

There's no harm in having too much: A comprehensive toolbox of methods in trophic ecology

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Abstract :

Trophic ecology is the study of feeding interactions and food acquisition by organisms. It includes the causes and consequences of those behaviours at all levels of biological organisation. As a field of research, it crosses many disciplinary boundaries and provides knowledge that is pertinent to many other areas of ecology. Here we list and categorise the methods available to trophic ecologists whose toolbox

has broadened considerably in recent years. They encompass empirical and numerical approaches with focus ranging from molecules to ecosystems. We further examine the relationship of each method to features such as the scale of observation (from microbes to largest organisms) and organisational level (from individuals to ecosystems) as well as the ecological question the method is capable of answering (from detecting predator-prey relationships to studying implications and consequences at different scales). Our survey reveals a very wide range of methodologies, each more-or-less appropriate for a particular line of research. It also identifies deficits, for example, trophic interactions at microscopic scales, for which empirical methods have hardly been used, as well as trophic models that have failed to consider fluxes at the ecosystem scale. Furthermore, we note that the combination of methodologies remains under-exploited despite great opportunities to solve complex ecological questions and to foster the emergence of new insights and hypotheses regarding organism, population and/or ecosystem properties.

Keywords : Food web, Feeding interactions, Flux of energy, Computer simulations, Trophic models

24 Introduction

25 Trophic ecology covers the ecological implications of feeding. As such, it embraces the act of
26 food acquisition and its consequences at the individual, population and community levels up to
27 functional outputs at the scale of the whole ecosystem. The field of trophic ecology, in which the
28 concept of food web is embedded, is broader than organismal detection and the description of
29 inter-species feeding relationships. Briefly, at the smallest organizational levels, feeding is
30 intimately linked to nutrition and ecophysiology, as the quantity and quality of mineral or
31 organic food resources regulates individual survival, growth and fecundity with upscaling effects
32 on population demography (Elser et al., 1996). Except for lithotrophic and saprophytic
33 organisms, food acquisition also implies that feeding interactions generate reciprocal effects on
34 predator and prey demography (Lotka, 1925 – Volterra, 1926). Trophic relationships are also
35 responsible for species inter-dependencies and contribute to shaping behaviours, driving
36 phenotype selection and eco-evolutionary feedbacks (Post and Palkovacs 2009, Clinchy et al.
37 2013). A trophic transition can also be biogeochemically regarded as a way to transfer mineral or
38 organic matter between two trophic levels with more-or-less efficiency (“trophic efficiency
39 concept” of Lindeman 1942, “ecological stoichiometry” see e.g. Elser et al., 1996), or
40 transformations in its biochemical quality (“trophic upgrading”: Klein-Breteler et al., 1999). The
41 concept of food web brings trophic ecology to the community and ecosystem scales. Food webs
42 allows exploring the network of consumer-resource interactions, considering its assemblage rules
43 and interaction strength and the consequences of network structure to overall community
44 composition and stability, up to emergent properties of the ecosystem — like carbon fixation
45 (see Layman et al., 2015, and references therein for a synthesis of major concept achievements in
46 food web ecology).

47 The broadness of trophic ecology implies a diversity of methodologies, along with considerable
48 improvements and developments both in field and laboratory methods. In addition, numerical
49 approaches have flourished and now support trophic ecologists in their efforts to conceptualise their
50 theories and to modify them based on empirical data (e.g. Proulx et al., 2005; D’Alelio et al., 2016).
51 Considering this large and fast-evolving bouquet of methodologies, we felt that an up-to-date overview
52 of existing methods, merging both empirical and numerical techniques, has been so far missing. Here, by
53 providing a technical overview, we hope to facilitate both upstream decision-making and the inclusion
54 of a broader diversity of research paths within otherwise well-defined methodological road maps.
55 Nevertheless, we do not pretend to provide either an exhaustive critical review of every method
56 relevant to trophic ecology or systematic pairwise comparisons of all methods. For this, we refer
57 readers to the comprehensive book by Garvey and Whiles (2017) and to more specific methodological
58 reviews referenced hereafter. Because the choice of a method primarily depends on its ability to
59 answer a question at hand, we have structured this review accordingly, grouping the methodologies
60 into four categories based on the trophic ecology question they are most suitable for addressing: (1)
61 empirical detection of predator-prey relationships or food sources, (2) connection of species within
62 networks based on empirical data (inference methods), (3) quantification of the consequences of
63 feeding, from individuals to ecosystems and (4) testing the implications of trophic interactions (trophic
64 models). For each method, we briefly describe the aims and principles, the advantages and drawbacks,
65 and we include estimates of human and financial costs, as time and money are often decisive in the
66 final choice. Beyond providing a methodological toolbox that will help identify the most appropriate
67 tool (Section 5), we seek to encourage an integrated research strategy that combines approaches
68 (Section 6) and to highlight the conceptual barriers (Section 7) in trophic ecology.

69 1. Detecting predator-prey relationships or food sources

70 1.1. Observations of feeding activity

71 The most straightforward and oldest approach to study feeding interactions relies on observations.
72 Feeding observations can be made with the naked eye and simple equipment (e.g., binoculars) or using
73 sophisticated, miniaturised, high-magnification optical devices, including remote underwater video
74 stations, camera traps and drones (e.g. Linchant et al., 2015). This allows large-scale records of feeding
75 behaviours in remote ecosystems that are poorly studied. In addition, animal-borne video systems offer
76 the animal's perspective (e.g. Moll et al., 2007). For microscopic or suspension-feeding animals, most
77 observations are restricted to laboratory conditions, for example using a camera attached to a
78 microscope (e.g. Dupuy et al., 2010) or by *in vivo* video endoscopy (e.g. Prasetya et al., 2017). To
79 complement direct observations, an emerging approach consists in remotely monitoring multiple
80 biological and environmental factors that constitute surrogates for feeding activity, such as the
81 movements of body parts, oesophageal or gastric temperatures and geographical positions, using
82 animal-attached bio-logging devices (Ropert-Coudert and Wilson, 2005). This should further progress
83 with the transfer of geo-referenced human mobility data analysis techniques to animals (Thums et al.,
84 2018). If direct observation of feeding activity is impracticable, food intake can be inferred from the
85 disappearance of food items. For example, suspension-feeder activity is most commonly assessed
86 using food-clearance experiments or flow-through chamber methods (see e.g. Ward and Shumway,
87 2004). Different parameters can be obtained this way, such as clearance rate, retention and sorting
88 efficiencies, ingestion, and egestion rates.

89

90

91 1.2. Gut content and faeces analysis

92 Observing the food remains in digestive tracts of animals is the most common approach to get a basic,
93 timely knowledge of predator-prey relationships. Some studies have used massive gut contents datasets
94 to evaluate and compare trophic networks in different ecosystems (e.g. Winemiller, 1990). Especially
95 in fishes, typical methodologies and indices have been developed, and some like the percentage of prey
96 occurrence may emerge as relatively reliable proxies of diet composition (see Baker et al., 2014).
97 Rejection pellets and faeces can also be collected and inspected for undigested prey items (e.g.
98 Kusmer, 1990). In most cases, a dietary assessment is based on the recovery of hard/recalcitrant prey
99 parts (e.g. bones, fur, diatom frustules), which makes a reference collection of such parts often
100 necessary to identify the respective prey organism.

101 The main advantages of this type of dietary analysis consist in: (1) being accessible, (2) being
102 applicable at relatively large spatial and temporal scales and (3) enabling assessments of prey size (e.g.
103 measuring otoliths or vertebrae). Amongst the main drawbacks are (1) the discrepancies in taxonomic
104 distinctness (as the ingested items can be identified either at the species level or at a higher taxonomic
105 level), (2) the inability to account for labile food items and (3) the requirement of comprehensive
106 taxonomic expertise. (4) Ethical issues are also raised by this approach, particularly when animals must
107 be dissected. Alternative techniques that avoid dissection can be used to recover stomach contents,
108 such as stomach flushing or regurgitation (e.g. Pierce and Boyle, 1991, Legler and Sullivan, 1979 ;
109 Duffy and Jackson, 1986). In addition, as many microscopic animals have transparent bodies, their gut
110 contents can often be examined under the microscope without dissection. For example, confocal laser
111 scanning microscopy can be used to detect the auto-fluorescence of micro-algal pigments in the gut of
112 rotifers (Mialet et al., 2013), and chromatography to quantify ingested biomarker pigments extracted
113 from guts (e.g. Majdi et al., 2012).

114 Molecular approaches can also be used to decipher ingested prey remains based on the use of
115 specific prey primers to amplify the prey DNA contained in the gut or faeces of the predator followed
116 by (meta)barcoding (for a review see King et al., 2008). The use of molecular gut content has really
117 expanded in recent years and has proved useful to assess, for instance, the diet of minute animals such
118 as soil micro- and meso-arthropods (e.g. Eitzinger et al. 2013; Heidemann et al. 2014), and
119 zooplankton (e.g. Ho et al. 2017). The major advantages of analysing gut content DNA are: (1) high
120 taxonomic resolution without taxonomic expertise, (2) the inclusion of partly digested, unidentifiable
121 prey chunks and, potentially, (3) the acquisition of data on the microbial assemblages ingested or
122 persisting in the gut (i.e. gut microbiomes, see, e.g. Derycke et al., 2016). However, besides substantial
123 costs, there are several disadvantages inherent to molecular approaches, especially (1) high risk of
124 sample contamination and false positives, (2) need for specific primers to identify uncommon prey
125 taxa, (3) absence in public gene repositories of sequence data for the DNA of numerous prey types, (4)
126 bias in quantitative extrapolations due to the differential timing of DNA degradation during digestion
127 or the specificity of certain DNA extraction protocols and (5) the inability to detect cannibalistic
128 behaviour (Traugott et al., 2013).

129

130 1.3. Parasites as biological tags

131 Since some parasites are transmitted only through food ingestion, they serve as evidence of a feeding
132 interaction and indicate that the host species has fed in geographical areas where the prevalence of this
133 parasite is high. Similarly, accurate information about the feeding grounds and past movements of
134 animal hosts can be surmised based on the presence of multiple parasite species differing in their
135 endemic areas (MacKenzie and Abaunza, 1998). Yet, to be reliable biological tags, parasites must
136 have: (1) distinct prevalences in different studied areas, (2) limited inter-annual or seasonal variations

137 in those prevalences, (3) a high specificity for the microhabitat within the host's body, (4) a lifespan
138 fitting the aim/scale of the study, (5) no strong pathological effects on the host and (6) preferably, a
139 direct and single-host life cycle (facilitating interpretations). They must also be readily detectable and
140 identifiable. Helminths generally fulfil all of these criteria and are thus the most commonly used
141 trophic tracers (see Mackenzie, 2002).

