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► **To cite this version:**

U Javourez, Michael O'Donohue, Lorie Hamelin. Waste-to-nutrition: a review of current and emerging conversion pathways. *Biotechnology Advances*, 2021, 53, 26 p. 10.1016/j.biotechadv.2021.107857 . hal-03426554

HAL Id: hal-03426554

<https://hal.inrae.fr/hal-03426554>

Submitted on 5 Jan 2024

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1 **Waste-to-nutrition: a review of current and emerging conversion pathways**

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6 7 **Abstract**

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

12
13 In order to provide a comprehensive overview of the technical possibilities to convert
14 residual biomasses into edible ingredients, we reviewed over 950 scientific and industrial
15 records documenting existing and emerging waste-to-nutrition pathways, involving over 150
16 different feedstocks here grouped under 10 umbrella categories: (i) wood-related residual
17 biomass, (ii) primary crop residues, (iii) manure, (iv) food waste, (v) sludge and wastewater,
18 (vi) green residual biomass, (vii) slaughterhouse by-products, (viii) agrifood co-products, (ix)
19 C₁ gases and (x) others. The review includes a detailed description of these pathways, as
20 well as the processes they involve. As a result, we proposed four generic building blocks to
21 systematize waste-to-nutrition conversion sequence patterns, namely enhancement,
22 cracking, extraction and bioconversion. We further introduce a multidimensional
23 representation of the biomasses suitability as potential as nutritional sources according to (i)
24 their content in anti-nutritional compounds, (ii) their degree of structural complexity and (iii)
25 their concentration of macro- and micronutrients. Finally, we suggest that the different
26 pathways can be grouped into eight large families of approaches: (i) insect biorefinery, (ii)
27 green biorefinery, (iii) lignocellulosic biorefinery, (iv) non-soluble protein recovery, (v) gas-
28 intermediate biorefinery, (vi) liquid substrate alternative, (vii) solid-substrate fermentation and
29 (viii) more-out-of-slaughterhouse by-products. The proposed framework aims to support
30 future research in waste recovery and valorization within food systems, along with stimulating
31 reflections on the improvement of resources' cascading use.

32 33 **Abbreviations**

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

40 **Keywords**

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

45 1. Introduction

46 The urgency to rethink the food system is increasingly attracting attention (IPCC,
47 2019; Searchinger et al., 2018; Willett et al., 2019). The current agrifood system consumes
48 about 70% of the world's freshwater (Sims et al., 2017), is responsible for at least 80% of
49 deforestation (Ramankutty et al., 2018), 30% of the overall energy consumption, annually
50 generates an estimated 20-30% of the anthropogenic greenhouse gas emissions
51 (Rosenzweig et al., 2020) and is currently depleting non-renewable phosphorous ores
52 (Schoumans et al., 2015). One underlying flaw of the current agrifood system is its overall
53 inefficiency (Alexander et al., 2017b). For example, Schramski et al. (2020) showed that
54 today, roughly six calories of input energy yield just one calorie of consumable food-based
55 energy. Projected climate trends combined with forecasted demographic changes (including
56 overall population growth and its dietary preferences) depict a challenging picture for food
57 production capacities in 2050. For instance, the World Resources Institute estimates that
58 food demand will grow by 56% compared to 2010 levels, leading to an additional agricultural
59 land twice the size of India for food production to keep pace with demand (Searchinger et
60 al., 2018). On the other hand, Gerten et al. (2020) calculated that if the current agrifood
61 system was to operate within the safe zone of all planetary boundaries, it would only feed 3.4
62 billion people. Yet, because food is not a luxury, it is vital to identify solutions to sustain the
63 future food demand of the world's population.

64 There is consensus that resolving the food conundrum requires simultaneous actions
65 aimed at regulating food demand and consumption, improving production efficiency and
66 diminishing food losses (Billen et al., 2021; Clark et al., 2020; van der Goot et al., 2016). To
67 achieve these goals, it is possible to sustainably intensify agriculture, increasing production
68 while lowering environmental impacts (Hamelin et al., 2021; Pretty, 2018; Rockström et al.,
69 2017). Moreover, the emerging digitalization of agrifood systems is foreseen to boost
70 outputs, increase nutritional quality and enhance environmental performance (Herrero et al.,
71 2020; World Economic Forum, 2018). Finally, the adoption of advanced technologies, such
72 as biotechnology, can procure novel foods and feed ingredients, providing nutritional
73 services comparable to those of current food- and feedstuffs (Alexander et al., 2017a; Ercili-
74 Cura and Barth, 2021; Parodi et al., 2018; Torres-Tiji et al., 2020). The present study focuses
75 on the latter strategy, and particularly on solutions allowing to loop residual biomasses back
76 into the food chain, thereby decoupling food production from the demand of additional arable
77 land. In this work, such solutions are generically referred to using the term "waste-to-
78 nutrition", and "residual biomass" denominates both unused and underused biogenic wastes,
79 residues and co-products.

80 Residual biomass is a constrained resource (Hamelin et al., 2019), and many streams
81 are already supplying energy (e.g. via the biogas from anaerobic digestion), materials (e.g.
82 woodchips panel) and food-related services, either indirectly through agronomic valorization
83 (e.g. manure and straws used as organic fertilizers) or direct use in animal diets (e.g. meals
84 from vegetable oil extraction) when feed standards are met (Mottet et al., 2017). Given the
85 foreseen importance of residual biomass in future development narratives such as
86 bioeconomy (Muscat et al., 2021), competing value chains for these streams are emerging
87 (e.g. fine chemicals for cosmetics and pharmaceuticals), prompting the need to ensure the
88 implementation of the most efficient and cascading uses of these resources (Baldoni et al.,
89 2021; Duque-Acevedo et al., 2020; Venkata Mohan et al., 2016). Valorization hierarchies
90 constitute a useful framework to tackle this challenge (EC Directive, 2008; Teigiserova et al.,
91 2020). These suggest to privilege pathways where functional properties (e.g. proteins) are
92 safeguarded and directly valorized (e.g. into ingredients) before the implementation of lower-

93 value cascading recovery pathways (e.g. nutrients or energy) (Garcia-Bernet et al., 2020;
94 Gómez-García et al., 2021).

95 The potential of residual biomass to directly (i.e. not through an agronomic valorization)
96 produce food and feed ingredients has already been explored for specific cases such as
97 space travels (Clauwaert et al., 2017), agricultural catastrophes (Denkenberger and Pearce,
98 2015) or through livestock recycling (i.e. direct inclusion in farmed animal diets) (Rajeh et al.,
99 2021; Van Hal, 2020; Van Zanten et al., 2019). Yet, to our knowledge, no comprehensive
100 attempts have been made to collate data and identify the multiple conversion pathways that
101 allow this. In an endeavor to fill this gap, the aim of the present work is to provide an
102 extensive overview of current and emerging waste-to-nutrition pathways. Overall, 660
103 scientific papers and 270 records from industrial literature, including patents, were reviewed
104 (review methodology available in Supplementing information; SI). The approach developed
105 does not allow to directly conclude on the environmental or economic relevance of the
106 reviewed value chains. Indeed, those aspects are beyond the scope of the present work and
107 are context-specific, requiring specialized assessment methodologies (e.g. life cycle or cost-
108 benefit assessments). Nevertheless, as a stepping stone, this work is the first to detail,
109 classify and systematize in a single framework the main waste-to-nutrition pathways,
110 facilitating their further comparisons.

111 **2. Scope: ingredients and biomasses considered**

112 The umbrella categories of residual biomasses considered in this study are illustrated
113 in figure 1. The terminology used (i.e. waste, residue, co-product and by-product) for these
114 categories, as well as throughout this study, is carefully chosen and based on the EU
115 legislation as further detailed in the SI. The scope of categories is an expansion and
116 harmonization of the streams described in Hamelin et al. (2019), also described in the SI and
117 briefly reported here. The category “Wood-related residual biomass” shown in figure 1
118 includes primary forestry residues (defined in Karan and Hamelin, 2020), pruning residues,
119 wood-processing wastes (e.g. sawdust) and some packaging waste (e.g. cardboard). The
120 “Primary crop residues” category only includes straws, stalks and corn stover; tuber’s top
121 fractions (e.g. potato leaves) are included within the “Green residual biomass” category along
122 with garden- and park wastes (e.g. mowed grass). “Food waste” (discarded food stemming
123 from households or the service sector such as restaurants, etc.) and “Manure” (including all
124 types of livestock excreta, whether managed as slurry, solid or deep litter) are stand-alone
125 categories. “Sludge” and “Wastewater” (WW) are grouped in a single category that includes
126 streams coming from both industrial (e.g. potato WW) and municipal (e.g. sewage sludge)
127 origins. The “Agrifood co-products” category encompasses streams from primary
128 transformation (e.g. bran, pulp, peels, spent grains, etc.) and secondary transformation (e.g.
129 fruit canning, bakery, etc.) of agrifood industries. Despite their frequent valorization as feed
130 (Chapoutot et al., 2019), these co-products host upgrading valorization potentials (Garcia-
131 Bernet et al., 2020) and are therefore included in the scope of waste-to-nutrition pathways.
132 Because of their specific composition and of the regulation they are subjected to,
133 “Slaughterhouse by-products” (e.g. feather, carcass, bristle, etc.) are gathered in a distinct
134 category. Additionally, bioeconomy-related wastes (e.g. insect frass, digestates, etc.) and
135 specific wastes not stemming from the food sector (e.g. scrap newspapers) are added under
136 the category “Others”. Finally, nutrient looping pathways building on C₁ gaseous feedstocks
137 (CH₄, CO₂) are considered given their potential to decouple food production from land use
138 (Pikaar et al., 2018), whether these stem from a biogenic (e.g. resulting from biomass
139 processing) or fossil origin.

