or fossil-based gases used for microbial biomass production	• Potential land-free biomass production (e.g. coupling direct-air capture, Haber-Bosch process and electrolysis) • Potential integration to biogas, syngas and other industrial facilities • MOB meal already authorized in EU	• Gas-transfer and light-penetration limiting yields • Safety and organoleptic properties of microorganisms (limited inclusion as feed, low acceptance as food)** • Eventual competition with energy and chemical sources	5-8
Liquid substrate alternative  Submerged fermentation fed with residual-based nutrients	• Lowering fermentation industries dependency on raw carbohydrates and nutrients	• Risk assessment of novel strain-substrate associations required** • GMO acceptance to enter the food chain**	3-6
Solid-substrate fermentation  Direct microbial culture on solid residual biomass, harvested or used as a whole	• Allow to increase share of residual biomass in livestock diets • Direct use of the versatility of microorganisms	• Risk assessment of novel strain-substrate associations required** • Heterogeneous substrates modeling and operation	3-4
More-out-of-slaughterhouse by-products  Full recovery of animal-based by-products (incl. slaughterhouse and aquaculture)	• Improve overall performance of livestock production • Potential to recover valuable functional TC	• Limited acceptance • Safeguard functionality while ensuring safety (e.g. prion-related risks)	4-6