142 The use of parasites as trophic tracers has thus far been limited to marine ecosystems, but,
143 given the ubiquity of parasites (Marcogliese, 2004), implementation of this method in other ecosystems
144 is certainly possible (see Holmstad et al., 2004). Additional advantages of parasites are that they
145 provide information even when their host's stomach is empty (Baldwin et al., 2008) and indicate long-
146 term feeding, as they can accumulate in their hosts for months or longer (Marcogliese and Cone 1997).
147 However, this method also requires that the animals are killed and dissected, the method is time-
148 consuming and considerable taxonomic expertise is required. Some of these shortcomings might be
149 overcome using DNA barcoding, which is inexpensive (~5€ /parasite), or by coupling behavioural and
150 molecular approaches (Poulin, 2010). However, the use of a parasite as a biological tag relies on an at
151 least partial understanding of the parasite's life cycle, which probably explains their use mostly in fish
152 species so far.

153

154 1.4. Tracers of biomass

155 Trophic tracers of biomass origin are elements or molecules that an organism can gain only from its
156 trophic resources. The presence of a tracer in the biomass of an organism indicates the consumption
157 and assimilation of a resource containing that tracer, as well as whether and how much the different
158 trophic resources have contributed to the biomass of the organism (or its targeted tissue), provided that
159 the potential resources differ in their tracer composition. Moreover, the presence of a tracer not only

160 reflects the consumption of a resource, it can also provide an information on how the tracer is retained
161 and transferred within the consumer, such as by selective digestion or assimilation (Gannes et al. 1997)
162 or routing to different tissues (Carleton et al. 2008).

163

164 *1.4.1. Stable isotope composition of bulk tissues*

165 One of the most common trophic-tracer-based methods is the determination of the stable isotope
166 composition of bulk tissues, such as muscle, blood, liver, feather, hair, fin, or whole organism. In
167 trophic ecology, C, N and S are the tracers most frequently used in stable isotopic analysis (SIA) (Fry,
168 2006), but H/D and O isotopes are also employed (Vander Zanden et al., 2016). The method is based
169 on predictable differences (trophic discrimination factors, TDFs) between the isotopic composition of
170 an organism and that of its food resources. For C and S, the difference is limited and these elements are
171 mainly used to trace the origins of the food resources from which the consumers' biomass has been
172 synthesized (Boecklen et al., 2011), whereas the TDF for N is larger, allowing its use in estimates of
173 trophic position (Post, 2002). However, the variability in the TDFs depending on environments, trophic
174 levels, taxa, tissues, etc. (Bond and Diamond 2011) is a potential confounding factor, that has been
175 highlighted in several studies (e.g. Bastos et al. 2017). In addition, the high variability of stable isotope
176 compositions in space and time (e.g. Hyndes et al. 2013) must also be considered. Several tools are
177 used to analyse stable isotope data. Their most recent versions generally adopt a similar Bayesian
178 approach to account for the sources of uncertainty (e.g. Parnell et al., 2013) and include associated
179 confidence intervals. Bayesian approaches also allow introducing informative priors, increasing the
180 accuracy and precision of the estimates. We distinguished three main types of tools: (1) those devoted
181 to the estimation of trophic position (e.g. tRophicPosition, Quezada-Romegialli et al. 2018), (2)
182 isotopic metrics to measure specimen or species positions in the isotopic space and to compare the

183 variability of isotopic signatures across individuals, populations and communities (SIBER, Jackson et
184 al. 2011; Cucherousset and Villegger 2015) and (3) mixing models to estimate the contribution of each
185 potential trophic resource to the biomass of an organism (see Philips 2012 for a review). The relevance
186 of SIA-derived results is thus strongly tied to isotopic discrimination between resources, the spatial and
187 temporal variability of the isotopic compositions captured by resource/consumer sampling and an
188 accurate estimate of the TDF. SIA is not well suited to situations involving large numbers of potential
189 resources (e.g. Robinson et al. 2018). The integration of the food isotopic signal into the consumer's
190 tissue depends of the rate at which tissue are renewed, by somatic growth or metabolic tissue
191 replacement (which determines isotopic turnover). Issues related to isotopic turnover thereby limit the
192 relevance of the method for individuals (i.e. adults) or seasons of reduced somatic growth (gonadic
193 growth or maintenance metabolism, Perga and Gerdeaux, 2005). Issues related to differential isotopic
194 routing (Gannes et al., 1998, Del Rio et al. 2009) and unequal TDF in plant *versus* animal food sources
195 (Perga and Grey 2010) also limit the detection of omnivory for individuals and species exploiting both
196 plant and animal resources. As a result, SIA enables quantitative estimates of elemental fluxes within
197 the different steps and habitats of a food web, but it is a less than ideal method with which to assess the
198 diversity and specificity of a consumer's diet.

199 When natural isotope abundance does not provide the necessary discrimination between sources,
200 for example, to overcome uncertainties linked to TDF variability, small quantities of isotopically
201 labelled sources (stable or radioactive) can be injected *in-* or *ex-situ* to track C and/or N pathways. This
202 method of isotope labelling, or Stable Isotope Probing (SIP) aims to track the integration of the
203 labelled elements within food webs (Pace et al., 2007). Primary producers can be selectively labelled
204 through addition of ¹³C-enriched bicarbonate/carbon dioxide or ¹⁵N-enriched ammonium or nitrate
205 directly *in situ* (see e.g. Middelburg et al., 2000) to track the fate of primary production through food

206 webs. Similarly, SIP based on dissolved organic matter (e.g. Hall and Meyer, 1998), phytodetritus (e.g.
207 Scharnweber et al. 2014) or animal feces (e.g. Dungait et al., 2009) are used to label microbial
208 decomposers and the fate of dead organic matter through “brown” food webs. The mode (single
209 addition, pulse chase, or constant levels) and the duration (a few hours to several months) at which the
210 label is introduced into the system determine the time and scale at which the fate of the labelled
211 substrate is tracked (from microbial interactions up to the whole ecosystem), and eventually to
212 document the dynamics of the processes (when performed in pulse chase) (e.g. Maxfield et al., 2012).
213 If studies using isotope labelling are relieved from the issues of TDF uncertainties encountered for SIA
214 in natural abundances, they also suffer for issues related to isotope routing. Indeed, structural
215 components of plant material behave differently than metabolic components in terms of microbial
216 utilisation, grazing, and assimilation (see e.g. Soong et al., 2014). The success of isotope-labelling
217 experiments is thereby strongly tied to the ability to uniformly label throughout the food source, or
218 instead to differentially label the structural and metabolic components of the source (Soong et al,
219 2014). SIP studies have proven powerful in documenting microbial involvement in biogeochemical
220 processes in soils and sediments and in quantifying the trophic links between the microbial and macro-
221 faunal worlds (e.g. Crotty et al. 2012; Middelburg, 2014).

222

223 *1.4.2. Fatty acid trophic biomarkers*

224 Since the early 1980s, fatty acids (FAs) have been widely used to study predator-prey relationships and
225 to trace the origin and transfer of organic matter in food webs (St-John and Lund, 1996). The use of
226 FAs as trophic markers relies on the specific FA patterns exhibited by basal resources that are then
227 transferred to and identifiable in consumers. As such, FAs have been analysed in many species to infer
228 feeding relationships in aquatic environments for example (Arts et al., 2009). They are increasingly

229 used to shed light on feeding channels in soil environments (e.g. Ruess et al., 2007). Most often, this
230 method requires tracing specific FAs of prey that cannot be synthesized *de novo* by the targeted
231 community of consumers/predators (e.g. 16:4 ω 3 for chlorophytes, 16:4 ω 1 for diatoms, 22:1 ω 11
232 biomarker for Calanoid copepods). The detection of those prey-specific FAs in the tissues of
233 consumers/predators thus reveals the assimilation pathway of the prey. However, many fatty acids (e.g.
234 16:0, 18:0, 18:3 ω 3, 18:2 ω 6) occur in a wide range of organisms restraining the accuracy of the
235 approach (Dalsgaard et al., 2003). For this matter, the comparison of FA ratios can improve the
236 interpretation of results (Parrish, 2003). For example tracking the 16:1 ω 7/16:0 ratio for diatoms or the
237 22:6 ω 3/20:5 ω 3 ratio for chrysophytes can be used to demonstrate that these microalgae are assimilated
238 by zooplanktonic microcrustaceans (Desvillettes et al., 1997; Pepin et al., 2011). Indeed,
239 the reliability of FA-based trophic markers requires in-depth knowledge of the lipid metabolism of
240 both primary producers and the targeted animal species as a prerequisite. However, while these
241 metabolic processes may obscure the identification of actual food resources, FA-based methods
242 generally provide sufficient information on foraging patterns.

243 To date, most studies using FA have been qualitative with the presence/absence of a
244 source-specific FA being used as an indicator of the existence of a trophic interaction between
245 this source and the consumer under study. A Quantitative FA Signature Analysis (QFASA) has
246 been more recently developed to enable the estimation of the proportions of different sources in a
247 predator's diet (Iverson et al. 2004). Basically, the FA signatures of consumers are modelled as a
248 mixture of the FA signatures of major food resources, which provides a quantitative estimate of
249 the proportions of those resources. The method is based on the calculation of the statistical
250 distance between predator FA signatures and mean prey FA signatures. The predator's FA
251 patterns are corrected according to the degree of modification linked to its FA metabolism.

252 Calibration coefficients are then necessary and calculated using experimental diet studies. These
253 studies are designed to assess the selective retention of dietary fatty acids, to detect fatty acid
254 bioconversion or *de novo* synthesis. The acceptance of this method by researchers studying the
255 trophic ecology of marine mammals for example will likely be broadened by the recent
256 development of a dedicated R-package (Bromaghin, 2017). According to Happel et al. (2016),
257 however, as for mixing models in SIA, the use of QFASA should be limited to the predators that
258 consume a small number of species and that can be studied experimentally as well as in the wild.

259

260 *1.4.3. Compound specific isotopic analyses (CSIA)*

261 Combining detection of biomarkers (lipids and amino-acids mainly, but also amino-sugars) to stable
262 isotope analyses, CSIA is able to trace the sources and pathways of numerous natural as well as
263 anthropogenic organic compounds. In ecology, first utilizations of CSIA focused on chemotaxonomic
264 markers of microorganisms. Although the role of microorganisms is crucial in processing and
265 transferring organic matter in food webs, their isotopic signatures were rarely reported due to the
266 difficulty of isolating specific microbial biomass from natural samples. Using ^{13}C labelled substrates
267 Boschker et al. (1998) described a CSIA approach to directly link specific microbial processes with the
268 organism involved, based on the stable carbon isotope labelling of individual lipid biomarkers. In the
269 same way, Werne et al. (2002) followed the ^{13}C depleted signal of methane in cold seep sediment
270 through different specific microbial markers and could trace with smart elegance the flow of methane-
271 derived-carbon through anaerobic methane-oxidizing archaea (archoleol and sn-3-hydroxyarcholeol) into
272 sulfate-reducing bacteria (C15 and C17 iso and anteiso fatty acids, dialkyl glycerol diethers), as well as
273 into aerobic methane-oxidizing bacteria (diploptene, diplopterol) up to bacterivorous ciliates
274 (tetrahymanol). Stable isotope probing of amino-sugars is regarded as a promising tool to investigate

275 fungal-bacterial interactions in soils (Bodé et al, 2013). Thus, CSIA can be used successfully for
276 elucidating source and fate of naturally or artificially labelled substrates.