140 Three general categories of ingredients supplying nutritional services are
141 distinguished. The first category encompasses macronutrient-rich concentrates (MRC) that

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

150 For animals, the specific nutritional characteristics of MRC, MPF and TC are
151 combined in formulations to furnish balanced meals, often referred to as compound feed.
152 Formulation is performed based on precise knowledge of the animal's gut physiology,
153 nutritional requirements, health needs, legislative constraints, and an endeavor to minimize
154 the overall cost (Saxe et al., 2018). In the case of animals farmed for human consumption,
155 optimization also includes specific performance parameters (e.g., carcass lean meat, milk
156 yield, feed conversion ratio, etc.). On the other hand, human food is mainly restricted to MRC
157 and TC, even if the inclusion of ingredients in human diets also depends on cultural and
158 social habits (Teigiserova et al., 2020), with consumer acceptability being a key factor in
159 relation to the commercialization of novel food ingredients (Aschemann-Witzel and Peschel,
160 2019; Rumpold and Langen, 2020). This present review does not explicitly address
161 consumer acceptability (figure 1), although it is reported when the issue is raised in the
162 literature. Similarly, regulation aspects related to the entry of specific streams into food- and
163 feed-related markets are not specifically covered in this work.

164

165 **Figure 1. Scope of the literature review**

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

168

169 **3. Bridging the gap between waste and nutrition**

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

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

186 Structural complexity is particularly prevalent in fibrous biomass, such as
187 lignocellulose or keratin. These structures are highly robust and resist the chemical and
188 enzymatic reactions of common digestive processes. Therefore, the ability of monogastric

189 animals to degrade MPF is quite limited, while the multiple intestinal tracts of ruminants (and
190 termites gut microbiomes) are adapted to the digestion of cellulose-based structures (Godon
191 et al., 2013). However, even ruminants only display very limited ability to digest lignin
192 (Chapoutot et al., 2010; Moore and Jung, 2001) which constitute a highly resistant,
193 hydrophobic barrier that survives most biodegradation processes (Triolo, 2013).

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

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

213

214 **Fig. 2. Waste-to-nutrition gap**

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

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

223 Background data is available in the SI database and icons are as defined in figure 1.

224

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

226 The systematic analysis of reviewed literature (see database in SI) revealed that the
227 series of unit operations and processes implemented in waste-to-nutrition pathways vary
228 according to two main considerations: (i) the degree to which the feedstock input
229 composition-structure is altered, and (ii) the targeted nutrient recovery ratio (i.e., input versus
230 desired output). These are represented as a scale gradient in the X-Y axis of figure 3. Along
231 this scale, four generic processes are proposed as pathway building blocks: (i)
232 enhancement, (ii) cracking, (iii) extraction and (iv) bioconversion. These are one key result
233 arising from the transversal interpretation of the present review, and were defined with the
234 aim to provide an interpretative framework highlighting common trends in waste-to-nutrition
235 pathways. In fact, conversion pathways can be described as a sequential workflow of
236 processes using these modular building blocks. Notably, the four building blocks proposed

237 herein are in line with previous classification works (Colonna, 2020). Importantly, these
238 blocks do not relate to specific technologies, but rather reflect the main macroscopic changes
239 resulting from a set specific process when applied on a feedstock or product. Finally, the
240 modular block representation (e.g. similarly used in Verstraete et al. 2016) reveals how
241 different unit operations can be combined to generate varying degrees of nutritional quality
242 and process intensity.

243 **4.1. Enhancement: low composition-structure change, high nutrient recovery**

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

252 Albeit minor losses might occur (typically ranging between 5-30% of the dry matter
253 during ensiling (Borreani et al., 2018) or other SSF (Castoldi et al., 2014; Rajesh et al.,
254 2010)), enhancement processes recover a major share of the initial nutrients in the final
255 product, while safeguarding the global composition-structure characteristics. Indeed,
256 modifications are generally limited to the macro- and mesoscopic scales (e.g. for
257 comminution or drying), although some impacts at the microscopic scale are possible. The
258 latter particularly applies for SSF as this process is based on microflora activities, hence
259 generating microscopic changes (e.g. lignin mineralization). However, these induced
260 changes remain partial and limited provided that the fermentation process is stopped before
261 significant quantities of nutrients are converted. When this condition is fulfilled, the product
262 displays compositional and structural properties that resemble that of the feedstock residue
263 (e.g., ensiled grass versus raw grass), and therefore enters the enhancement building block.

264

265 **4.2. Cracking: high composition-structure change, high nutrient recovery**

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

278

279 **4.3. Extraction: low composition-structure change, low nutrient recovery**

280 Extraction includes all unit operations and processes that selectively solubilize and/or
281 separate a target fraction from a matrix, while safeguarding its initial functional properties
282 (Jimenez et al., 2015). Some extraction processes are hybrid, combining the features of both

283 extraction and cracking processes (e.g., alkaline extraction). However, extraction processes
284 differ from cracking in as much that the targeted compound or fraction is not necessarily a
285 structural component of the feedstock and is generally a minor fraction (e.g., proteins in
286 tomato seeds). Unlike cracking, extraction does not induce generalized molecular-scale
287 disruptions (Gençdağ et al., 2020; Rodriguez-Lopez et al., 2020). Extraction often involves a
288 sequence of separation processes (e.g., precipitation and filtration) and isolation processes,
289 all included within the extraction building block.

290 According to the literature reviewed, the recovery potential of an extraction step is
291 limited by (i) the amount of the targeted TC available in the feedstock and (ii) the maximum
292 achievable yield using the extraction technique. The latter is heavily dependent on the
293 compound-structure interactions and inversely correlated to the desired purity (Colonna,
294 2020; Tamayo Tenorio et al., 2018). For example, considering proteins present in green
295 residual biomasses (<20%DM), only a fraction (5-45% of total) is recovered using the
296 extraction techniques described in section 5.3.3. (Santamaria-Fernández and Lübeck, 2020).
297 Similarly, all common downstream separation and purification processes used to obtain TC
298 such as valuable fatty acids (e.g. docosahexaenoic acid: DHA) compliant with market
299 specifications imply mass and nutrient losses. For example, in weight terms, 1 to 15 units of
300 DHA is obtained per 100 units of microalgae or aquatic protists (Russo et al., 2021;
301 Xiangping et al., 2019). The reviewed literature often highlighted this particular point:
302 extraction processes typically generate significant quantities of side streams whose
303 synergetic valorization is key to ensure economic sustainability (Teekens et al., 2016).

304

305 **4.4 Bioconversion: high composition-structure change, low nutrient recovery**

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

327 For convenience, microbial and farmed animal bioconversion sub-groups are further
328 distinguished. Microbial bioconversion encompasses the use of microorganisms both as
329 biocatalysts that produce enzymes and nutritional TC such as vitamins, amino acids or flavor
330 compounds (Specht and Crosser, 2020; Sun et al., 2021; Yang and Xu, 2016), and as final

331 standalone nutritional MRC themselves. Currently, this latter function is encountering
332 renewed interest, especially regarding so-called “single cell proteins” i.e., microbial proteins
333 and fungal proteins (Ciani et al., 2021; Hüttner et al., 2020; Linder, 2019; Singh et al., 2020;
334 Tubb and Seba, 2019) which cover organisms that generate high protein (up to 70-75%DM)
335 content (Pikaar et al., 2018). Similarly, single cell oils (Ochsenreither et al., 2016) and all
336 microbial-based fermentation and cell-culturing aiming at substituting common food products
337 (Crosser et al., 2019; Lv et al., 2021; Specht and Crosser, 2020) are also considered within
338 this bioconversion building block.

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

345

346

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

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

353

354 5. Waste-to-nutrition pathways debunked

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

366

367 5.1. Direct upgrading: nutritional enhancement pathways

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

371 For animal feed, enhancement pathways typically increase the digestibility of fibrous
372 materials by disrupting the complex plant cell wall matrix and releasing macromolecular
373 structures, such as polysaccharides in lignocellulosic feedstocks. In addition to breaking
374 down structural barriers, enhancement strategies sometimes achieve a net nutritional
375 enrichment of the feedstock. This is the case for ammonia-fiber expansion treatments
376 increasing the total nitrogen content of ruminant forage (MPF), but also for SSF treatments

377 provoking protein and/or lipid enrichment. SSF treatments are often applied after a first
378 mechanical enhancement step. Used on lignocellulosic residual biomass, SSF allows to
379 selectively degrade lignin while avoiding microbial polysaccharide consumption (e.g., using
380 white rot fungi) (van Kuijk et al., 2015; Villas-Boas et al., 2002), and thus provides access to
381 a wider range of lignocellulosic biomass for use as MPF. In the case of monogastrics,
382 enhancement pathways are employed to substitute MRC, using residual biomass with low
383 lignin content as feedstock for SSF aiming to convert part of the polysaccharide fibers into
384 assimilable nutrients (e.g., free sugars and proteins) (Patil et al., 2020; Villas-Boas et al.,
385 2002; Wongputtisin et al., 2014). Consequently, the product is characterized by higher
386 nutrient availability and content and displays improved palatability. As conventional
387 aquaculture uses high quality feed products (high protein and lipid digestibility), the inclusion
388 of mildly treated fibrous materials is often avoided (Leduc, 2018). Nevertheless, SSF
389 transformation units are used to generate alternative feed products for aquaculture, by
390 improving digestibility of non-lignocellulosic feedstocks such as feather meal and isolated
391 plant-based proteins (Dawood and Koshio, 2020; Hamidoghli et al., 2020).

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

400 **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: <i>Fusarium flocciferum</i> 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 <i>Colletotrichum spp.</i> , 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 <i>Kluyveromyces marxianus</i> 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 <i>Bacillus subtilis</i> 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: <i>Saccharomyces cerevisiae</i> strain, 30°C, 70% moisture 3. Homogenization and dried 55°C.	Protein content increased 11 times. Can be included in cereal bars with improved sensorial 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)

401 SSF: Solid Substrate Fermentation

402 **5.2. Cracking pathways: Unlocking nutrients in structural biomass**

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

408

409 **5.2.1. Lignocellulosic feedstock to sugars and dietary fibers**

410 Lignocellulosic feedstocks are characterized by three interlinked macromolecules: (i)
411 cellulose, (ii) hemicellulose and (iii) lignin representing 38-52%, 15-30% and 10-40% of the
412 dry matter, respectively (Kapu and Trajano, 2014). Cellulose is a homopolymer composed of
413 glucose, while hemicellulose is a generic term for β -1,4-linked non-cellulosic plant-based
414 polymers (Scheller and Ulvskov, 2010). The most abundant class of hemicelluloses are
415 xylans that are mainly composed of pentoses (i.e., C₅ sugars like xylose and arabinose).

