

Review

The role of vital dietary biomolecules in eco-evo-devo dynamics

Libor Závorka ^{1,*} Andreu Blanco,² Fernando Chaguaceda,³ Julien Cucherousset,⁴ Shaun S. Killen,⁵ Camilla Liénart,⁶ Margaux Mathieu-Resuge,^{1,7,8} Pavel Němec,⁹ Matthias Pilecky,^{1,10} Kristin Scharnweber,¹¹ Cornelia W. Twining,¹² and Martin J. Kainz^{1,10}

The physiological dependence of animals on dietary intake of vitamins, amino acids, and fatty acids is ubiquitous. Sharp differences in the availability of these vital dietary biomolecules among different resources mean that consumers must adopt a range of strategies to meet their physiological needs. We review the emerging work on omega-3 long-chain polyunsaturated fatty acids, focusing predominantly on predator–prey interactions, to illustrate that trade-off between capacities to consume resources rich in vital biomolecules and internal synthesis capacity drives differences in phenotype and fitness of consumers. This can then feedback to impact ecosystem functioning. We outline how focus on vital dietary biomolecules in eco-evo-devo dynamics can improve our understanding of anthropogenic changes across multiple levels of biological organization.

Ecological currency and commodity

Environmental changes induced by anthropogenic activities affect the flux and distribution of nutrients, including **vital dietary biomolecules** (see [Glossary](#)) such as thiamine [1] or **omega-3 long-chain polyunsaturated fatty acid (n-3 LC-PUFA)** [2], across ecosystems around the globe. The importance of these vital dietary biomolecules for consumer development has been thoroughly studied in veterinary and medical sciences, providing evidence of their role for animal health, reproduction, and neural tissue functioning (e.g., [3–5]). However, ecologists have rarely considered the substantial spatial [6,7] and temporal [8,9] variations in the availability of vital dietary biomolecules across the food webs. In addition, even closely related species and populations of consumers can differ in their physiological dependence on specific dietary biomolecules [10] and their capacity to **synthesize them internally** when they are not available in the diet [11–13]. Therefore, while energy is typically considered the common currency underlying numerous ecological and physiological phenomena, vital dietary biomolecules likely play the role of critically limiting commodities that are produced and transferred among consumers within and across food webs. Dietary biomolecules can be a key determinant of individual fitness and affect the functioning of ecosystems. Therefore, a greater focus on the role of vital dietary biomolecules in feedbacks between phenotypes of consumers and their environment, that is, **eco-evo-devo dynamics**, can improve our understanding of the effects of anthropogenic environmental changes across multiple levels of biological organization. There is, however, a notable lack of integrative work exploring the importance of vital dietary biomolecules in nature, causing researchers to overlook potentially critical links between the evolution and development of consumers and ecosystem functioning.

The role of vital dietary biomolecules in the evolution and development of consumer phenotype is largely determined by the trade-off between the capacity of a consumer to acquire food sources rich in a given dietary biomolecule and its capacity to synthesize that same molecule internally or

Highlights

Availability of vital dietary biomolecules, such as vitamins, amino acids, and fatty acids, is critical for the evolution and development of animals.

Extensive evidence indicates that anthropogenic changes influence the distribution of vital dietary biomolecules in food webs.

Shifts in the availability of these vital biomolecules can trigger far-reaching changes in phenotypes of consumers with potential cascading impacts on the functioning of the ecosystems.

There is no unified integrative framework to study the role of vital dietary biomolecules in feedbacks between phenotypes of wild consumers and ecosystem functioning.

We review evidence on omega-3 long-chain polyunsaturated fatty acids (n-3 LC-PUFA) in prey–predator interactions to illustrate how vital dietary biomolecules moderate the feedbacks between behavioral, physiological, and life-history traits of wild consumers and the higher levels of biological organization.