277 In other cases, the isotopic fractionation between substrates and chemotaxonomic markers must
278 be known. Food webs studies have thus applied CSIA on essential lipid compounds such PUFA or
279 sterols by assuming that TDFs would be negligible. However, an unpredictable fractionation ranging
280 from 0‰ to 4‰ still occurs during trophic transfer of essential lipid compounds such sterols
281 (Chamberlain et al., 2004) or PUFA (Bec et al., 2011, Gladyshev et al., 2016). Moreover, the
282 intermolecular variability of $\delta^{13}\text{C}$ values within the same sample may be relatively high, thereby
283 challenging again data interpretation. For example, the difference between fatty acids $\delta^{13}\text{C}$ values
284 within a single cultivated alga may be up to 7.6‰ (Schouten et al., 1998). Thus, interpretation of CSIA
285 data could be constrained in case the potential endmembers are not sufficiently isotopically different.
286 However, when the conditions are met, CSIA could trace limiting compounds and eventually detect
287 minor food sources unseen by classical methods. For example, CSIA has revealed an uncoupling
288 between essential compounds and major organic matter transfers highlighting functional importance of
289 minor food sources of great nutritional importance (Koussoroplis et al., 2010). An increasing attention
290 is now being paid to amino acids-CSIA since McClelland and Montoya (2002) showed that the $\delta^{15}\text{N}$
291 values of some amino acids such phenylalanine in consumers are very similar to those in the producers
292 while the $\delta^{15}\text{N}$ values of other amino acids such glutamic acid become enriched in ^{15}N with each
293 trophic transfer. Thus, due to this differential ^{15}N enrichment with trophic transfer, $\delta^{15}\text{N}$ of amino acids
294 in a consumer provide a measurement of the $\delta^{15}\text{N}$ baseline as well as its trophic position.

295 Coupled with stable isotopic probing (also coined SIP), ribosomal RNA or DNA can also be
296 used as integrative tracers. ^{13}C - or ^{15}N -labelled RNA or DNA is heavier and can be separated from
297 unlabelled material using isopycnic ultracentrifugation, for example. Further amplification and

298 barcoding of the isolated fractions allows an organism associated with the assimilation of a specific
299 resource or organic contaminant to be identified (Neufeld et al., 2007). In microbial ecology, this is a
300 promising approach to detect specific functional guilds of microbes (e.g. methanotrophic bacteria), but
301 it can also be scaled-up to other consumers, such as fungi and flagellates, to reveal matter flows in
302 microbial food webs (Lueders et al., 2003).

303

304 *1.4.4. Contaminants as trophic tracers*

305 Both trace metals (inorganic elements) and xenobiotic organic compounds can fulfil the role of trophic
306 tracers (Ramos and González-Solís, 2011) when these contaminants enter trophic pathways and
307 differentially bio-accumulate in food sources or prey and consequently in consumers or top predators
308 (e.g. Walters et al., 2008; Pitt et al., 2017). Selected contaminants can thus be used to infer trophic
309 relationships, including the prey preferences of consumers/predators, foraging areas or food webs
310 exploited by different individuals or populations (e.g., Larsson et al., 1990; Deshpande et al., 2016)
311 and even trophic positions and organic matter flux when bio-magnification occurs (Kelly et al., 2007).
312 Therefore, these indirect tracers can be particularly helpful when there is inherent difficulty of direct
313 observations of trophic relationships (e.g., for marine species). Another advantage of using
314 contaminants in a trophic perspective is that it also informs on the contamination status of the species
315 and food webs of concern, which may be very interesting for ecotoxicological and/or conservation
316 biology perspectives as well. For example, a survey of cadmium (Cd) in common dolphins from the
317 North-East Atlantic allowed neritic and oceanic populations to be distinguished based on the Cd
318 concentrations in their kidneys (long-term accumulation organ in mammals) and their distinct
319 preferential prey (Lahaye et al., 2005). Cephalopods and especially oceanic squids (i.e. the preferential
320 prey of oceanic dolphins compared to neritic ones) indeed display very high burden of this metal

321 relative to fish prey species, and were thus proved to constitute a significant vector of Cd for their
322 predators (Caurant and Amiard-Triquet, 1995; Bustamante et al., 1998).

323 However, while monitoring contaminants can yield information on both trophic interactions
324 and matter fluxes, good knowledge of the contaminants' characteristics (biogeochemical cycles, the
325 distribution and persistence of the contaminant in organisms and the environment), the target
326 organism's biology, and the structure of food webs are essential. Another prerequisite is an obvious
327 source of the contaminant and its clear partitioning. In fact, contaminants are rarely used alone as
328 trophic tracer tools, and rather complement other intrinsic trophic markers such as C, N, S isotopic
329 ratios or FA profiles (e.g., Krahn et al., 2007; Hebert et al., 2009; Praca et al., 2011). For example, in
330 prey with similar FA but different contaminant profiles, use of the latter allows the discrimination of
331 different diets in the predator (while the use of FA alone did not). Nevertheless, the use of
332 contaminants as trophic tracers requires that the analysed tissues be carefully chosen, because the type
333 of tissue strongly influences the turnover rate of the contaminant-containing compound, which in turn
334 modifies the integration time of the contaminant itself. Finally, like parasites-based approaches, the
335 toxic effects of a contaminant may alter the feeding strategy of the organism. However, as long as the
336 contaminants are able to track these potentially altered foraging behaviours, they fulfil their role as
337 trophic tracers. With the recent development and improvement of modelling tools such as the
338 "Ecotracer" module (Walters and Christensen, 2018) in the Ecopath with Ecosim software package
339 (see Sections 2.3 and 4.1), the potential of contaminants as trophic tracers could be further extended.

340

341

342

343 2. Connecting species within networks from ecological data (inference methods)

344 Because establishing complete inventories of trophic interactions within a system is virtually
345 impossible, inference methods can be used to reconstruct trophic networks when the ecological
346 datasets are incomplete (Jordano, 2016). Inference methods are thus specifically useful when empirical
347 approaches (such as those described in section 1) cannot be implemented to assess trophic interactions.
348 In that case, inference methods combine empirical data about the community composition (mostly
349 occurrence/abundance of the different species) and theoretical knowledge about trophic ecology (e.g.
350 trophic behaviour of the species) to infer the trophic interactions within the community. It is worth
351 noting that inference methods were not specifically developed for trophic interactions, but for all kinds
352 of interactions (from causal relationships among variables, to social networks). Several ways are
353 available to infer interactions (e.g. using Gaussian distributions, logical interaction rules or likelihood
354 postulates), each leading to a different method that can be applied to trophic interactions. In the
355 following, we only focus on the inference methods that are mainly used in the reconstruction of trophic
356 networks.

357

358 2.1. Graphical models

359 A Graphical model is a probabilistic model using a graph to represent the dependencies among variables.
360 In the case of trophic networks, the variables are species abundances or occurrences and the edges in
361 the graph can be interpreted as trophic interactions. Generally, the graph structure is given by expert
362 knowledge, and graphical models are used to make predictions about species persistence. Conversely,
363 it is also possible to learn the graph structure, in our case the trophic network, using empirical data.
364 The principle is to draw an edge between two species in the community, whenever their
365 abundances/occurrences are not independent. Two main kinds of graphical models are used in trophic

366 ecology: Gaussian Graphical Models (GGMs) (Højsgaard et al., 2012) and Bayesian Networks (BNs)
367 (Jensen and Nielsen, 2007).

368 With GGMs, independence between two species is assessed from the empirical data with the
369 precision matrix (i.e. the inverse of the covariance matrix of the model). The resulting network is an
370 undirected interaction network whose edges are weighted by the coefficient of the precision matrix.
371 Expert knowledge is then required to determine the nature and the direction of the inferred interactions
372 (trophic or non-trophic links). In addition, it is often necessary to limit the number of inferred
373 interactions to the most relevant ones. To do so, GGMs are coupled with sparse regularisation
374 techniques, such as the graphical LASSO (for Least Absolute Shrinkage and Selection Operator;
375 Friedman et al., 2008). Faisal et al. (2010) tested different GGM procedures on large-scale spatial data
376 sets describing abundance records for 39 species of European Warblers. They were able to reconstruct
377 *in silico* the ecological networks, and from the inferred networks, they could compare the relative role
378 of bioclimatic *versus* biotic interactions on the species spatial distribution.

379 Unlike GGMs, BNs and their temporally explicit extension, dynamic-BNs (Dean and Kanazawa,
380 1989) rely on directed graphs. Concretely, it means that an edge can be interpreted directly as a
381 predation link. BNs also differ from GGMs by the learning process of the graph. In the case of BNs,
382 every possible graph is used to assess species abundances/occurrences. Then, each graph receives a
383 score, depending on both the fit between observed and inferred abundances/occurrences and graph
384 complexity. Scores are calculated using different statistical score functions (e.g. Bayesian information
385 criterion), but the underlying principle is the same: to find a graph (in our case a trophic network) that
386 maximises the score, exactly or approximately. In trophic ecology, BNs and dynamic-BNs have been
387 successfully applied to infer feeding interactions among species based on synthetic data (Aderhold et
388 al., 2012), by combining expert knowledge and field data, such as long-term catches per unit effort of

389 fisheries (Trifonova et al., 2015), or based on the presence-absence time series of a fish community
390 (Sander et al., 2017).

391

392 2.2. Logic-based approaches

393 Logic-based approaches differ from graphical models by the way they reconstruct trophic networks.
394 The principle is not based on statistical approaches, but on a set of logical rules (in the form of: “if”
395 *premise* “then” *consequence*) that is used to reconstruct trophic networks. The main advantage of such
396 approaches is to establish the rules by combining background knowledge about the species and their
397 environment and empirical data. In trophic ecology, two techniques are commonly used to determine
398 the set of logical rules: Inductive logic programming (Muggleton, 1991) when background knowledge
399 is available; or meta-interpretive learning (Muggleton et al., 2014) when background knowledge is
400 incomplete or lacking, (e.g. when the trophic ecology of the species is not known and is actually the
401 object of the attention). Logic-based approaches have been successful employed to automatically
402 generate trophic networks. For instance, Bohan et al. (2011) reconstruct the trophic network of
403 invertebrate communities within arable fields in Great Britain, using logic-based machine-learning
404 algorithms, species occurrence data and background knowledge, such as species body-size and
405 functional groups.