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

435 For food applications, product purity is of prime importance, because high severity
436 (e.g. high temperature, pH changes) cracking processes often generate undesirable products
437 and neoformed chemical species, such as furfural or acetic acid (Venkateswar Rao et al.,
438 2016). The hydrolysates detoxification stage (i.e., removal of anti-nutritional compounds) is
439 thus often a prerequisite for commercialization (Domingos et al., 2020; Dupoirion et al.,
440 2017). In this regard, the use of alternative strategies, such as preventive pretreatment
441 and/or enzyme-mediated hydrolysis might be advantageous and provide economically more
442 viable routes to target food ingredients from lignocellulose (Paës et al., 2019; You et al.,
443 2013). Enzymes act as highly selective catalysts that operate in mild (e.g., low temperature
444 and near neutral pH) conditions and do not generate neoformed compounds, thus potentially
445 positively influencing costs (Ingle et al., 2020; Roth et al., 2020). Consolidated bioprocesses
446 involving the *in-situ* production of enzymes are often preferred for economic reasons, albeit
447 requiring an additional stage of bioconversion to produce them.

448

449 5.2.2. Amino acids recovery from slaughterhouse by-products

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

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

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

497

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).

514

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).

544

545 **5.3.2. Protein recovery from activated sludge**

546 Activated sludge is the solid fraction remaining after the biological treatment of WW.
547 Activated sludge is mainly composed of microbial biomass and is rich in proteins (up to
548 60%DM). Albeit sometimes directly reused for example in “sewage fish farms” (Verstraete et
549 al., 2016), the presence of noxious compounds (e.g., pathogenic bacteria or detergent)
550 usually prevent its direct use as animal feed (Vriens et al., 1989). Therefore, several studies
551 have investigated the means to extract proteins implementing “sludge-to-proteins route”
552 (Xiao and Zhou, 2020). In addition to the high moisture content of sludge, another
553 disadvantage is that sludge proteins are contained within microbial cells. Therefore, it is
554 necessary to use a first stage, such as hydrothermal and ultrasound treatments, to
555 disintegrate microbial cells and release proteins. Afterwards, the recovery stage yields up to
556 90% of the proteins and the removal of most noxious compounds, such as heavy metals
557 (Gao et al., 2020; Liang et al., 2020; Zhang et al., 2018). The resulting sludge protein
558 concentrates display a complete amino acids profile and are investigated to supply the
559 animal feed markets (Belyaev et al., 1978; Hwang et al., 2008; Markham and Reid, 1988).
560 However, to drive sludge proteins into the food sector, it is necessary to implement more
561 intensive, cost prohibitive purification methods (Xiao and Zhou, 2020). Nevertheless, to
562 obtain food-grade proteins, it might be more reasonable to focus on sludge derived
563 exclusively from WW treatment facilities associated with food transformations units (e.g.,
564 brewer effluent, bakery effluent), with the drawback of limited available volumes (Vriens et
565 al., 1989).

566

567 **5.3.3. Protein recovery from green residual biomass**

568 Green biomass refers to all photosynthetic organs of plants, such as grass, vegetable
569 tops and leaves. Those all harbor significant quantities of Rubisco, which is the key CO₂-
570 fixing enzyme in plants. Although crude protein levels vary among species and as function of
571 pedoclimatic conditions, they nevertheless represent 10-25% DM of green biomass, of which
572 up to 50% is soluble (Solati et al., 2018). A specificity of green biomass compared to general
573 plant-based biomass, is their low lignin content (<10%DM) coupled to high moisture, typically
574 well above 70% of total weight (Tamayo Tenorio et al., 2018; Triolo, 2013). These
575 characteristics are compatible with the mechanical separation of the freshly harvested green
576 biomass into two fractions: a nutrient-rich juice and a fiber-rich cake, each harboring around
577 50% of the initial proteins (Kromus et al., 2008). This first mechanical extraction process is
578 the starting point of most protein recovery in green residual biomass conversion pathways.

579 To maximize protein recovery, common extraction units such as thermal coagulation
580 followed by centrifugation and drying are commonly performed on the green juice. The
581 resulting leaf protein concentrate (LPC) (Davys et al., 2011; Pirie, 1971) targets monogastric
582 livestock market, as a substitute for soy meal (Stødkilde et al., 2019). The implementation of
583 additional refining steps can lead to food-grade extracts (Di Stefano et al., 2018; Martin et al.,
584 2019). The fiber-rich cake mostly contains non-soluble proteins, hence preventing their direct
585 recovery. However, this cake can be used as a substitute for raw grass in ruminant diets,
586 while additionally providing the means to reduce nitrogen excretions (Damborg et al., 2020;
587 Lucci et al., 2019). Advantageously for this fraction, the initial mechanical fractionation of
588 e.g., grass increases the overall accessibility of grass proteins and thus offsets the absence
589 of soluble proteins present in the green juice fraction (Damborg et al., 2018).

590 While a wide panel of residual biomass for LPC production had been historically
591 screened (Pirie, 1971; Rosas Romero and Diaz, 1983), to-date commercial-stage

592 developments are only based on premium green crops such as alfalfa. Monogastric-grade
593 alfalfa LPC is already commercialized (Andurand et al., 2010) while alfalfa food-grade
594 extracts are recently entering markets (Luzixine, 2020; Tereos, 2020). However, numerous
595 European-based consortia attach to widen the panel of LPC production feedstocks, such as
596 LPC production from raw grasses (Agroväst, 2020; Go Grass, 2020), green cuttings
597 (GrasGoed, 2020) and vegetable tops such as sugar-beet (Green Protein Project, 2020;
598 Tamayo Tenorio, 2017). The seasonality, heterogeneity and perishability of green biomass,
599 coupled to energy-intensive technologies that procure insufficiently high protein yields are
600 increasingly driving LPC production towards green biorefinery schemes in which LPC is just
601 one of several added-value products (Corona et al., 2018b; Djomo et al., 2020; Santamaría-
602 Fernández et al., 2020). Depending on local contexts, diverse green biorefinery setups and
603 schemes exist, each aiming to supply energy, material and chemicals (e.g. lactic acids) from
604 the LPC co-products (i.e. fiber-rich cake and supernatant “brown” juice) (Corona et al.,
605 2018a; Kamm et al., 2016; Kiskini, 2017; Parajuli et al., 2018). Similarly, focus has also been
606 put on the recovery of proteins in cellulosic bioethanol biorefineries (Bayat et al., 2021), using
607 for this purpose non-residual biomass streams, such as switchgrass (Bals and Dale, 2011;
608 Kammes et al., 2011; Laser et al., 2009).

609

610 **5.4. Microbial bioconversion pathways**

611 The literature survey revealed that the use microorganisms to recover and
612 concentrate nutritional products from residual biomass is a well-studied route. Obviously, the
613 term “microorganism” embraces an extraordinarily large number of species. Therefore,
614 waste-to-nutrition pathways reviewed herein are classified according to the main metabolic
615 processes involved, consistent with previous works (Jones et al., 2020; Spalvins et al.,
616 2018). Resulting sub-categories are displayed in figure 4, and mainly differ regarding the
617 preferred carbon and energy sources of the microbes. The categories are indicative,
618 because some microorganisms are mixotrophs, being capable of several metabolic
619 processes (e.g., purple bacteria), while other conversion pathways involve simultaneously
620 more than one microbial culture (Alloul et al., 2021a; Rasouli et al., 2018; Yang et al., 2019;
621 Zhu et al., 2020).

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

627

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

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

633

634 **5.4.1. Direct microbial bioconversion pathways**

635 Direct microbial bioconversion pathways are heavily dependent on the characteristics
636 of the feedstock. Accordingly, two main approaches are distinguished, in which the substrate

637 is either under a solid or a liquid (i.e., wastewater) form. The proposed unit operation pattern
638 is displayed in SI (figure S4) and corresponding examples are presented in table 2.

639

640 **5.4.1.1. Fungiculture**

641 In the review, SSF processes to generate harvestable nutritional metabolites targeting
642 both TC and MRC ingredients were reported. Regarding TC production, identified pathways
643 mainly focus on enzymes and flavors (Aggelopoulos et al., 2014; Sharma et al., 2020;
644 Teigiserova, 2020) which are not the purpose of the present study. On the other hand, the
645 production of MRC is principally achieved through fungiculture, as further detailed. The
646 fruiting bodies of fungi (i.e., mushrooms) are commonly cultivated on moisturized
647 lignocellulosic materials, meaning that food grade foodstuff (e.g., *Pleurotus spp.* ranging 15-
648 45%DM protein content) is obtained in a single unit operation from non-food feedstock
649 (Bellettini et al., 2019; Chanakya et al., 2015; Ritota and Manzi, 2019). The fungiculture unit
650 operation can be decomposed into two main sub-stages corresponding to mycelium
651 colonization of the substrate, followed by fructification (cf., table 2). The spent mushroom
652 substrate displays a reduced lignin content, and is enriched in proteins and lipids (Khan et
653 al., 2015; Wang et al., 2001). Therefore, depending on the initial feedstock, it is possible to
654 use the spent substrate in animal feed regimes (Mhlongo et al., 2021; Wanzenböck et al.,
655 2017), mix it with fresh feedstock to generate new SSF substrate (Hamed et al., 2020), or
656 implement subsequent transformation steps. In this case fungiculture acts as a pretreatment
657 for cellulosic sugar recovery for example (Chen et al., 2021). The time period required to
658 convert residual biomass into mushrooms is generally at least three to four weeks when
659 using optimized strains and culture conditions, but this often extends to several months,
660 especially when it is necessary to first compost the feedstock (i.e., a prolonged bioconversion
661 process).