¹WasserCluster Lunz – Biologische Station, Inter-university Centre for Aquatic Ecosystem Research, A-3293 Lunz am See, Austria

²Centro de Investigación Mariña, Universidade de Vigo, EcoCost, Campus de Vigo, As Lagoas, Marcosende, 36310, Vigo, Spain

³Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Box 7050, 750 07 Uppsala, Sweden

⁴Laboratoire Evolution et Diversité Biologique (UMR 5174 EDB), CNRS, Université Paul Sabatier - Toulouse III, 31062 Toulouse, France



via endosymbiosis from more accessible dietary precursors [4,14]. While many examples in this review concern predator–prey interactions, this trade-off is intrinsic to most consumers including parasites [14] and detritivores [15]. The fact that many consumers do not simultaneously invest in both dietary acquisition and synthesis of vital biomolecules is likely driven by high energetic cost of synthesis [16,17]. Moreover, adaptation toward one end of this trade-off may relax selection pressure and lead to a loss of traits associated with the other [18,19]. Consumers can limit this trade-off by reducing their physiological dependence on a given dietary biomolecule. For example, by reducing growth of nutrient-demanding tissues, such as n-3 LC-PUFA-rich brain [3], or by adopting behavioral and physiological strategies that increase the retention of scarce dietary biomolecules [20]. However, reducing physiological dependence on vital dietary biomolecules in the short term can reduce the biological fitness of the consumer and limit its potential to adapt to environmental change [21]. Importantly, these changes in consumer phenotype can then feedback to the functioning of ecosystems. Traits of consumers related to dietary acquisition and internal synthesis of the vital biomolecules (e.g., food source selectivity or organismal stoichiometry) likely have direct impacts on ecosystem functioning and thus can be considered **functional effect traits**, which determine the per-capita ecological impacts of consumers [21,22] (Figure 1). Traits of consumers that drive the physiological need for specific dietary biomolecules (e.g., brain or gonad size) have direct impact on fitness of consumers and thus can be considered **functional response traits** that affect population growth and feedback to the community and ecosystem levels as density-dependent ecological effects [22,23] (Figure 1).

We summarize emerging evidence of the ecological, evolutionary, and developmental importance of vital dietary biomolecules using n-3 LC-PUFA as a specific example. While we focus on n-3 LC-PUFA, the general concepts that we cover can guide research of eco-evo-devo dynamics on numerous other vital biomolecules such as vitamins [24], sterols [25], and amino acids [26], which are not as well studied from ecological and evolutionary perspectives as n-3 LC-PUFAs.

At the biochemical level, n-3 LC-PUFAs are critical for functioning of cell **membrane lipids** which have direct impacts on the efficiency of signal transfer in tissues [27] (Box 1). This key biochemical function is why n-3 LC-PUFAs are important for a broad range of physiological [28], cognitive [27], and life history [29] traits. There are ecologically meaningful differences in the availability of n-3 LC-PUFA at the base of food webs at different spatial and temporal scales [7,9]. Globally, the main source of dietary n-3 LC-PUFA is produced by aquatic primary producers [7,30], and in some environments, also by bacteria [31] and protists [32]. Omega-3 LC-PUFAs from aquatic primary producers are transferred to higher trophic levels [33], and a large part of this aquatic production is transferred to terrestrial ecosystems [34,35]. The availability of n-3 LC-PUFAs is generally higher in marine than in freshwater ecosystems [30,36]. It has been shown that the availability of n-3 LC-PUFAs within marine ecosystems is closely linked to the algal community assemblage [7,37]. There are numerous marine gradients in n-3 LC-PUFA availability with latitude, from poor oligotrophic open ocean to rich coastal upwelling systems, from rocky to sandy coasts, or from brackish estuary to salt marine waters [7,37,38]. In freshwater ecosystems, there is higher n-3 LC-PUFA availability in lentic than in lotic ecosystems [39]. At finer spatial scales, n-3 LC-PUFA availability is greater in pelagic than in littoral areas of lentic ecosystems [40,41] and increases with stream order in lotic ecosystems as freshwater primary producers become the dominant source of energy [6]. In terrestrial ecosystems, the availability of dietary n-3 LC-PUFA for consumers generally decreases with the distance from aquatic ecosystems [10]. Together, the heterogeneous spatiotemporal distribution of dietary n-3 LC-PUFA, a consumer's physiological dependence on n-3 LC-PUFA, and a consumer's position along the synthesis and acquisition trade-off create a strong selection gradient that can drive developmental and evolutionary changes in traits that have a direct impact on ecosystem functioning (Figure 1).