406

407 2.3. Linear inverse inference

408 In linear inverse inference, trophic networks are represented in a steady state, as static webs of model
409 compartments (e.g. species or group of species) that are linked together by linear interactions (Van
410 Oevelen et al., 2010). The approach is particularly suited to infer the magnitude of missing
411 interactions, a very common situation in many ecosystems given the high-dimensionality of trophic
412 networks and the scarcity of information across all trophic levels. Linear inverse inference estimates

413 the missing interactions by ensuring mass-balance across all compartments. Practically, different kinds
414 of techniques can be used (see Van Oevelen et al., 2010) to select the set of parameters that produce
415 the best fit between the modelled abundances (or biomasses) of each compartment and empirical
416 observations. The Ecopath software (see Christensen and Pauly, 1992) constitutes a typical example of
417 this approach. In addition, linear inverse inference can be coupled with ecological stoichiometry or
418 stable isotopic analysis to further constrain the solution range of the reconstructed food webs. For
419 instance, Pacella et al. (2013) associated isotope data with linear inverse modelling to reconstruct the
420 feasible food webs within the Marennes-Oléron intertidal seagrass bed.

421

422 2.4. Approximate Bayesian computation

423 Bayesian inference methods rely on the computation of a likelihood, which is the probability density of
424 the observed data under the studied model. It is associated with the parameter values of the model. As
425 a likelihood computation is not always possible, approximate Bayesian methods can be used instead,
426 with the most common one being the Approximate Bayesian Computation (ABC). This approach
427 originates from the field of population genetics (Tavaré et al., 1997) but it has been successfully
428 applied in trophic ecology to decipher the impacts of trophic interactions on the spatial structure of
429 communities (e.g. Jabot and Bascompte, 2012). In an ABC, the likelihood computation step is replaced
430 by intensive simulations of the model with variable parameter values, so as to select the values that
431 lead to the best match between simulations and empirical data. ABC can be further coupled to efficient
432 algorithms, such as sequential or traditional Markov Chain Monte Carlo methods (Jabot et al., 2013).
433 This approach was used to evidence the presence of density-dependent dispersal in spatially distributed
434 food webs, as well as its implication for food web spatial structure (Melián et al., 2015).

435

436 3. Quantifying the consequences of feeding from individuals to ecosystems

437 3.1. Ecophysiological markers

438 Nutritional status and/or body condition can be assessed using diverse types of information, such as
439 foraging success or the energy stored by individuals (Schulte-Hostedde et al., 2001). Using
440 ecophysiological approaches among others, nutritional status and body condition can be helpful to (1)
441 infer feeding activities and foraging history of individuals and populations, and (2) the consequences of
442 trophic relationships and availability of resources on individual health and fitness as well as population
443 and community dynamics. Despite the existence of extremely invasive or lethal methods currently
444 available to assess body condition, body composition and nutritional status, non-lethal techniques are
445 increasingly used. As described in recent reviews, these techniques include body condition indices,
446 body fluid biochemistry, chemical dilution techniques (isotope dilution: change in concentration of
447 isotopes of hydrogen and/or oxygen in body water, and gas dilution: change in concentration of lipid
448 soluble gas), electrical approaches such as body electrical conductivity and bioelectrical impedance,
449 scanning methods (e.g. magnetic resonance imaging, ultrasound scanning, dual-energy X-ray
450 absorptiometry, computed tomography), molecular analyses (e.g. gene expression) and measurements
451 of stress hormones and immune responses (Stevenson and Woods, 2006; Wilder et al., 2016).
452 In addition, animal performance (i.e. various life-history traits related to fitness, such as survival,
453 development rate and growth, resistance to starvation, tests of stamina, and reproductive success) can
454 be measured. These data are often used to assess the physical condition of the animal, or to evaluate
455 the “quality” of its food and/or habitat and determining factors of trophic interactions or driver of diet
456 selection (Harrison et al., 2011; Jakob et al., 1996; Raubenheimer and Simpson, 2004; Visanuvimol
457 and Bertram, 2011). Metabolism is also a physiological indicator; it can be determined through
458 respirometry, which measures the basal metabolic rate (at rest) or the maximum oxygen consumption

459 rate during forced exercise (Sadowska et al., 2008; Urrejola et al., 2011). Among this wide range of
460 techniques, our focus here is on those most widely used, easy to conduct, least invasive and least
461 expensive, namely, body condition indices and body fluid biochemistry.

462

463 *3.1.1. Body condition*

464 Body composition, or the amount of fat vs. fat-free body mass, is probably one of the most direct
465 indicators of body condition. It provides a quantitative assessment of energy storage because lipid
466 stores constitute the principal form of energy reserves in animals (Schulte-Hostedde et al., 2001;
467 Walsberg, 1988). Thus, the body's energy reserves are measured through analyses of body fat content
468 or body composition. The latter is mostly based on two or three compartments: fat mass, lean dry
469 mass/water mass and protein and ash mass (Jakob et al., 1996; Peig and Green, 2009; Reynolds et al.,
470 2009; Schulte-Hostedde et al., 2005). Alternative, but destructive methods, that can be conducted in
471 study designs based on carcass collection for instance include the sampling and weighing of specific
472 subcutaneous fat depots during dissection or the use of complementary somatic indices such as those of
473 the liver or pancreas (Stevenson and Woods, 2006). However, such methods are tedious, time-
474 consuming and intrusive as well as destructive.

475 Consequently, other methods have been proposed to measure body composition or fat stores,
476 notably total body electrical conductivity (Reynolds et al., 2009; Walsberg, 1988), magnetic resonance
477 imaging (McGuire and Guglielmo, 2010) and body composition modelling (Molnar et al., 2009). In
478 certain taxonomic groups (such as birds), subcutaneous adipose depots can be assessed by simple
479 visual inspection (Labocha and Hayes, 2012), whereas others (small mammals) require simple
480 measurements, such as pelvic circumference, considered representative of fat content (Labocha et al.,

481 2014). In microscopic organisms, coherent anti-Stokes Raman spectroscopy can be used to non-
482 invasively observe lipid droplets in tissues (e.g. Fueser et al., 2018).

483 Body condition indices based on morphometrics have also been developed. Most discriminate
484 between the mass of the individual associated with body structural size (body weight) and the mass
485 related to energy reserves (Green, 2001; Peig and Green, 2009; Schulte-Hostedde et al., 2005).

486 Accordingly, the greater the body weight is, the larger are the energy reserve, and the better is the body
487 condition. Body condition indices thus allow the relative size of the body's energy stores to be
488 computed, taking into account body structural size components. Historically, this was achieved using
489 the residuals of the regression (typically, ordinary least squares regression) between body weight and
490 some index of body size, or by calculating the scaled mass index (Green, 2001; Peig and Green, 2009,
491 2010; Schulte-Hostedde et al., 2005). Although much debated (Wilder et al., 2016), body condition
492 indices based on morphometrics have been, and are still, widely applied (Labocha et al., 2014;
493 Labocha and Hayes, 2012; Wilder et al., 2016).

494

495 3.1.2. *Body fluid biochemistry*

496 Several (micro-) nutrients needed to fulfil basic energetic requirements and metabolism cannot be
497 synthesised *de novo* and can only be acquired from food (Kohl et al., 2015; McWilliams, 2011). These
498 essential trace elements include dietary minerals (e.g. Cu, Co, Fe, Mn, Mo, Se, Zn), carotenoids,
499 vitamins and some amino acids and FAs (Costantini et al., 2010; Harrison et al., 2011; Kohl et al.,
500 2015; McWilliams, 2011). By measuring the levels of certain metabolites, electrolytes and enzymes,
501 the depletion of some essential or limiting dietary element, and thus the health state (or the presence of
502 food deficiencies) of the individual, can be determined directly. Moreover, information are given on

503 how the resource balance is oriented toward the use (and even storage) of nutrients from the acquired
504 food or toward the mobilisation of endogenous reserves.

505 With the aid of diagnostic tools similar to those used in human and veterinary medicine, body
506 fluid biochemistry can be used to assess body condition and individual health in other organisms
507 (Resano-Mayor et al. 2016; Schoepf et al. 2017), especially for micro-nutriments only acquired by
508 food. Since the late 1990s, interest in non-lethal methods to evaluate the physiological state of
509 individuals has grown and has stimulated the development of technical devices and commercial kits
510 compatible with the measurement of micro-volumes. Thus, biochemical analyses of plasma/serum or
511 hemolymph can be conducted by measuring various markers related to nutrition and digestion,
512 metabolism, nutrient storage, osmoregulation, liver or kidney function and immunity. Specifically,
513 nutritional status and patterns of energy utilisation can be assessed by measuring the levels of the
514 products of intermediary metabolism related to diet and detectable in body fluids. This is the case for
515 total proteins, glucose, albumin, urea, creatinine, uric acid, essential minerals and trace elements. Lipid
516 metabolism can be assessed by measuring the concentrations of lipids and ketones, homeostasis,
517 energetic metabolism or the functioning of tissues involved in digestion based on the activities of
518 specific enzymes (e.g. alkaline phosphatase, lactate dehydrogenase and creatine kinase). There are also
519 markers specifically associated with starvation, such as bile acids, bilirubin and globulin, and those that
520 allow accurate assessments of hepatic, renal and pancreatic function or electrolyte levels (major and
521 dietary minerals). Analyses of body fluids may also target specific micronutrients essential for normal
522 metabolic processes and thus potentially indicative of health status. An example is carotenoids. These
523 fat-soluble pigments originate from plants, algae or fungi but cannot be synthesised *de novo* by
524 vertebrates, which must acquire them exclusively from dietary sources. Hence, carotenoid-based traits

525 can reveal the foraging ability, resource availability and trophic interactions as well as the nutritional
526 and immune status of their bearers (Sternalski et al., 2010).

527 The main drawback of these techniques lies in the difficulty of interpreting the data obtained
528 from the battery of markers. The measured parameters must be chosen carefully to obtain convincing
529 evidence of a metabolic pattern or change in nutritional status. Furthermore, some parameters can be
530 interpreted only in the light of variations in others (for instance lipids or hepatic enzymes), and body
531 fluid biochemistry can be affected by several confounding factors in the relationship with food
532 acquisition (for instance, blood/hemolymph metabolite concentrations may change after food
533 ingestion, and age, sex, and reproductive stage can affect metabolic levels and enzymatic activities).
534 Given these considerations, an integrated assessment is critical and should be based on the use of
535 several body fluid biomarkers, other metrics of body condition and could be dependant of individual
536 and ecological factors as well (Resano-Mayor et al., 2016; Wilder et al., 2016). Changes in
537 physiological conditions are not always food-related but may be driven by other abiotic stressors (e.g.
538 temperature changes, contaminants) that might be considered carefully but that are important in trophic
539 ecology as well as to get further insights into the consequences of the interactions between
540 environmental factors and trophic relationships (see for instance Bustnes et al., 2015). Such issues are
541 raising growing interest within the framework of stress ecology. Nutritional ecology is one side within
542 trophic ecology framework that is perhaps not enough considered to build integrated approaches and
543 may deserve further attention in studies on food webs and trophic ecology (Raubenheimer et al., 2009).