662

663 **5.4.1.2. Wastewater to nutrition**

664 WW has been successfully used as microbial bioconversion medium, mostly using
665 WW from: (i) food (e.g., vegetable oil) and beverage (e.g., brewing) processing
666 (Amenorfenyo et al., 2019; Marchão et al., 2018; Patsios et al., 2020), (ii) animal effluents
667 from farms and slaughterhouses (Li et al., 2019) and (iii) certain non-food industries, such as
668 fertilizer manufacture (Chavan and Mutnuri, 2020) or paper pulp mills (Romantschuk, 1975).
669 These WW have in common to host rich organic loads and a low carbon-to-nitrogen ratio
670 (Spalvins et al., 2018; Vethathirri et al., 2021). However, the presence of toxic compounds
671 can vary greatly depending on their specific origin. The services supplied by microbial
672 bioconversion on such residual liquid substrate are thus two-fold: (i) production of microbial
673 biomass from WW and (ii) removal of the nutrient charge (i.e., WW treatment) (Muys et al.,
674 2020; Tomlinson, 1976). Mixed-culture mixotrophic microalgae and purple bacteria are
675 particularly adapted to such diluted media (Cao et al., 2020; Capson-Tojo et al., 2020;
676 Solovchenko et al., 2020). They combine atmospheric carbon capture with the use of soluble
677 organics and nutrients, reducing the need for additional inputs (Hülßen et al., 2018; Shahid et
678 al., 2020).

679 The aquaculture market is a prime target for wastewater-to-nutrition pathways,
680 because microorganisms are already part of the fish trophic chain (Glencross et al., 2020;
681 Milhazes-Cunha and Otero, 2017). However, if not deployed *in-situ* (e.g., through activated
682 sludge-derived biofloc technologies) (Alloul et al., 2018; Bossier and Ekasari, 2017), the
683 requisite harvesting and dewatering of low concentration microbial biomass using a series of

684 energy-intensive extraction steps rapidly becomes cost ineffective. Furthermore, the final
685 market is currently dependent on the quality of the initial WW, because technical
686 specifications (e.g., fecal contamination) drive the requirements of additional intensive
687 prior/post purification treatment steps (Verstraete et al., 2016). In this respect, food-grade
688 applications are mainly limited to high quality food-processing WW (e.g., from starch
689 production, table 2), which is only available in limited volumes.

690 **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 <i>Chlorella pyrenoidosa</i> and yeast <i>Rhodotorula glutinis</i> 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 <i>Paecilomyces varioti</i> 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 <i>Chlorella vulgaris</i> , 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 (<i>Shiitake</i> , <i>Pleurotus sp...</i>) 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 <i>Agaricus bisporus</i> 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 <i>Pleurotus</i> : 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)

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

692 **5.4.2. Indirect microbial bioconversion pathways**

693 In the field of nutritional services, direct microbial bioconversion is restricted to small
694 number of microorganisms and the use of quality feedstocks (cf., 5.4.1. and 5.1.). The
695 delivery of nutritional services from residual biomass through microorganisms can be
696 extended by adapting the feedstock to the specific requirements of the fermentative microbial
697 cultures. The common objective of these indirect bioconversion pathways is the substitution
698 of high-grade nutrients (commonly used to formulate fermentation medium) with lower grade
699 materials. However, the scientific literature mainly focuses on the use of mixed feedstocks
700 where only a part of the nutrient requirement is furnished from lower grade materials and
701 completed with quality ingredients. Nonetheless, the conversion pathways included in this
702 section all share the feature of at least partially supplying the energy, carbon and nutrients
703 required for microbial bioconversion from residual biomass or C₁ gases.

704 Indirect microbial bioconversion pathways can be subdivided into two categories. The
705 first group relates to bioconversion of C₁ gases, while the second group targets the
706 elaboration and bioconversion of alternative soluble fermentable compounds (C₁ to C₆).

707

708 **5.4.2.1. Gas-to-nutrition conversion pathways**

709 The gas-to-nutrition pathways employ C₁ gases (mainly CH₄ or CO₂) as carbon
710 source for microbial biomass production. The generic unit operation pattern is illustrated in SI
711 (figure S5). The energy source defines the exact nature of the pathway: phototrophic
712 bioconversion fixes carbon dioxide using light (representative examples in SI, table S3),
713 while chemotrophic bioconversion converts high-energy gases such as dihydrogen into
714 biomass (table 3).

715 Phototrophic pathways are similar to wastewater-to-nutrition pathways (section
716 5.4.1.2.), especially regarding post-treatment. However, phototrophic pathways usually focus
717 on the capture of concentrated CO₂ streams (figure 4). Accordingly, phototrophic organisms
718 (mainly microalgae and cyanobacteria) are operated in reactors optimized for light
719 penetration and gas transfer and fed with essential nutrients (e.g., N, P, K, etc.) in order to
720 produce proteins and omega-3 fatty acids. According to the literature, these nutrients are
721 often sourced from high grade products (e.g., glutamate, peptone, fertilizers) instead of being
722 upcycled from residual biomass streams. However, in addition to the use of waste C₁ gases,
723 some gas-to-nutrition pathways also harness nutrients from underused streams (e.g.,
724 predominant N leakages such as animal and human effluents) to satisfy the nutritional
725 requirements of the microorganism (Matassa et al., 2015; Yang et al., 2021). The versatility
726 of bacterial strains, which can use different forms of nitrogen such as NH₃, NH₄⁺ (Dou et al.,
727 2019) and N₂ (Hu et al., 2020; Pfluger et al., 2011) provide the basis for a whole range of
728 pathway variants.

729 Chemotrophic pathways mainly rely on either hydrogen-oxidizing bacteria (HOB) or
730 methane-oxidizing bacteria (MOB), both of which use gases as their carbon and energy
731 sources and hence provide the basis for “full-gas” pathways (Matassa et al., 2020).
732 Importantly, chemotrophic processes are characterized by high conversion efficiencies
733 (Claassens et al., 2016; Liu et al., 2016; Pander et al., 2020) in large part because, unlike
734 phototrophic processes, they are not limited by energy availability. Additionally, chemotrophic
735 bacteria can fix between 80% and 100% of their N supply (Pikaar et al., 2017) into microbial
736 biomass, which yields a protein content of approximately 70%-80% and an amino acids
737 profile analogous to that of fish meal (Matassa et al., 2015; Øverland et al., 2010). For these
738 reasons, HOB and MOB strains have been arousing interest for some time, with their

739 proteins being studied for human nutrition, especially in the context of space travel (Alvarado
740 et al., 2021; Foster and Litchfield, 1964; Steinberg et al., 2017). The suitability of MOB meals
741 as a substitute for conventional high-protein ingredients in monogastric animal diets has
742 been demonstrated (Øverland et al., 2011, 2010) and these are already close to
743 commercialization unlike HOB routes. However, one cause for concern is the significant
744 presence of anti-nutritional RNA/DNA and endotoxins in bacterial biomass. Therefore, if not
745 mitigated through genetic engineering, this often must be eliminated before the microbial
746 biomass is considered fit for consumption. Nucleic acids removal can be achieved through
747 heat treatments, as already performed during the industrial production of *F. venenatum* (RNA
748 content reduced from 8-9% down to 1% in weight) (Whittaker et al., 2020).

749 The origin of C₁ gases is key to the economy of chemotrophic pathways (García
750 Martínez et al., 2021; Huizing, 2005; Verbeeck et al., 2020). While scaling projects currently
751 focus on the use of fossil-based methane and electrolysis-based hydrogen, syngas and
752 biogas are also investigated (cf., table 3). The inherent variability and heterogeneity of these
753 biogenic gases are attenuated through scrubbing, removing undesirable gas components,
754 such as carbon monoxide and hydrogen sulfide (Tsapekos et al., 2019; Xu et al., 2020).
755 Accordingly, gases for chemotrophic pathways can be derived from residual biomass through
756 a sequence of cracking and/or bioconversion units (e.g., anaerobic digestion, gasification)
757 followed by refining units.

758 The low solubility of H₂ (De Vrieze et al., 2020) and the safety issues related to the
759 simultaneous presence of H₂ and O₂ for aerobic HOB production (Molitor et al., 2019) are
760 also questions that are addressed by current research work. Often, to meet these
761 challenges, additional processes are envisaged for chemotrophic pathways (Sakarika et al.,
762 2020). For example, gases are first converted into organic compounds (e.g., acetic acid or
763 methanol) using either biocatalysis (e.g., fermentation using an acetogenic bacteria) or
764 physico-chemistry (e.g., hydrogenation) (Linder, 2019; Mishra et al., 2020). The resulting
765 organic compound is then used as substrate to support the growth of a common
766 heterotrophic organisms such as yeast. Alternatively, the overall process can be achieved in
767 a single step using the co-culture of several microorganisms (Du et al., 2020). An emerging
768 route is the use of volatile fatty acids (VFAs) as platform intermediates instead of end-gases.
769 This novel approach, described in Alloul et al. (2018) targets acidogenic fermentation on
770 dissolved carbon sources (obtained through prior cracking or conversion of residual biomass)
771 to recover VFAs. These are further converted into edible biomass through flexible
772 microorganisms such as purple bacteria (Capson-Tojo et al., 2020; Lu et al., 2021) or
773 filamentous fungi (Uwineza et al., 2021).

774

775 **5.4.2.2. Alternatives to common microbial bioconversion medium**

776 The previous section describes processes that require the use of novel substrate-
777 microbe associations regarding nutrition. However, axenic microbial bioconversion is already
778 a core technology of the feed and food industries, being widely used to produce amino acids,
779 lipids or mycoproteins from well-defined substrates such as raw glucose or methanol.
780 Nevertheless, with increasing pressure to deliver cost-competitive carbohydrates in a
781 framework of environmental sustainability and food/feed security, analysis of the literature
782 reveals that considerable focus is put on the investigation of alternative carbon sources
783 (Siben et al., 2018; Specht, 2020; Specht and Crosser, 2020). Accordingly, this section
784 provides a description of attempts to drive low-cost residual biomass into common microbial
785 bioconversion pathways, using a series of conversion processes to ensure that nutrient and

786 end-product quality and safety are maintained, as represented in figure 5. A selection of
787 examples from the literature is available in SI, table S4.

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

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

809 Finally, synthetic pathways to produce fermentable TC are reported in the literature.
810 Also called power-to-food or power-to-protein (Mishra et al., 2020; Sillman et al., 2020),
811 these approaches use electricity to produce the reducing power further converted by a target
812 microorganism. A first application is to extend the possibilities of gas-to-nutrition pathways,
813 for example through the "CO₂-to-CH₄-to-protein" route (Xu, 2021) or converting hydrogen into
814 methanol and acetic acid as mentioned in section 5.4.2.1.. Similarly, synthetic pathways are
815 also engineered to fix CO₂ through "biological-inorganic" (Nangle et al., 2017) or "microbial
816 electrosynthesis" (Dessi et al., 2020) processes into non-gaseous fermentable TC such as
817 formate or methanol (Mishra et al., 2020; Sakarika et al., 2020).