544

545

546 3.2. Trait-based trophic ecology

547 Focusing on functional features rather than on taxa helps describing biodiversity from a functional
548 point of view (Levine, 2016). Trait-based approaches can be an adequate theoretical framework for
549 understanding and predicting food webs dynamics and properties (Bartomeus et al., 2016; Gravel et al.,
550 2016). Thus, trait-based trophic ecology investigates both (1) trophic interactions *per se* and (2) their
551 ecosystem implications. First, functional traits allow inferences regarding the most probable
552 interactions occurring within a community. A common first approach uses phenological traits or
553 ecological preferences to detect species that co-occur and to discard unlikely trophic interactions
554 (González-Varo and Traveset, 2016). The morphological and/or physiological traits of the co-occurring
555 partners are then used to infer the probability of realised trophic interactions (see Gravel et al., 2016 for
556 a useful framework distinguishing foraging, vulnerability and consumption traits). Because
557 determining all interactions among individuals, even in simple systems, is fairly unattainable,
558 narrowing those interactions using functional traits provides an alternative and can make the
559 mechanistic underpinnings of interactions understandable (e.g. Ibanez et al., 2013). In addition,
560 functional traits enable the different dimensions of the trophic niche to be investigated individually or
561 simultaneously by examining the morphological, physiological, phenological and behavioural
562 determinants of the trophic niche of a particular species (e.g. Spitz et al., 2014).

563 Two tenets of functional-trait-based approaches are essential in interpreting the implications of
564 the identified trophic interactions. First, ‘response and effect traits’ link the response of individuals to
565 higher trophic levels or to environmental stressors with the potential effects on lower trophic levels.
566 For instance, plant diversity changes affects functional diversity of arthropods across trophic levels
567 (Ebeling et al., 2018) which might affect ecosystem processes. Second, functional-trait-based
568 approaches can explicitly address intra-specific variability at the individual level (Albert et al., 2011;

569 Rota et al., 2018) and the findings then scaled up to the community and ecosystem levels (e.g. Lavorel
570 and Grigulis, 2012).

571 The development of functional-traits-based approaches in trophic ecology is still hampered by
572 several limitations and drawbacks, but with recent progress these are being overcome e.g. by using
573 methodological standardization (Moretti et al., 2017). Further, it remains difficult to assess the strength
574 of species interactions (the direct effect that species have on their mutual demography). Nevertheless,
575 it is possible to estimate functional food web relationships by distinguishing (1) the life-history traits
576 which may modulate the strength of an interaction on population growth, from (2) the topological traits
577 which may modulate the pairwise interactions between the predator and its prey, and from (3) the
578 consumption traits which may modulate the *per capita* interaction strength (Gravel et al. 2016, see also
579 Brousseau et al., 2018). Additionally, the correlation between individual traits and how this lack of
580 independence among traits reflects phylogenetic (evolutionary) constraints remain poorly understood
581 (Poff et al., 2006). Thus, the validity of linking traits to actual trophic functions continues to be a
582 source of debate, as the causal link between them is often far from obvious, quite variable, and/or has
583 yet to be definitively demonstrated.

584

585

586 3.3. Ecological stoichiometry (ES)

587 The consequences of elemental imbalances in ecosystems can be explored using ES approaches, in
588 which the elemental compositions of heterotrophic organisms (generally expressed as C:N or C:P
589 ratios) are considered as far less variable than those of primary producers, at least for most similarly
590 sized taxa (Persson et al., 2010). Based on the law of conservation of matter, ES approaches can
591 predict how organisms are influenced by the mismatch between consumer demand and the elemental
592 supply available in resources (Sterner and Elser, 2002). At the ecosystem scale, measuring imbalances
593 can be used to estimate nutrient transfer efficiency and secondary production (Cebrian et al., 2009). In
594 the presence of excess elements in their food, consumers make use of several coping strategies such as:
595 (1) selecting food with elemental ratios close to their requirements and/or (2) eating food of different
596 qualities but assimilating only those elements that fulfil their requirements while rejecting those
597 available in excess. In the latter case, mass balance models can estimate the amount of excess elements
598 released. Experimental measurements of metazoan's nitrogen and phosphorus excretion rates showed
599 that animals can supply nutrients at rates similar to those of other major nutrient sources and support a
600 large portion of primary production by nutrient recycling (Vanni, 2002; Vanni et al., 2002). Excreted
601 elements reduce nutrient limitations and impact ecosystem processes in a predictable manner (Danger
602 et al., 2009). Accordingly, ES is a powerful conceptual framework for predicting both the
603 consequences of resource ingestion on consumers' life history traits and the ecosystem consequences
604 of elemental imbalances. To date, most ES studies have focused on C, N and P; however, the
605 consideration of other essential elements (e.g. As or Cu, see Karimi and Folt, 2006) might provide a
606 better understanding of nutrient transfer and the potential limitations for consumer growth or
607 ecological processes (Welti et al., 2017).

608

609 3.4. Resource quality

610 Parameters other than the C:N:P ratios of resources can influence consumers' growth and physiological
611 status as well as the efficiency of nutrient and energy transfer into food webs. These include several
612 essential compounds as crucial drivers of diet selection (Kohl et al., 2015). For example, the lack of
613 certain polyunsaturated FAs of the $\omega 3$ series and/or phytosterols limits *Daphnia* growth and/or
614 reproduction (e.g. Martin-Creuzburg et al., 2009). Micronutrients are another example and include
615 carotenoids, described in Section 3.1.2. These pigments are important stimulators of immune responses
616 and show antioxidant properties (e.g. Lucas et al., 2014). Integrative approaches that include large
617 classes of biochemical compounds (proteins, lipids, glucids) have been proposed to relate resource
618 composition and organism fitness within a conceptual framework referred to as "nutritional geometry"
619 (Simpson and Raubenheimer, 1993). Its advantage is that it directly relates consumers' feeding
620 strategies to their life history traits (e.g. optimal carbohydrate/protein ratios that optimize either
621 individual growth or reproduction) and thus nutritional geometry allows evolutionary questions to be
622 explicitly related to trophic ecology. Moreover, a combination of all of these resource-quality-based
623 approaches has been proposed (Sperfeld et al., 2017) and is a promising methodological strategy for
624 research in trophic ecology.

625

626

627 4. Testing the implications of trophic interactions (trophic models)

628 While inference methods are used to reconstruct trophic interactions within community (Section 2),
629 modelling approaches presented in this section allow investigations of the consequences of feeding
630 interactions on various ecosystem features, ranging from population to ecosystem dynamics. The
631 assumptions underlying the different models include continuous/discrete, mechanistic/statistical and
632 individual-/population-based systems. The common goal is to simulate food web functioning from a
633 set of given conditions, such as network structure, which can in some cases be determined through
634 inference methods. Modelling approaches can be used to investigate the potential implications of
635 feeding interactions in terms of community dynamics and/or organic matter/energy transfers (e.g. Rall
636 et al. 2008) and thus contribute to an improved understanding and management of ecosystems. The use
637 of models also allows the testing of hypotheses that cannot be tested in natural systems (e.g. Gaucherel
638 et al., 2017) as well as the formulation of predictions regarding ecosystem responses to management
639 decisions (e.g. Marzloff et al., 2016). In this section, we present the main modelling approaches
640 currently used for hypotheses testing in trophic ecology.

641

642 4.1. Ordinary differential equations and qualitative models

643 Ordinary differential equations (ODEs) simulating species dynamics, such as the Lotka-Volterra
644 equations, can be adapted for food web models. The latter have been central to understanding indirect
645 interactions in food webs and in studying the consequences of predator-prey interactions on population
646 dynamics (e.g. Rall et al., 2008). Food web models based on ODEs allow investigations of the
647 relationship between food web complexity and stability (e.g. McCann and Rooney, 2009). During the
648 last two decades, models based on ODEs have been expanded to include allometric constraints on
649 species traits, such as metabolic rates and feeding rates, leading to the so-called bioenergetic or

650 allometric trophic network model (Brose et al., 2017). Ecosim, the time dynamic simulation module
651 associated with Ecopath, is a well-known application of this approach and it is commonly used to
652 explore policy options in the ecosystem-based management of fisheries, such as the effects of fishing
653 on ecosystems and the establishment of marine protected areas (see Walters et al., 1997).

654 Qualitative modelling focuses on the feedback structure of food webs and is used to assess both
655 stability and ecosystem responses to perturbations (Puccia and Levins, 1985). This method, which is
656 also based on ODEs, is particularly well suited for trophic ecology studies, as it does not rely on the
657 quantification of all trophic interactions within a system. Indeed, based only on qualitative assessments
658 of the interactions among major trophic compartments (e.g. positive, neutral or negative), qualitative
659 models of food webs can provide a general understanding of ecosystem stability and dynamics based
660 on network topology (Hulot et al., 2000). For instance, they can be used to predict the overall
661 responses of a community to long-term disturbances, as the spatial shift of multiple marine species due
662 to ocean warming (e.g. Marzloff et al. 2016). However, the predictions are most useful for simple
663 networks (< 15 nodes) as they become ambiguous in more complex systems (e.g. Dambacher et al.,
664 2003).

665 4.2. Statistical approaches 666

667 Statistical approaches are based on graphical models (see section 2.1), but in the present case, the
668 graph structure (i.e. the trophic network) is known and is not an output of the model. Trophic
669 interactions are represented as edges in the graph and are interpreted as statistical interactions between
670 species by the model. Using the resulting graph, statistical approaches are able to model the probability
671 of species persistence, explicitly, without a mechanistic model of the extinction dynamics. Unlike
672 Lotka-Volterra or structural food-web models that are based on material fluxes, statistical approaches
673 can be built from simple “on-field” observations of individual occurrence. The required experimental

674 set-up is thus simpler than the one for computing the parameters and structure of Lotka-Volterra or
675 structural models. Another advantage is the possibility to evaluate the resilience of trophic networks
676 using the probabilities of species persistence, and not only the trophic structure. McDonald-Madden et
677 al. (2016) adopted this approach to study the conservation management of 6 real food webs (the
678 Alaskan, Baltic Sea, Lake Vattern, Chesapeake Bay, Arizona Montane forest and Long Island Salt
679 Marsh food webs) and 40 hypothetical food webs. The resulting predictions allow estimating the effect
680 of management strategy directly at the scale of food-web and their study provide a computationally
681 efficient way of identifying the important species to manage in large food webs.

682

683 4.3. Discrete approaches

684 In discrete approaches, networks of trophic interactions are represented by systems made of distinct
685 and separate components, and characterised by temporally distinct and separated events (e.g. Campbell
686 et al. 2011). As such, discrete approaches, more than classical trophic models, are particularly
687 appropriate to consider complex interaction networks (i.e. networks with a high number of direct and
688 indirect processes), while their behaviour remain under rigorous control. A strong advantage of
689 discrete models is thus the possibility to model the evolution of trophic networks over time. Studying
690 ecosystem trajectories constitutes a potential fruitful research avenue for discrete approaches that
691 could help identifying sustainable paths (the ecosystem is able to persist and evolve) from dead-ends
692 (the ecosystem disappears or is stuck in a specific state with less interacting species). Gaucherel et al.
693 (2017) followed such an approach, using Boolean networks, to study the trajectories of a theoretical
694 termite colony. By removing different numbers and types of nodes, the authors simulated different
695 disturbances of the colony and examine the effects on the interaction network. By doing so, they
696 showed that the colony was highly sensitive to the trophic part of the interaction network. In addition,

697 this example illustrates the conceptual shift permitted by discrete approaches toward broader (spatial
698 and temporal) scales of ecological processes (Wallach et al., 2017).

699

700 4.4. Individual-based models

701 In an individual-based model (IBM), each individual and its associated behaviour are represented,
702 which allows interactions among individuals to be approximated. IBMs are commonly used in ecology
703 (Grimm et al. 2005). An important research activity surrounding IBMs consists in understanding how
704 patterns at the population or community scale emerge from the interactions among individuals (Durrett
705 and Levin 1994). In trophic ecology, IBMs can be used to reveal the consequences of intraspecific
706 variations in diet on community trophic structure (Bolnick et al., 2011) or eco-evolutionary dynamics
707 (Melián et al., 2011). Another application consists in scaling from trait-based interactions between
708 individuals to the global structure of ecological networks (Jabot and Bascompte, 2012).

709

710 4.5. Dynamic energy and mass budget approaches

711 The dynamic energy and mass budget (DEB) theory describes the organisation of metabolism within
712 organisms (Sousa et al., 2008) by modelling its quantitative facets (assimilation rate,
713 growth/maintenance, and maturity/reproduction) based on common rules of allocation and the
714 processes occurring at the organism level. Standard DEB model consists in a system of three ordinary
715 differential equations following first order dynamics. Assimilated products first enter a reserve pool
716 which is then mobilized to fuel two pathways following the kappa rule: a fixed kappa fraction is
717 allocated to perform growth and maintenance and the remaining fraction (1-kappa) is available for
718 maturity (i.e. increase of complexity and its maintenance) and reproduction (Van der Meer, 2006). A
719 set of 12 primary parameters is calibrated from life history traits and univariate data (Lika et al., 2011).

720 Common model inputs are temperature and food availability and outputs are size, shape, full life cycle
721 dynamics, reproduction rate and composition of the organism (C, H, O, N). Standard DEB models (one
722 reserve, isometric organism) are commonly used at the level of the individual organism (e.g. Grangeré
723 et al., 2010) but they can be scaled up to population level (Martin et al, 2012) or to food web and
724 ecosystem levels including trophic interactions (e.g. Marques et al., 2014). Interesting applications of
725 DEB models in trophic ecology are related to diet reconstructions (Picoche et al, 2014), the effect of
726 food stoichiometry on growth (Muller et al, 2001), the effect of prey selection on organism
727 bioenergetics (Lavaud et al, 2014) and spatio-temporal dynamics of predator-prey interaction
728 (Grangeré et al., 2010). With some more parameters, they also include the dynamics of body isotope
729 composition (Pecquerie et al, 2010) and thus offer promising perspectives in understanding
730 metabolically induced variations in TDFs and in the dynamics of isotope incorporation (Emmery et al.,
731 2011), in turn allowing better inferences using natural stable isotope ratios.

732

733 5. A comprehensive toolbox of methods

734 Trophic ecology is a vibrant field of research supported, as discussed extensively above, by a diverse
735 and ever-growing array of methodological tools. For ecologists seeking to answer specific trophic
736 questions, we examine this set of tools (Table 1) based on our own experience and background (Fig.
737 1). For the empirical methods, our discussion includes the results of a multiple correspondence analysis
738 (MCA) based on an evaluation of the price, investment, and affinities of each method with key criteria,
739 such as the observational scale, organisational level, type of ecological question to be tackled and the
740 type of data produced (Fig. 1A; the procedure is detailed in the Appendix). The first axis of the MCA
741 was mainly driven by the type of ecological question and the second axis was related to the investment
742 needed to implement the methods. On the same figure (Fig. 1A), we also displayed the methods'
743 affinity with organisational level and a rough evaluation of their costs. We completed this analysis with
744 a subjective classification of the various trophic models (after C. Gaucherel and E. Thebault, pers.
745 com.). On the resulting Fig. 1B, we focused on the models' affinity with the type of ecological
746 question and organisational level for the sake of consistency with the classification of empirical
747 methods. Not included into this classification were inference methods, because they could not be
748 discriminated by these two axes. The resulting roadmap (Fig. 1A and B) provides an overview of the
749 affinities of the methods for the different criteria. As an example, from Fig. 1A it can be deduced that
750 the use of observational methods is more appropriate than stoichiometry if the nature of feeding
751 interactions is the subject of interest. This visual overview also highlights the gaps (i.e. the absence of
752 available method to address a specific issue), such as the modelling of fluxes at the integrated scale of
753 ecosystems (and not only between species, see Fig. 1B). An advantage of the roadmap is that it
754 facilitates the selection of the best combination of methods with which to investigate (or triangulate) a
755 specific issue in trophic ecology (see below).

756 6. Interconnecting approaches to advance ecological research

757 The abundance of methods currently available to trophic ecologists offers opportunities such as the
758 triangulation referred to by Munafò and Smith (2018), i.e. the intentional use of multiple approaches
759 which complementarity offers less-biased, multiple lines of evidence. In other words, combining two
760 or more methods allow overcoming the shortfalls of each one alone, and initiating interdisciplinary
761 collaborations that will enrich our knowledge and perspectives. More than combining several methods
762 at the same integration level (e.g. SIA + FA + Gut contents), we recommend more interconnection of
763 approaches, for example by creating first a topology using traits, then modelling and using
764 ingestion/assimilation tracers as validations. Only a few comparative studies of methodologies have
765 been published (but see Nielsen et al, 2018), in the following we present several examples in which
766 complementary methods were merged or interconnected successfully and led to novel insights.

767 Combinations of methods have been used to improve empirical descriptions of food webs,
768 especially as there are recurring issues related to the integration of trophic processes over time. These
769 can be addressed by complementary approaches. For example, while assimilation tracers such as
770 isotopes and FAs are regularly combined, the addition of complementary behavioural observations and
771 ingestion tracers would favour the emergence of comprehensive theories and models describing
772 tropho-dynamics in food webs (e.g. Woodward et al, 2010, McMeans et al, 2016). Direct field records
773 (motion-sensitive cameras, Robinson et al, 2018) are also useful additional measurements to obtain
774 inferred food webs with a much better temporal accuracy. At the individual level, SIAs can be coupled
775 to DNA-based analyses of gut contents to enable the detection of possible cannibalistic behaviour, as
776 this is not possible with molecular methods (Traugott et al, 2013), and to overcome the lack of dietary
777 resolution inherent to stable isotope methods (e.g. Hambäck et al, 2016).

778 Other examples show that interconnecting trait-based concepts with stable isotope methods
779 sheds light on the interplay between interactions and fluxes. In fact, this has contributed to the
780 emergence of the concept of isotopic trophic niches (Bowes et al, 2017, and references therein). Also,
781 placing predator-prey functional traits (e.g. predator biting force vs. prey cuticle toughness) within a
782 phylogenetic framework (e.g. evolutionary distance between trophic levels) can give rise to models of
783 predator-prey interactions (Brousseau et al, 2018). Observational data can contribute to inference
784 methods and models to obtain a characterisation of the ecosystem-level properties emerging from
785 trophic interactions (e.g. Pacella et al, 2013, de Vries et al, 2013). For example, a Bayesian model
786 using topology and isotopes was specifically dedicated for the elucidation of trophic strengths in
787 trophic networks (IsoWeb, Kadoya et al., 2012). Models tested against empirical data can be employed
788 to reveal the mechanisms operating within food webs and to re-assess the relevant level of complexity
789 (guilds) at which food webs should be scrutinised in the field (Hulot et al, 2000). Theoretical
790 modelling and empirical data, connected through a trait-based approach to species and metabolic rates
791 within allometric trophic networks, can successfully reproduce complex multi-species dynamics in
792 natural environments (Boit et al. 2012). Among the most recent attempts involve hybrid modelling, in
793 which models of the overall dynamics of the ecosystem are combined with realistic individual-based
794 models to link responses at the individual and population levels (Strauss et al, 2017). Also worthy of
795 mention are stoichiometry-based approaches, which offer a powerful and promising perspective from
796 which to extend our knowledge about food webs to include biogeochemical consequences and effects
797 on ecosystem services (Boit et al, 2012, Strauss et al, 2017). A stoichiometric-trait-based approach was
798 recently described (Meunier et al, 2017), although it requires further development (Welti et al, 2017).
799 Multivariate DEB models (several substrates, or/and reserves and structures) offer new perspectives to
800 integrate nutritional geometry and ecological stoichiometry into a metabolic theory through the

801 concept of organisms' homeostasis (Sperfeld et al., 2017). Capturing complex trophic interactions
802 within or between species could then be modelled by embedding multivariate DEB models in agent-
803 based modelling approaches (Sperfeld et al., 2017). Finally, DEB models estimate key morphological
804 traits, such as size, weight, shape, ingestion rates, and range of temperature tolerance. By doing so,
805 they provide connections to biophysical models (e.g. temperature, wind speed and radiation) and to
806 nutritional geometry that allow modelling trophic and ecological niches of organisms (Kearney et al.,
807 2010).

808

809

810 7. Including the microbial world in trophic ecology

811 The microbial world has long been treated almost independently from the macroscopic world (Prosser
812 2007). Conversely, studies of microbial diversity do not explicitly consider the concepts of trophic
813 ecology. The emergence of molecular approaches has enabled microbial cryptic diversity to be
814 revealed through genomics, by mapping co-occurrence networks within microbial communities
815 (Barberán et al, 2012, Peura et al, 2015). However, the implications of the results in terms of trophic
816 interactions within microbial communities or in relation to the metazoan food web remain poorly
817 explored (Peura et al, 2015). On the other hand, trophic ecology has not yet explicitly integrated the
818 role and contribution of complex microbial communities even though the participation of microbes in
819 aquatic and marine food webs was described more than four decades ago (Pomeroy, 1974), and
820 heterotrophic protists have been recognized as the major grazers in the oceans (Calbet and Landry,
821 2004, Sherr and Sherr, 2007). Bacterial and micro-eukaryotic communities are for the most part
822 included in food web models as broad, unresolved taxonomic or functional groups, with very few
823 exceptions (Peura et al, 2015, D’Alelio et al, 2016, Weitere et al, 2018). Furthermore, estimates of
824 trophic chain length fail to consider heterotrophic microbes (Post, 2002), while recent CSIA-based
825 assessments register heterotrophic microbes in food webs at the same trophic positions as animals
826 (Steffan et al., 2015).