818

819 **Fig. 5. Producing alternative fermentation mediums from residual biomass: unit** 820 **operations pattern**

821 The indicative ranking of residual biomass families in the nutritional quality scale is derived from figure 2., and
822 allows to visualize the estimated chain of unit processes required to bridge the gap between the initial
823 composition-structure of a feedstock and the composition-structure which is adequate to deliver a nutritional
824 service. Icons are as defined in figure 1. The identified conversion pathways are rather straightforward when
825 starting from sugar- or lipid-rich residual biomass, but can be more complex, involving prior cracking and
826 extraction operations to release fermentable compounds. Albeit limited by economic considerations (Kwan et al.,
827 2019), purification technologies are often required to detoxify feedstocks and bring them up to nutritional
828 specifications. C₁ 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 <i>Curpiavidus necator</i> 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. Homogenization 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 <i>M. Capsulatus</i> MOB (and conversion of excess NH ₃ into NO ₂) 2. Effluents from MOB reactors and treated digestate are sent to denitrifying bioreactor (<i>Halomonas desiderata</i> 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 ₂ S	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 <i>Methylophilus sp.</i> , or <i>Methylococcales</i> and <i>Methylophilales</i>	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 <i>Clostridium ljungdahlii</i> HOB acetogenic strain (35°C, pH 6, anaerobic) 3. Fermentation of edible <i>Saccharomyces cerevisiae</i> 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)
-----------------------------------------	----------------------------------------------------------------------------------------	--------------	--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------	-------------------------------------------------------------------	-------------------------------------------------------------------------------------

830
831

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

832 **5.5. Farmed animal bioconversion pathways**

833 A wide range of residual biomass has already been tested as direct animal feed,
834 ranging from fruit wastes (Wadhwa and Bakshi, 2013) to manure (Mueller, 1980). Not only
835 limited to circumstances of extreme necessity (De Groot and Bogdanski, 2013; Makkar et al.,
836 2018), the wide adoption of residual biomass to sustain animal husbandry has been explored
837 in recent literature (te Pas et al., 2021). Animal farming, or rather the farmed animal
838 themselves can then be considered as a bioconversion process in waste-to-food pathways.

839

840 **5.5.1. Waste-to-meat, milk and eggs**

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

847 Provided that the use of residues and co-products does not affect performance and
848 food safety, and that it does not require intensive pretreatments, the use of livestock as direct
849 bioconverters is a viable option and indeed is already widely implemented (Mottet et al.,
850 2017; Wilfart et al., 2019). Residual feedstocks still need to meet feed standards, and
851 therefore mainly consist of agrifood industry co-products, which on average represent 10%
852 and 20% of compound feeds used in France for monogastric and ruminants respectively
853 (Agreste, 2019, 2017). Monogastric animals are restricted to low-lignin feedstocks
854 (Chapoutot et al., 2019), but ruminants can also convert green biomass and pretreated crop
855 residues. Direct bioconversion of slaughterhouse by-products is also reported, especially for
856 aquaculture in some regions, but in others this is considered unacceptable (Leduc, 2018;
857 Meeker, 2006). Besides direct enhancement techniques such as grass ensiling (cf., section
858 5.1.), a common strategy involves the inclusion of specific enzymes in diets. These degrade
859 anti-nutritional compounds (e.g., mycotoxins) and increase the digestibility of fibrous
860 components (Nunes, 2018).

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

877 The main challenge of using livestock as residual biomass bioconverters is the fact
878 that the current key determinant of stakeholder practices and choices is performance, mainly

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

894

895 **5.5.2. Insect bioconversion pathways**

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

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

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

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

948

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

950 **6.1. Building block framework: implications and limits**

951 Overall, waste-to-nutrition pathways involve diverse technologies and different degree
952 of nutrients and energy circularity, using different schemes of unit operations of increasing
953 intensity and complexity. In general, the less edible the feedstock (as defined in section 3),
954 the more processing is required to derive an edible foodstuff from it, as it can be visualized in
955 figures 5 and S1-S7. Bioconversion can sometimes be used to circumvent this, providing
956 foodstuff in a reduced number of steps (e.g. figures S4, S6 and S7). This is because living
957 organisms can be considered as complex reactors performing a series of unit operations
958 (Godon et al., 2013). However, in the case of highly structured and chemically complex plant-
959 based feedstock, most organisms display only limited direct conversion capabilities. As a
960 result, a pretreatment sequence to render the feedstock suitable for subsequent
961 bioconversion is often needed (e.g. figures 5 and S7). One notable exception to this rule are
962 fungi, as these secrete complex arsenals of biomass-degrading enzymes (Kuyper et al.,
963 2021; Souza Filho, 2018). Mushrooms cultivated on wood residues (figure S4) exemplify
964 such shortened bioconversion pathways that bridge the gap between an inedible feedstock
965 and edible nutrient production.

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

975 (details in SI). Second, animals are able to autonomously capture and concentrate diluted
976 nutrients. For example, some insects efficiently concentrate residual biomass proteins (<50-
977 60% recovery efficiency, see SI) and are themselves easily harvestable. As a second
978 example, farming fishes within microalgae production systems is an indirect way of collecting
979 microalgae biomass (as fish) otherwise diluted in production pond/reactor (Verstraete et al.,
980 2016). In this case, conventional energy-intensive microalgae harvesting and drying
981 techniques are replaced by fishing techniques, yet at the expense of a significantly lower
982 overall nutritional output yield. It is also important to point out the ability of some edible
983 microorganisms to grow in biomats at the liquid-air interface, removing the need of energy-
984 intensive extraction stage (Kozubal et al., 2020).

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

992 As the effects and drawbacks of each unit operation are cumulative, it is still unclear
993 to what extent the foreseen advantages associated with waste-to-nutrition strategies would
994 offset their drawbacks if massively implemented (Guthman and Bilekoff, 2020; Helliwell and
995 Burton, 2021; Van Eenennaam and Werth, 2021). The building blocks framework proposed
996 herein is intended to simplify the representation of processes involved in waste-to-nutrition
997 pathways, systematizing their transformation sequence patterns and grouping these into
998 large categories. Accordingly, this framework is a stepping stone to further assessments,
999 providing a convenient way to visualize available options when comparing different
1000 feedstocks. However, as key aspects such as energy demand or greenhouse gas emissions
1001 are technology- and operation-specific, further state-of-the-art life cycle assessments (LCA)
1002 accounting for all inputs, outputs including wastes and co-products generated during a
1003 process are required to quantitatively estimate their full environmental performance.
1004 Accounting for services provided by co-products in waste-to-nutrition pathways is key,
1005 because these are potential sources of energy, chemicals, materials and even feed. When
1006 feedstock give rise to multiple pathways and multiple products and services it is appropriate
1007 to use the term biorefinery.

1008

1009 **6.2. Waste-to-nutrition pathways into eight large families**

1010 Earlier (cf., section 5) waste-to-nutrition pathways were grouped based on their core
1011 building block. To refine the analysis, the classification is here extended by grouping
1012 pathways into large families on the basis of belonging to the same biorefinery scheme or
1013 addressing the same challenge (figure 6). These families are not defined based on the use of
1014 specific feedstocks, nor do they deliver specific services. Moreover, livestock-based
1015 bioconversion was not considered as a waste-to-nutrition family, being rather a plug-in often
1016 present at the end of the other families.

1017 Value chains built on the extraction of rubisco, or the cracking of plant fibers are well-
1018 studied, constituting respectively the green and lignocellulosic biorefinery families. Similarly,
1019 insect farming is increasingly studied from the angle of biorefining, because use of the co-
1020 products will form part of the business model (da Costa Rocha et al., 2021; Hubert and
1021 Berezina, 2020; Ravi et al., 2020), hence the insect biorefinery proposed herein. Likewise,

1022 we propose a “gas-intermediate biorefinery” family, as gas-based proteins can be part of
1023 larger anaerobic digestion and gasification platforms (Matassa et al., 2020), but also because
1024 it positions C₁ gases as key basic bricks for nutrition. Besides proteins and fats,
1025 slaughterhouse by-products already constitute a source of ingredients for cosmetics and
1026 medical products. However, a “more-out-of-slaughterhouse by-products” family is defined
1027 with the aim to convey the idea of valorizing such hitherto underused streams (cf., 5.2.2.).
1028 The remaining categories are not related to specific value chains, but are rather challenge-
1029 oriented. These include the development of (i) non-soluble protein extraction from diverse
1030 residual biomass feedstocks, (ii) solid substrate fermentation for nutrition and (iii) alternative
1031 liquid substrates for fermentation. Importantly, the eight families proposed herein can interact
1032 and are likely complementary to achieve a better use of resources from a circular economy
1033 standpoint. For example, cellulosic sugars, or organics remaining in the liquid fraction of
1034 anaerobic digestion, can be used as alternative fermentation substrates. Furthermore,
1035 because the families are not defined by specific technologies, they should be amenable to
1036 future technology innovations, for example biotechnology-based processes.

1037

1038 **Fig. 6. Identified waste-to-nutrition conversion pathway categories and current status**

1039 * Technology Readiness Level (1-9): based on information available to date (SI).

1040 ** Valid for all pathways involving microorganisms.

1041

1042 **7. Criteria for waste-to-nutrition pathways assessments**

1043 Obviously, the waste-to-nutrition pathways reviewed herein do not hold the same
1044 potential to supply novel food and feed resources and further studies are required to
1045 ascertain their true relevance and feasibility. To perform a quantitative prospective
1046 assessment, common criteria are required.

1047 First, a clear hierarchy of residual biomass valorization must be established and
1048 respected. From a sustainability standpoint it is unacceptable to use avoidable wastes and
1049 residues as feedstock, especially when these are directly derived from food (Leipold et al.,
1050 2021; Mourad, 2016; Redlingshöfer et al., 2020). Similarly, residual biomass prioritization is
1051 essential to prevent the risk of rebound effects (i.e. encouraging additional waste and
1052 residues generation to ensure feedstock availability for biorefineries) (Teigiserova et al.,
1053 2020).