827 Consequently, our understanding of the “green” and “brown” food webs, including the tropho-
828 dynamic processes of the detritosphere, emphasised already by Lindeman (1942), remains deficient,
829 and the potential contribution of the topology of microbial and metazoan networks to ecosystem
830 stability and resilience barely known (Peura et al, 2015). Several recent methodological developments
831 may be the first steps in ground-breaking advances in our understanding of micro-macro food webs:
832 (1) Recent developments in DNA-SIP (Pepe-Ranney et al, 2016) and RNA-SIP (Kramer et al, 2016)

833 allow the tracking and identification of microbial metabolisers of organic substrates up to primary
834 consumers (see section 1.4.3), thereby improving empirical descriptions of the links within prokaryotes
835 and protists but also allowing a quantification of the connection to higher trophic levels. (2) By taking
836 advantage of the surge of metagenomic and metatranscriptomic approaches, microbial ecologists have
837 been able to link microbial genetic diversity with the functionalities and biogeochemical processes
838 determined in field samples (see Morales and Holben 2011 and references therein). (3) Information on
839 taxon-specific feeding selection and the rates measured in experimental settings from microbial and
840 metazoan organisms can be used as input in Ecopath-like food web models adapted to explicitly
841 include highly resolved protozoan contributors (D'Alelio et al, 2016). These models can then be
842 applied to explore the functional consequences of the switches in microbial food web structure on the
843 overall trophic transfer of matter across the micro-macro continuum (D'Alelio et al, 2016). Ecological
844 stoichiometry (Welti et al., 2017) or the application of trait-based approaches to microorganisms
845 (Litchman et al., 2015) may serve as a bridge between the microbial food web and the energetics and
846 biogeochemistry of the ecosystem, while allometric scaling could connect processes at the food web
847 scale, thus merging the “green” and “brown” food chains (e.g. Mulder et al., 2013).

848 For trophic ecologists, these elements well evidence the so-far-unrealised opportunity to fully
849 consider vertical biodiversity based on an explicit representation of the micro- and macroscopic actors
850 and their roles. With the improvement of the collaboration between microbiologists and trophic
851 ecologists many long-standing questions will finally be answered and “complexity made simple”
852 (Pomeroy, 2001).

853

854

855 Conclusion

856 In a world of fast and dynamical changes in environmental conditions, there is a crucial need to
857 understand and anticipate changes in biodiversity in both space and time. Direct effects of changes in
858 physical factors on species depend on specific tolerance, physiological acclimation, phenotypic
859 plasticity and evolutionary processes (Angert et al, 2013), likely to create local changes of biodiversity
860 such as spatial redistribution of species (Marzloff et al, 2016). Yet, evidences are piling that indirect
861 effects of global changes through alterations in species interactions overweight direct effects (see Holt
862 and Barfield, 2009, Angert et al, 2013), or that species range shifting can induce new trophic cascades,
863 inflating the ecological consequences of multiple species redistribution (Marzloff et al, 2016). Such
864 observations of the crucial role of feeding interactions in the biodiversity response to global changes
865 place trophic ecology at the core of the issue (see R. Holt contribution to Nature 2020 visions, Norvig
866 et al, 2010). Recent conceptual and methodological developments in trophic ecology now allow to
867 explore all the dimensions of such changes, but also to draw cross-scale linkages, at least for some
868 pilot sites and case studies. Numerical improvements and machine-learning technics offer the
869 opportunity to test theories and capitalize on these laboriously obtained field- or lab- data by expanding
870 the time- and space scales of processes and predictions (Faisal et al, 2010; Angert et al, 2013). We
871 hope this synthesis will convince our colleagues that we have at hand the perfect toolbox to finally deal
872 with the enormous complexity of trophic implications.

873

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1479 Figure's Captions:

1480 Fig. 1 (A) Multiple correspondence analysis showing the general distribution of empirical methods
1481 used in trophic ecology (see Table 1 for data and abbreviations). Arrows indicate the affinity of the
1482 methods with the selected features: organisational level (from individuals to ecosystems), ecological
1483 questions (interaction vs. flux of energy/matter), or commitment of budget, time and efforts (investment,
1484 price). Observational scale (i.e. microscopic to macroscopic) was mostly discriminated by axis 4, not
1485 shown here, but scores are in appendix. (B) Subjective classification of trophic models based on their
1486 affinity with the organisational level and ecological question (after C. Gaucherel and E. Thebault, pers.
1487 com.). ODE: ordinary differential equation, IBM: individual-based model, DEB: dynamic energy and mass
1488 budget.

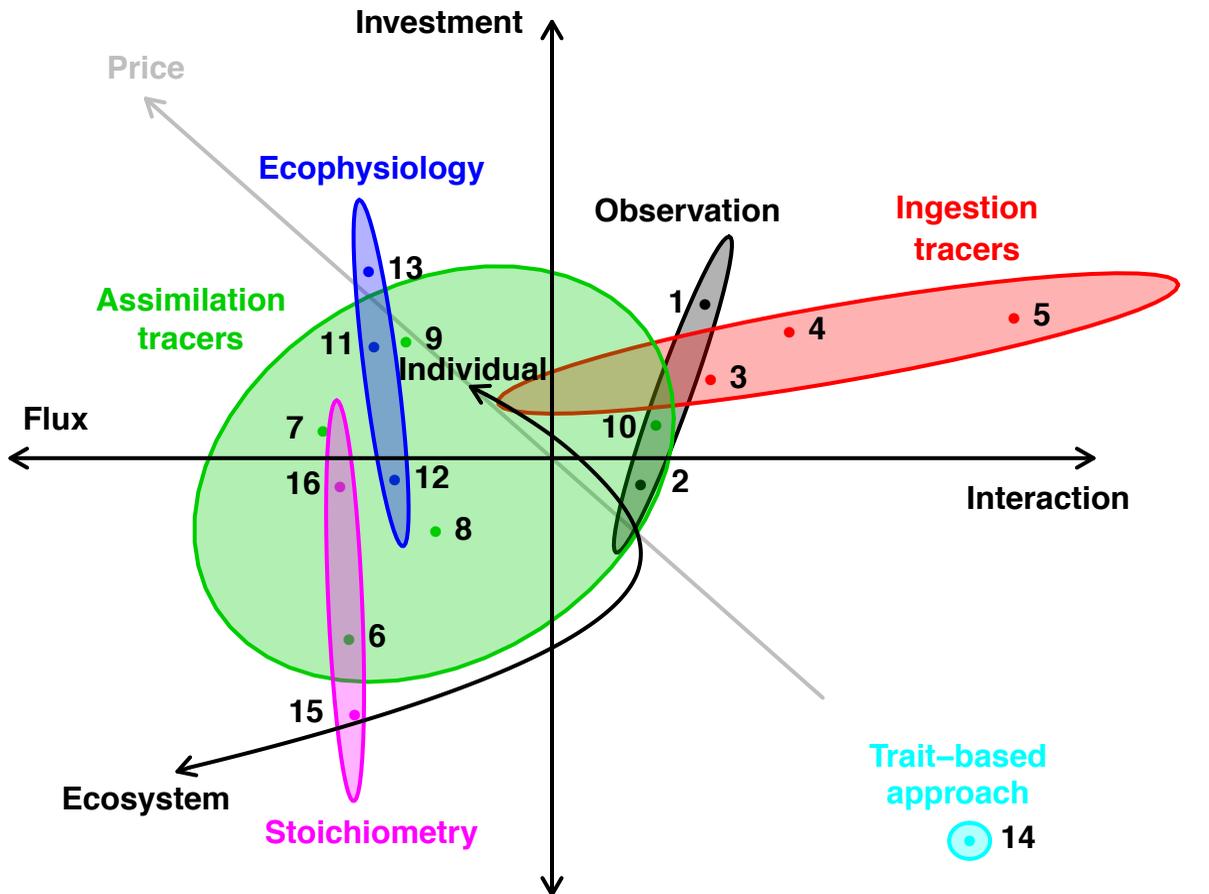
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1491 Table 1. Synthesis of the main advantages and drawbacks of several methods commonly used in trophic
1492 ecology. Expert assessment of empirical methods according to 12 variables is also shown: price, investment
1493 (is it a turnkey method? or does it require further development?), observational scale (from microscopic to
1494 large organisms), organisational level (from individuals to ecosystem), type of ecological question
1495 (interaction vs. flux of energy/matter), and type of produced data (qualitative vs. quantitative). 0 indicates
1496 "not adapted" and 1 indicates "strong affinity". The exceptions are the variables "price" and "investment",
1497 where 0 and 1 stand for "low" and "high" respectively, and the "data" variable, where 0 and 1 stand for
1498 "qualitative" and "quantitative" data respectively.