1054 A second criterion must consider potential drawbacks and disruptions of diverting
1055 biomass streams from their current value chain (Abel and Blanc, 2017; Hedegaard et al.,
1056 2008). In this respect, a sensitive point is related to biomass that already sustain the food
1057 production system either directly (e.g. co-products as animal feed) or indirectly through
1058 agronomic valorization (e.g., composting, ploughing, fertilizing). The latter, not dealt with in
1059 this review, echoes the numerous incentives to close nutrient cycles through the promotion of
1060 organic fertilizers, among others those widening the scope of streams able to enter
1061 agronomic valorization pathways (European Union, 2019). Examples of their uses in urban
1062 farming are increasingly put forward (Billen et al., 2021; Stoknes et al., 2016; Van Zanten et
1063 al., 2019). Therefore, not only is it necessary to carefully compare waste-to-nutrition
1064 pathways between themselves, but also with conventional scenarios, also referred to as
1065 counterfactuals in LCA involving constrained resources (Pehme et al., 2017). Another trade-
1066 off of waste-to-nutrition pathways is the burden shifting between resource efficiency and
1067 utilities requirements. Indeed, previous analyses revealed that, depending on the scenario,
1068 novel ingredients do not necessarily always perform better (environmentally) than

1069 conventional ones, mainly because of higher requirements in energy, water, chemical and
1070 material (Bohnes and Laurent, 2021; de Boer et al., 2014; Sillman et al., 2020; Smetana et
1071 al., 2015; Spiller et al., 2020).

1072 A third criterion must capture the spatio-temporal and context-dependent dimension
1073 (Dries et al., 2020). The demand for alternative practices that reduce pressure on arable land
1074 use is urgent and cannot be delayed for an indefinite period. However, different waste-to-
1075 nutrition pathways are characterized by different technology readiness and feasibility levels
1076 (Tuomisto, 2019). Some technologies are immature, while other are perhaps quite mature,
1077 but face major regulatory hurdles, stakeholder risk aversion or consumer rejection (Cameron
1078 et al., 2019; Specht et al., 2019; Tubb and Seba, 2019). In this regard, while synthetic
1079 “cultured” animal products (e.g. cultured meat) are still far from widespread
1080 commercialization (Post et al., 2020; Zhang et al., 2020), rapidly evolving socio-cultural
1081 considerations are likely to push innovation and accelerate development in the area (Crosser
1082 et al., 2019). Similarly, novel waste-to-nutrition pathways will not be deployable everywhere
1083 in the same way, either because of local availability of feedstock (see below) and technical
1084 skills, and/or because of socio-cultural trends. It is generally recognized that neophobia,
1085 cultural values and disgust are the major barriers for the widespread consumer acceptance
1086 of novel food (Fischer and Van Loo, 2021; Siegrist and Hartmann, 2020; Tuorila and
1087 Hartmann, 2020). These barriers make market uptake projections quite challenging,
1088 particularly when genetic engineering is involved (Boccia et al., 2018; Lähteenmäki-Uutela et
1089 al., 2021). Therefore, the challenge is to motivate change in people’s perception so that they
1090 can progressively accept such novel ingredients at their tables. For example, the inclusion of
1091 bacterial meal in astronauts’ diets could trigger a wider acceptance of microbial-based food
1092 (Verstraete et al., 2016). Similarly, many initiatives investigate the organoleptic
1093 enhancements of novel food such as plant-based proteins and upcycled agrifood co-products
1094 (cf. table 1 and SI database), aiming to increase their attractiveness. Safety considerations
1095 (see below) will also condition market uptake, especially in the case of ingredients stemming
1096 from feedstocks currently covered by waste regulations. About 75% of the pathways
1097 reviewed in this study target inclusion of novel ingredients in animal diets, suggesting a
1098 foreseen trend of waste-to-nutrition approaches development preferentially towards feed
1099 rather than food markets.

1100 Another spatially related criterion concerns the potential impact and development
1101 pattern of a given waste-to-nutrition pathway. The feasibility of a pathway is intrinsically
1102 linked to the availability and processability of an appropriate residual feedstock. Many
1103 biomass feedstocks are characterized by high moisture content, which limits transport and
1104 increases perishability (e.g., sugar beet leaves). For these reasons, it is often preferable to
1105 process biomass close to the site of production. In the case of industrial streams, it might be
1106 even preferable to process them onsite. When waste-to-nutrition pathways are implemented
1107 in stand-alone facilities, it is necessary to carefully balance biomass availability and storage
1108 constraints with considerations related to the economy of scale, either opting for small-scale
1109 decentralized facilities or large-scale centralized ones (Maity, 2015). In this regard, although
1110 technology considerations partially dictate which option is most appropriate, this is not
1111 always the case. For example, insect biorefineries are economically feasible at both scale
1112 (Chia et al., 2019; Kröncke et al., 2020). Moreover, biotechnology-based processes also offer
1113 scope for downscaling and decentralization, with microbial bioconversion being feasible in
1114 transportable containers (Kernel.bio, 2020) and even domestic scales (Shojinmeat Project,
1115 2020). Therefore, it is crucial to understand the ways in which waste-to-nutrition pathways
1116 are likely to be deployed, because evidence-based future narratives and scenarios on food
1117 transition are essentials to the proper context-dependent prospective comparison of different
1118 pathways (Antonsen and McGowan, 2021). Finally, one important future narrative to consider

1119 is the degree to which meat will still be produced and will coexist with its alternatives (plant-
1120 based, microbe-based). Change in meat production will have implications both on the
1121 feedstock side of waste-to-nutrition pathways, but also on the market side, eventually
1122 reducing the relevance of producing feed ingredients.

1123 The final criterion relates to safety and the way this affects the substitution potential of
1124 novel nutritional services. Safety is a complex issue because it covers potential and real risks
1125 and needs to be addressed using technical and regulatory means. The application of the
1126 principle of precaution means that the introduction of any novel nutritional services will be
1127 confronted by strict institutional barriers (Lähteenmäki-Uutela et al., 2021; Tzachor et al.,
1128 2021). Overcoming these requires the compilation of large amounts of background data on
1129 risk assessment, so the “Generally recognized as safe” or “Novel food” labels can be granted
1130 (EFSA Panel on Dietetic Products, Nutrition and Allergies (NDA), 2016). In cases where the
1131 risk is patent (e.g., use of sludge or other feedstocks under the Waste Regulation), the
1132 hurdles will be higher and advanced technical solutions (e.g., sequence of cracking, refining
1133 and conversion units) will likely be required to attenuate the presence of noxious substances,
1134 viruses and microorganisms (Alloul et al., 2018; Verstraete et al., 2016). Therefore, safety-
1135 related barriers to implementation of novel waste-to-nutrition pathways must be assessed to
1136 properly compare these, establishing the plausible timeline to implementation and the likely
1137 technology cost involved. Additionally, because safety often involve purity and intense
1138 refining, it is necessary to assess a collateral risk, which is that of the market product being
1139 part of a cracking-building food chemistry pattern, likely leading to ultra-processed food
1140 ingredients (Fardet, 2018; van der Goot et al., 2016).

1141

1142 **8. Conclusion**

1143 To enhance food system resilience and limit its environmental impacts, pathways
1144 transforming residual biomasses and C₁ gases into food and feed ingredients are gaining
1145 increasing attention. As a first step to assess their potential, this study classifies the main
1146 waste-to-nutrition pathways through the review of 950 literature records. The analysis reveals
1147 that most nutritional services can be provided through pathways built on different residual
1148 feedstocks, and reversely, one residual biomass can lead to a variety of nutritional outputs.
1149 Identified waste-to-nutrition pathways employ a sequence of unit operations workflow to
1150 adapt the initial composition-structure (i.e. nutritional, anti-nutritional and structural contents
1151 triangle) of the input to the end-market requirements while ensuring safety and regulations
1152 compliance. This study proposes a qualitative four-quadrant building block framework,
1153 composed by bioconversion, cracking, extraction and enhancement processes to
1154 systematically compare value chains, and classifies the reviewed waste-to-nutrition
1155 approaches into eight generic families.

1156 Waste-to-nutrition pathways directly target the reduction, closing and shortcutting of
1157 nutrients flows loops, and should therefore be integrated within the broader context of
1158 transition towards low fossil carbon and planetary boundaries-compliant economies. In this
1159 regard, this comprehensive review highlights the wide span of the basket of solutions, where
1160 traditional residual biomass recycling approaches (e.g. livestock, compost) are likely
1161 complemented with emerging biotechnologies and extraction processes. Yet, further work
1162 remains necessary to capture the economic- and environmental relevance of a wide
1163 deployment of waste-to-nutrition strategies, considering context-dependencies.

1164

1165 **CRedit authorship contribution statement**

1166 U. Javourez: Conceptualization, Data curation, Formal analysis, Investigation, Methodology,
1167 Visualization, Writing – Original Draft.

1168 M. O'Donohue: Validation, Writing – Review & Editing.

1169 L. Hamelin: Conceptualization, Funding acquisition, Resources, Supervision, Validation,
1170 Writing – Review & Editing.

1171

1172 **Declaration of competing interests**

1173 The authors declare no conflict of interest.

1174

1175 **Acknowledgement**

1176 This work was carried out within the framework of the research project Cambioscop
1177 (<https://cambioscop.cnrs.fr>), partly financed by the French National Research Agency,
1178 Programme Investissement d'Avenir (ANR-17-MGPA-0006) and Region Occitanie
1179 (18015981). U. Javourez was additionally funded by the Metaprogram GLOFOODS (INRAE-
1180 CIRAD).

1181

1182 **Credits**

1183 Figures of the present manuscript have been designed using free icons resources from
1184 Flaticon.com (authors: Surang, Linector, Good Ware, Monkik, Smashicons, Smalllikeart,
1185 Itim2101, DinosoftLabs, Roundicons, Vector markets, Darius Dan) and Wikipedia commons.

1186

1187

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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. C₁ gases can either have a fossil or biogenic origin, as represented in figure S5.