Figure 1

A



1: Observation of feeding activity

6: Bulk stable isotope analysis

11: Body composition

2: Incubation experiments

7: Isotopes as labels

12: Body condition index

3: Gut & feces content

8: Fatty Acids

13: Body fluid biochemistry

4: Gut DNA

9: Compound-SIA

14: Trait-based approach

5: Parasites as biological tags

10: Contaminants

15: Ecological stoichiometry

16: Resource quality

Figure 1

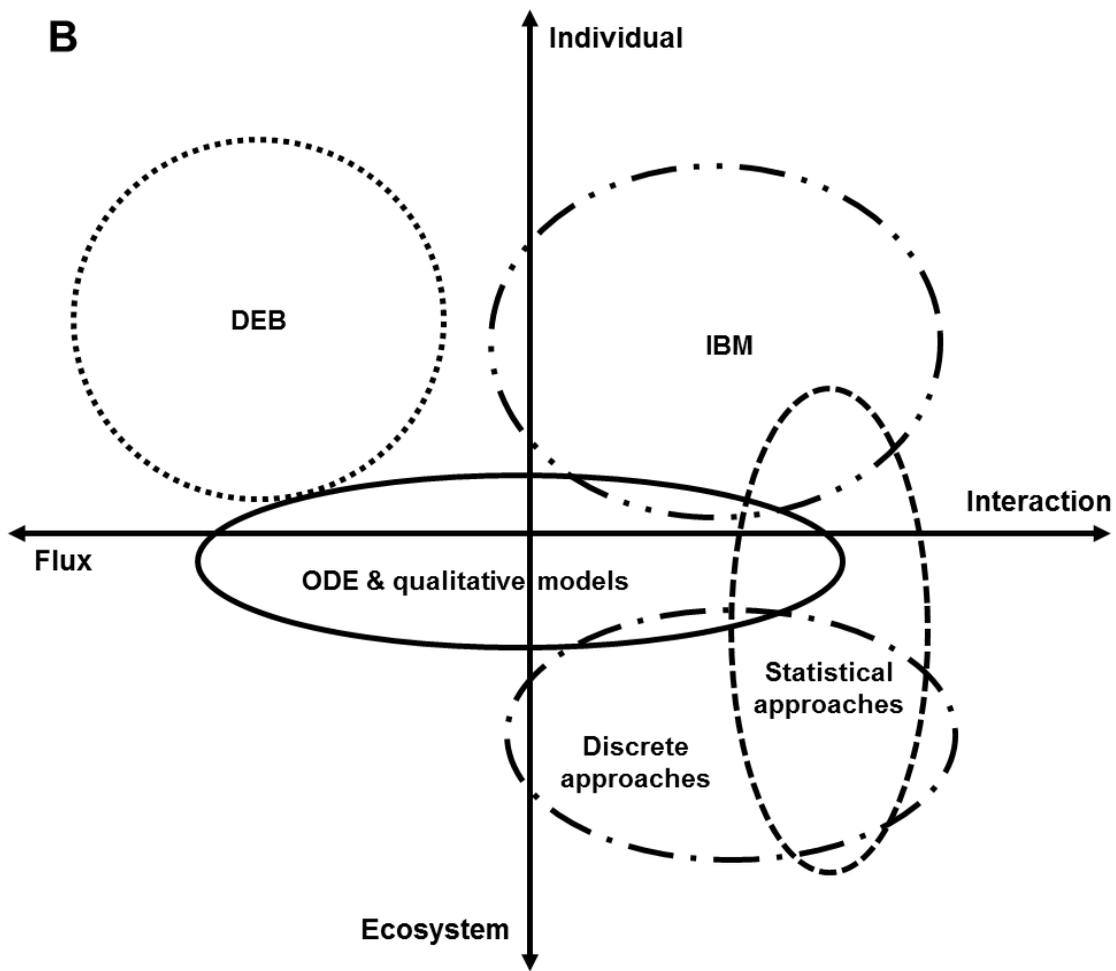


Table 1 - Empirical and experimental methods for trophic ecology

Detecting prey-predator relationships, or food sources	Price	Investment	Micro	Small	Large	Individual	Population	Community	Ecosystem	Interaction	Flux	Data
	Observation of feeding activity	0	1	0	1	1	1	1	0	0	1	0
Incubation experiments	0	1	1	1	0	1	1	1	0	1	1	1
Gut & feces content	0	1	1	1	1	1	1	0	0	1	0	1
Gut DNA	1	1	0	1	1	1	1	1	0	1	0	0
Parasites as biological tags	0	1	0	0	1	1	1	1	0	1	0	0
Bulk Stable Isotope Analysis	0	0	0	1	1	1	1	1	1	0	1	1
Detecting prey-predator relationships, or food sources	Price	Investment	Micro	Small	Large	Individual	Population	Community	Ecosystem	Interaction	Flux	Data
	Isotopes as labels	1	1	0	1	1	1	1	1	0	1	1
Fatty Acids	1	1	1	1	1	1	1	1	1	0	1	0
Compound-Specific Isotopic Analysis	1	1	0	1	1	1	1	1	0	0	1	1
Contaminants	1	1	1	1	1	1	1	1	0	1	1	0

Table 1 - Empirical and experimental methods for trophic ecology

Quantifying the consequences of feeding from individuals to ecosystems	Price	Investment	Micro	Small	Large	Individual	Population	Community	Ecosystem	Interaction	Flux	Data
Body composition	1	1	1	1	1	1	1	0	0	0	1	1
Body condition indices	0	0	0	1	1	1	1	0	0	0	1	1
Body fluid biochemistry	1	1	0	1	1	1	1	0	0	0	1	1
Traits	0	0	1	1	1	0	1	1	0	1	0	0
Ecological Stoichiometry	0	0	1	1	1	1	1	1	1	0	1	1
Resource quality	1	0	1	1	1	1	1	0	0	0	1	1

Table 1 - Empirical and experimental methods for trophic ecology

Advantages	Drawbacks
Straightforward and well-established / Relatively cheap / Various interactions and scales (incl. intraspecific variability) / <i>In situ</i> or under controlled conditions / Large scale records of feeding-behaviors are possible with miniaturization of loggers	Temporal & spatial scales are design-dependent/ Difficult to measure assimilation
Effect-size of specific variables / Suitable for filter-feeders	Mostly laboratory-based, so deviation from natural conditions might occur
Well-established / Relatively cheap / Information on nature and size of ingested food items	Snapshot of diet (does not reveal interaction strength) / Time consuming / Labile tissues or prey might be overlooked
Identification of gut microbiomes / Works on partly digested, poorly recognizable, food items	Expensive / Susceptible to typical drawbacks associated to molecular approaches
Host specificity / Integration of diet over long time periods / Potential information on diet provenance	Lethal / No information on prey size / Needs empirical knowledge of life-cycles (and potentially biogeography) of parasites / Bias due to side-effects of parasites on hosts' health and behavior
Well-established / Relatively cheap / Traces the carbon and nitrogen food sources in consumers / Important replication is possible / suited for <i>in situ</i> as well as laboratory studies	Turnover times and isotopic discrimination might vary among species, tissues and the environment studied / Not well-suited when a large number of potential resources are considered
Advantages	Drawbacks
Trace the fate (timing and scale) of carbon and nitrogen from microbes to macroscopic consumers / Differentiation between N and C uptake from unlabelled C and N pools	Difficult to provide quantitative fluxes / Needs to know turnover incorporation and routing in tissues (e.g. issue of uniformly labeling the food source) / Can be relatively expensive depending on the scale or nature of the labeling
Well-established / Traces flux and nutritional quality	Non-specific biomarkers / Needs <i>a priori</i> knowledge of producers' and consumers' metabolism / relatively expensive
Integrative tracers when coupled with a labeling / Target analysis promising in Microbial Ecology / Ideally it can trace limiting compounds and eventually detect minor food sources unseen by classical methods / Better knowledge in fractionation and turnover times for specific compounds	Needs a good understanding of the biochemical and physiological pathways in investigated organisms or tissues / Relatively expensive
Might trace spatio-temporal ingestion and assimilation depending on the persistence of compounds within tissues (e.g. lipophilic contaminants might biomagnify along food chains) / Potentially information on foraging area, and on contamination status of species and ecosystems	Needs a source of contamination / Biases due to side-effects on health and behavior / Needs knowledge of contaminants' biogeochemical cycle, distribution and persistence in organisms and in the environment / Relatively expensive

Advantages	Drawbacks
Measuring energy storage is one of the most direct and quantitative indicator of body condition	Dissection might be time-consuming and tedious / Alternative techniques are less invasive but more expensive and require further development
Cheap / Estimation of energy storage / Applicable <i>in situ</i> and in the lab from various data sources / Can be non-lethal (allometry) and applied on endangered wildlife	Indirect measure, non-specific marker of trophic interactions / Large temporal variations (e.g. depending on annual and circadian cycle)
Integrative assessment of physiological state (health, diet deficiencies)	Physiological state can be affected by other factors than nutritional stress / Difficult interpretation that needs integrated assessment (combination of markers) / Expensive / Less suitable on small animals
Cheap / Morphological repositories widespread / Adapted for paleo-trophic ecology / Useful to infer the dimension of trophic niches	Difficult to assess strength in species interactions / Little understanding of how traits are inter-correlated / Little consensus and practical guidance in methodology
Cheap / Permits to scale up processes from molecules to ecosystems, from physiology to ecosystem functioning / Predictive	Cannot be used as a tracer of biomass / Sometimes too general and missing important information (e.g. nature of C compounds)
Essential compounds are key drivers of diet selection along the life of an organism / Existence of a "nutritional geometry" framework	Young field of research / Needs integrative, and thus potentially expensive, measures

Table 1 - Modelling methods for trophic ecology

Connecting species within networks from ecological data (inference methods)	Advantages
Gaussian graphical models	Popular framework to infer interactions among continuous variables / Obtained precision matrix is a direct proxy of network structure
Bayesian networks & dynamic Bayesian networks	Adapted to class-occurrence data / Suitable to represent directed interactions (trophic, parasitic...) / Can be used to infer ecosystem static states or dynamics / Numerous heuristics are available to reach efficient approximate inference
Logic-based approaches	Adapted to qualitative data / Can incorporate background (expert) knowledge on the interactions / Describes directed interactions / Requires relatively less data than others
Linear inverse inference	Particularly suited to infer the magnitude of missing interactions based on simple assumptions
Approximate Bayesian computation	Replaces the step of likelihood computation by simulations of the model with variable parameter values
Testing the implications of trophic interactions (trophic models)	Advantages
Ordinary Differential Equations and qualitative models	Understanding of indirect interactions and species dynamics in food webs / Qualitative models useful when the quantification of each trophic interaction is unreachable / Useful to investigate potential consequences of perturbations on food web functioning and stability
Statistical approaches	Can be built from simple field observations of individual occurrences / Useful to evaluate management strategies dedicated to increase food web resilience (operational models)
Discrete approaches	Adapted to discrete and qualitative interactions / Well adapted to large interaction networks, whatever the nature of components and processes / No need of calibration, except the expert knowledge defining the model / Relevant to deduce all possible trajectories and stabilities the system may experience.
Individual-based models	Help understanding how patterns emerge from inter-individual interactions / Able to scale up from trait-based interactions to structure of ecological networks
Dynamic energy and mass budget approaches	Model the quantitative facets of metabolism by depicting rules of allocations and processes at the organism level / Application to diet reconstructions

Table 1 - Modelling methods for trophic ecology

Drawbacks
The network is undirected (unlike trophic/parasitic relations) / High computational complexity (sparse matrix inversion) / Unsuitable for classes-occurrence observations / Assume a gaussian distribution of interactions
Not adapted to continuous observations / Exact inference is out of reach given the combinatorial nature of the underlying optimization problem.
The learnt network describes "deterministic" interactions / Accuracy of learning is hard to validate because the learning process is rather "black box"
Relies on a known network topology and on the static assumption of mass balance between all network compartments at equilibrium.
Requires substantial computing time
Drawbacks
ODE models for large food webs often require a disproportionate number of parameters, and all parameter combinations are impossible to test through sensitivity analysis / Predictions of the effects of perturbations with qualitative models become ambiguous for large networks (< 15 nodes)
Not process-based, thus no mechanistic understanding / Dependant on collected data (over- and under-fitting)
Hardly adapted to continuous quantitative abundances, biomasses or fluxes in the network
Often require very intensive numerical simulations (calibration and validation stages) / Not adapted to heavy individual or multiscale networks / Hardly provide rigorous and demonstrated analyses
Huge personal investment required / Decreasing interest when used for complex applications at community or ecosystem levels