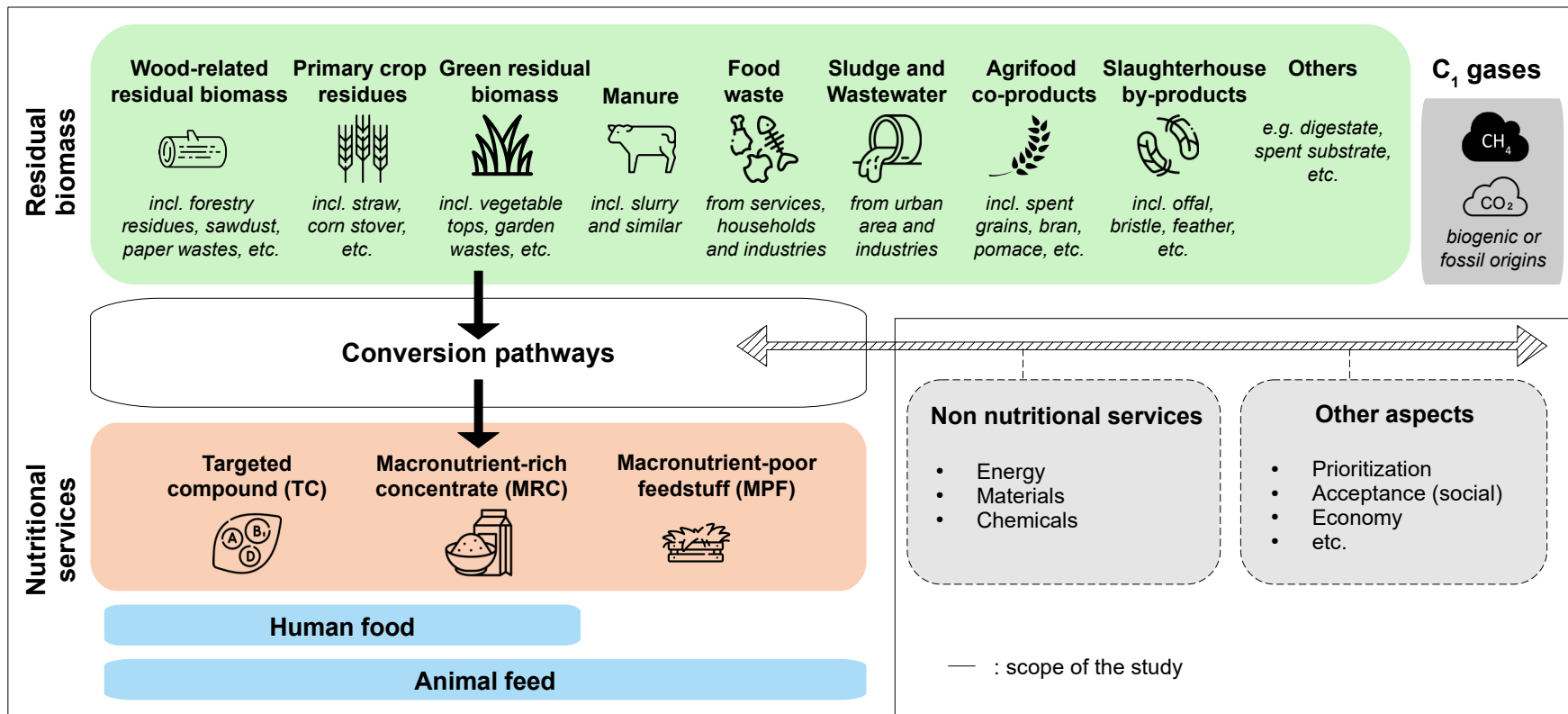
Fig. 6. Identified waste-to-nutrition conversion pathway categories and current status

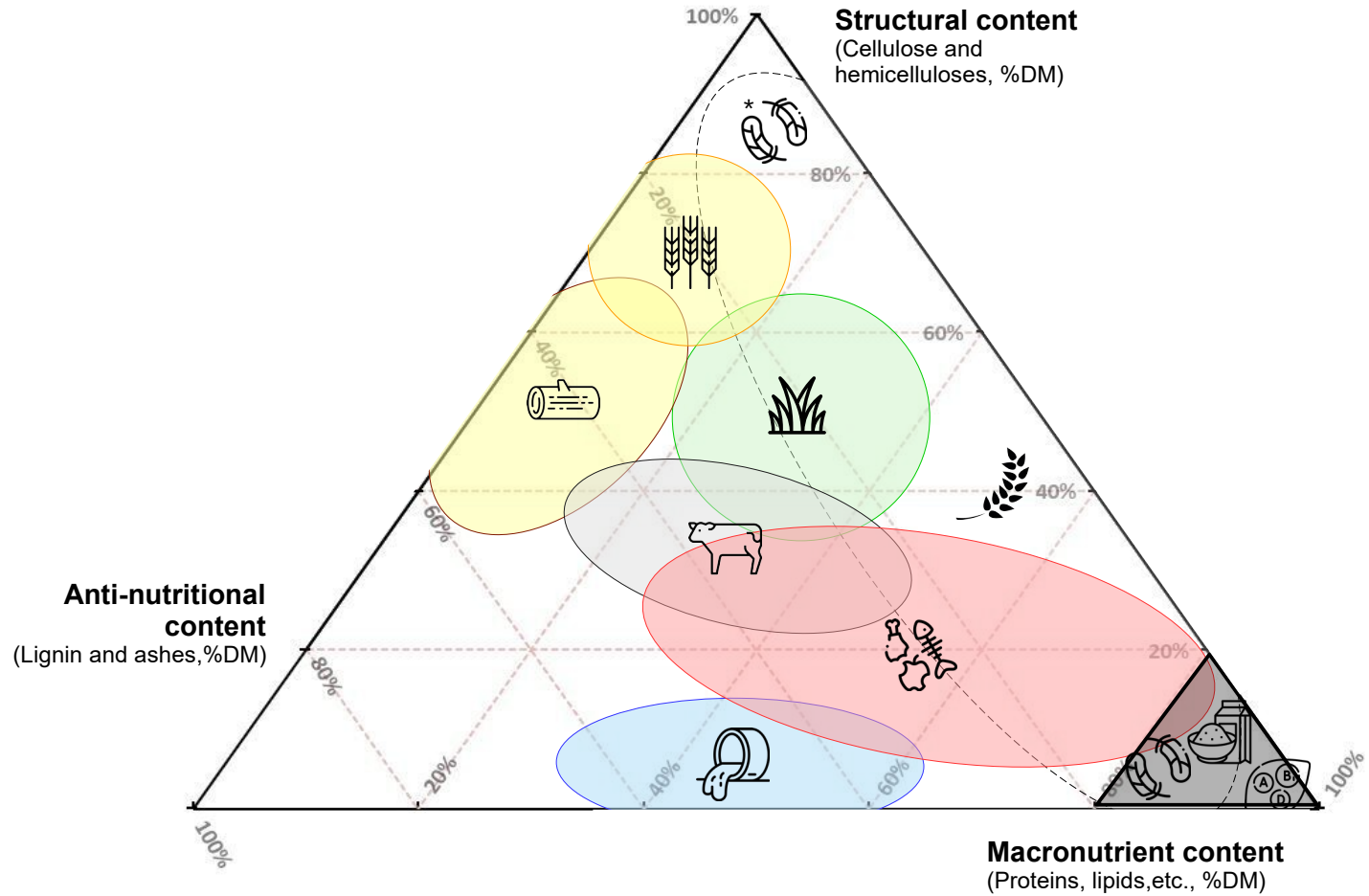
* Technology Readiness Level (1-9): based on information available to date (SI).

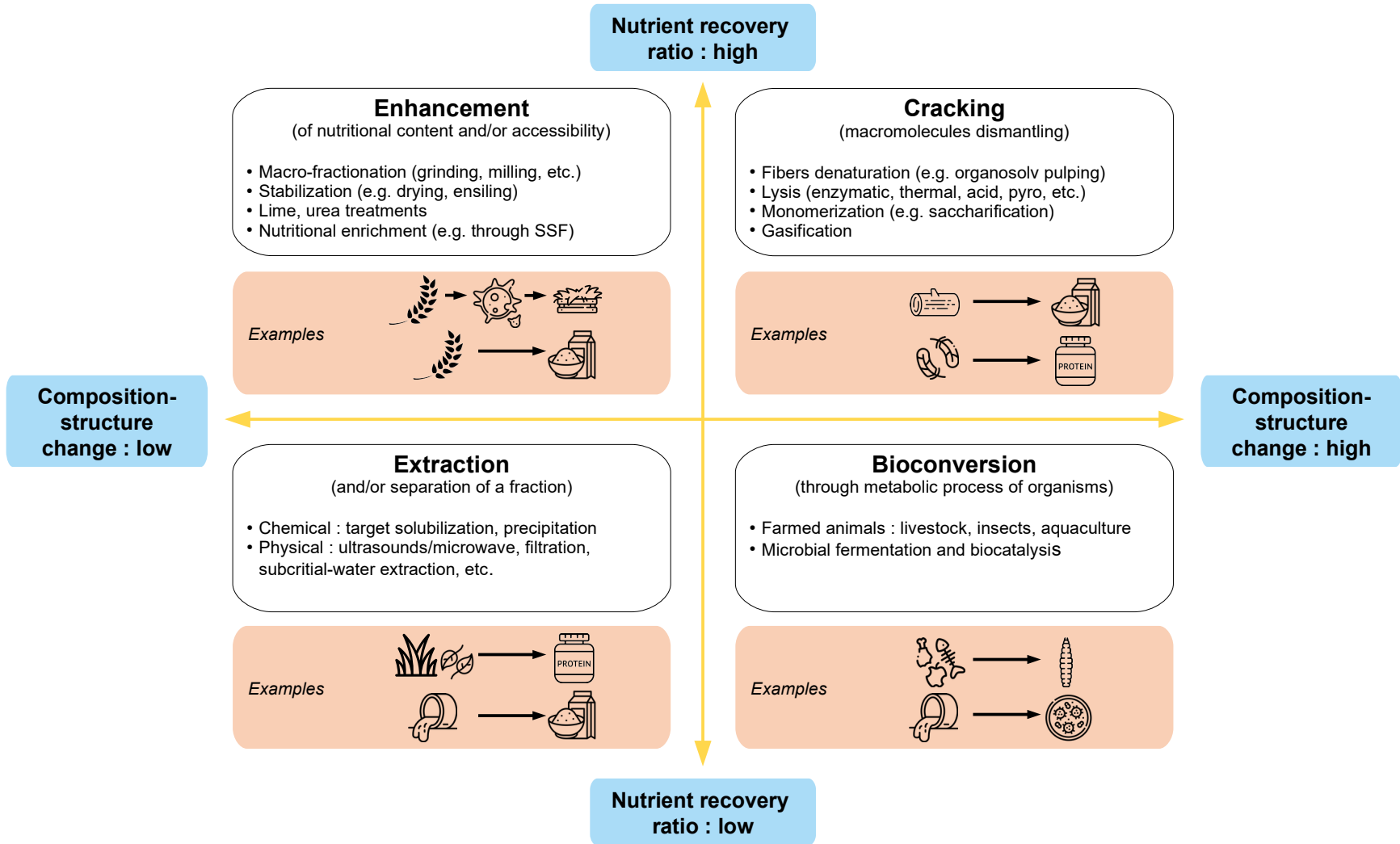
** Valid for all pathways involving microorganisms.

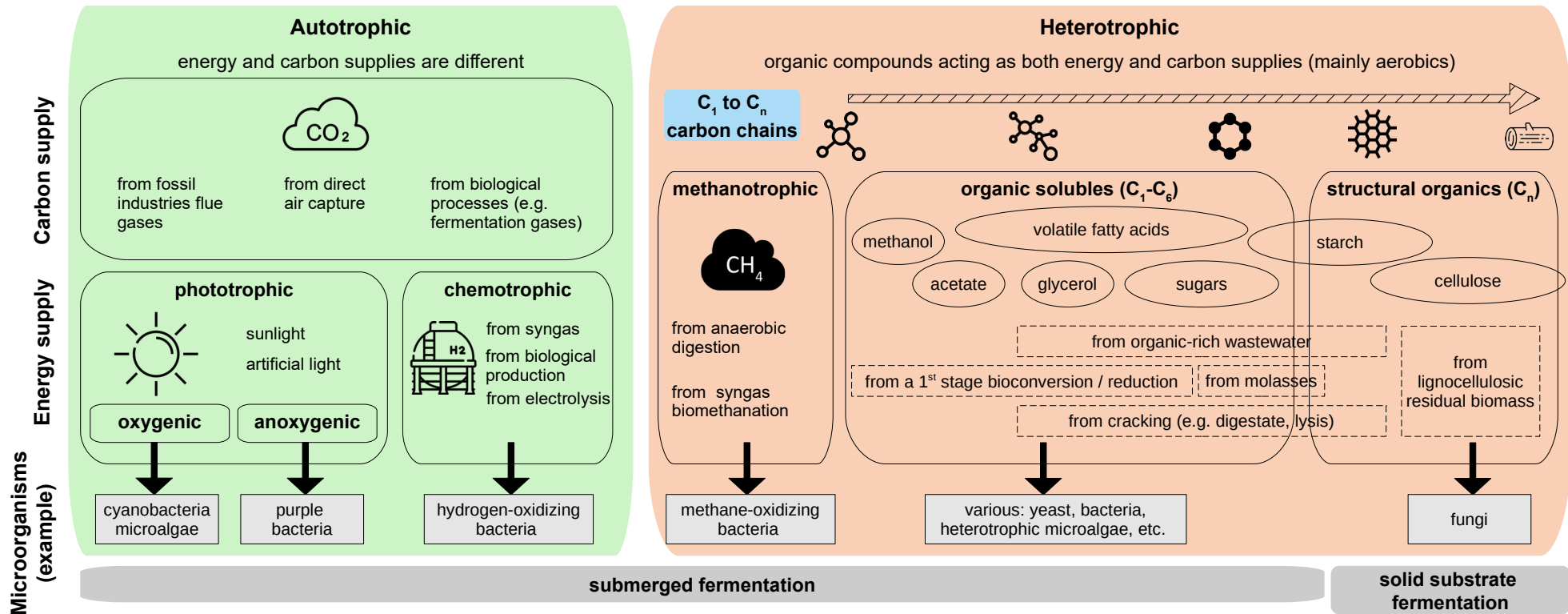
References

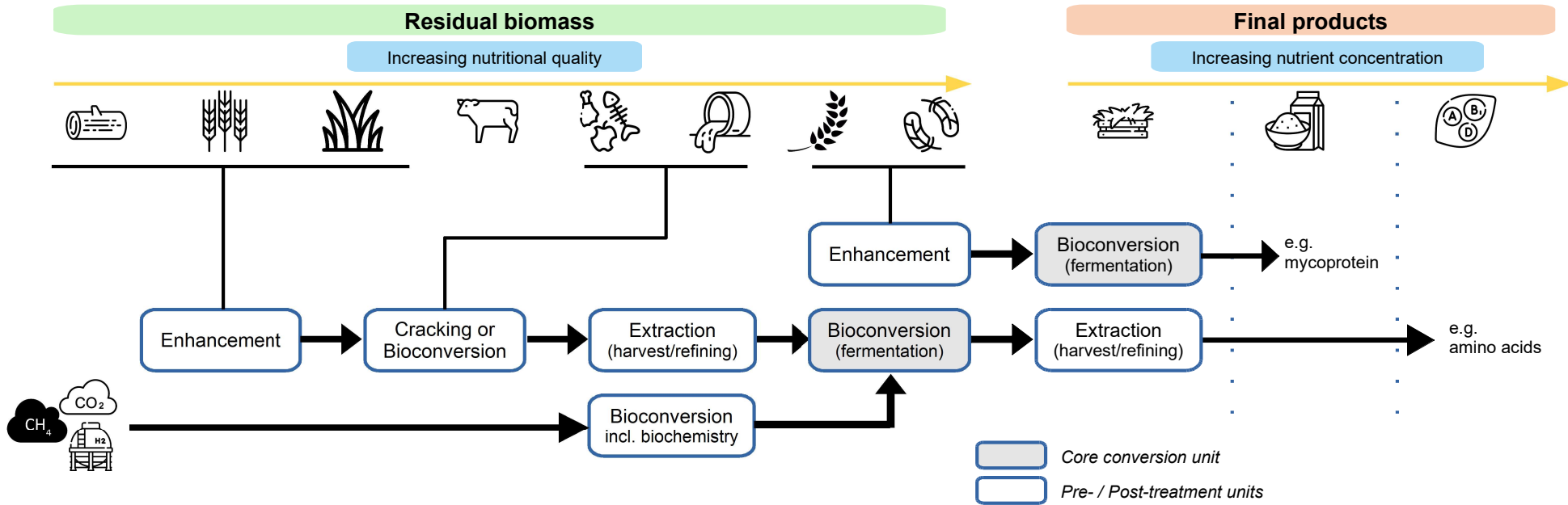
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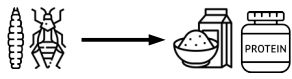

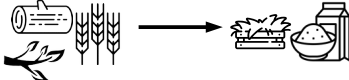


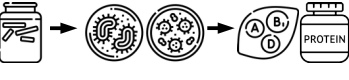
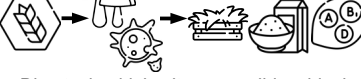
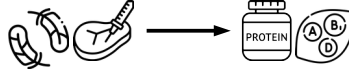










Waste-to-nutrition families	Arguments	Challenges	TRL*
<p>Insect biorefinery</p>  <p>Residual biomass digested by insects, further fractionated or used as a whole</p>	<ul style="list-style-type: none"> • Animal proteins with reduced impacts • Markets for co-products (e.g. chitin and frass) • Insect proteins approved for swine and poultry markets, three species approved as novel food in EU to date 	<ul style="list-style-type: none"> • Influence of feed on insect characteristics, risk of bio-accumulation • Acceptance as food limited • Risk of livestock-competing feed use 	8-9
<p>Green biorefinery</p>  <p>Separation of juice and fibers from green residual biomass</p>	<ul style="list-style-type: none"> • Rubisco is the most abundant protein • Opportunity to directly grow it (if land is made available) • Markets for co-products (e.g. press-cake) 	<ul style="list-style-type: none"> • Seasonality, heterogeneity and short shelf-life • Polyphenols interaction with proteins: trade-off between purity and yield 	6-8
<p>Lignocellulosic biorefinery</p>  <p>Cracking of lignin-based biomass into its basic compounds</p>	<ul style="list-style-type: none"> • Highly available and no current direct use in nutrition • Integration potential within biofuel and biomaterial production platforms 	<ul style="list-style-type: none"> • Utilities-intensive processes • Under-developed use of C₅-derived products 	6-8
<p>Non-soluble protein recovery</p>  <p>Techniques to extract structure-tied proteins (e.g. sludge and press-cake)</p>	<ul style="list-style-type: none"> • Widely available streams • Under-efficient current use (if not hazardous) • Rapeseed meal protein extract approved as novel food in EU 	<ul style="list-style-type: none"> • Low protein recovery efficiency • Costs of purification / refining • Legal barriers for streams not currently used as feed 	5-9
<p>Gas-intermediate biorefinery</p>  <p>Biogenic- or fossil-based gases used for microbial biomass production</p>	<ul style="list-style-type: none"> • 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 	<ul style="list-style-type: none"> • 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
<p>Liquid substrate alternative</p>  <p>Submerged fermentation fed with residual-based nutrients</p>	<ul style="list-style-type: none"> • Lowering fermentation industries dependency on raw carbohydrates and nutrients 	<ul style="list-style-type: none"> • Risk assessment of novel strain-substrate associations required • GMO acceptance to enter the food chain 	3-6
<p>Solid-substrate fermentation</p>  <p>Direct microbial culture on solid residual biomass, harvested or used as a whole</p>	<ul style="list-style-type: none"> • Allow to increase share of residual biomass in livestock diets • Direct use of the versatility of microorganisms 	<ul style="list-style-type: none"> • Risk assessment of novel strain-substrate associations required • Heterogeneous substrates modeling and operation 	3-4
<p>More-out-of-slaughterhouse by-products</p>  <p>Full recovery of animal-based by-products (incl. slaughterhouse and aquaculture)</p>	<ul style="list-style-type: none"> • Improve overall performance of livestock production • Potential to recover valuable functional TC 	<ul style="list-style-type: none"> • Limited acceptance • Safeguard functionality while ensuring safety (e.g. prion-related risks) 	4-6