⁵School of Biodiversity, One Health & Veterinary Medicine, Graham Kerr Building, College of Medical, Veterinary & Life Sciences, University of Glasgow, Glasgow G12 8QQ, UK

⁶Tvärrinne Zoological Station, University of Helsinki, J.A. Palménin tie 260, Hanko, 10900, Finland

⁷Université de Brest, CNRS, IRD, Ifremer, LEMAR, 29280 Plouzané, Brittany, France

⁸UMR DECOD (Ecosystem Dynamics and Sustainability), Ifremer, INRAE, Institut Agro, Plouzané, France

⁹Department of Zoology, Faculty of Science, Charles University, CZ-12844 Prague, Czech Republic

¹⁰Danube University Krems, Dr. Karl Dorrek Straße 30, A-3500 Krems, Austria

¹¹University of Potsdam, Plant Ecology and Nature Conservation, Am Mühlenberg 3, 14476 Potsdam, Germany

¹²Department of Fish Ecology and Evolution, Eawag – Swiss Federal Institute of Aquatic Science and Technology, Seestrasse 79, CH-6047 Kastanienbaum, Switzerland

*Correspondence: libor.zavorka@wcl.ac.at (L. Závorka).

Ecological keystone genes for synthesis of n-3 LC-PUFA

Ecological keystone genes are those with disproportionately large effects on community and ecosystem functions, and most of the known examples of ecological keystone genes are species specific [42], for example, genes for rapid leaf litter decomposition in a flowering evergreen tree *Metrosideros polymorpha* [43]. The increasing knowledge of genetic mechanisms leading to the synthesis of n-3 LC-PUFAs and other vital biomolecules across taxa [24,44–46] provides a unique opportunity to study the impact of ecological keystone genes in whole communities of consumers. The capacity of consumers to synthesize n-3 LC-PUFAs [e.g., docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA)] from the short-chain alpha-linolenic acid (ALA) is determined by the function of multiple independent synthetic pathways regulated by genes for two sets of enzymes, fatty acyl desaturases (Fads) and elongase (Elovl) [45,46]. In vertebrates, evidence suggests that duplication and neofunctionalization of the genes coding different types of these enzymes have repeatedly led to evolution of fully functional synthetic pathways [46]. The genetic architecture of fatty acid synthesis in invertebrates is more diverse than in vertebrates, but still poorly understood [44,45].

Much of the empirical evidence on the evolutionary dynamics of n-3 LC-PUFA synthesis in natural systems is currently based on comparison of populations and closely related species of fishes such as three-spined sticklebacks (*Gasterosteus aculeatus*) [11–13] or American sole fishes (Achloridae) [47]. These studies have shown that colonization of habitats with lower availability of dietary n-3 LC-PUFA is associated with increasing number of copies of Fads genes, facilitating higher synthesis of n-3 LC-PUFAs [11–13,47]. Evolutionary changes in genes regulating n-3 LC-PUFA synthesis could affect communities and ecosystems by shifting functional effect and response traits of consumers [36,48] (Figure 1), therefore Fads and Elovl genes are strong candidates for ecological keystone genes [42].

Omega-3 LC-PUFA-deficient food sources increase basal metabolic rate of consumers

Foraging on prey deficient in n-3 LC-PUFA is likely to increase metabolic rates of consumers, due to an increased need for internal synthesis of these vital biomolecules and reduced energy production efficiency of mitochondria deprived of n-3 LC-PUFA. Synthesis of n-3 LC-PUFA from dietary precursors has metabolic costs associated with elongation and desaturation of ALA and the maintenance of the enzymatic apparatus [36,41]. In addition, a low n-3 LC-PUFA content in membrane lipids in vertebrates has been shown to reduce energy production efficiency of mitochondria, and therefore, consumers require more O₂ to produce ATP [49,50]. Low n-3 LC-PUFA content in mitochondrial membranes can also lead to elevated production of reactive oxygen species, resulting in high oxidative stress and shorter consumer life spans [51]. These cellular-level processes can then influence the metabolic rate of the whole organism as n-3 LC-PUFA-deficient diets have been shown to increase the **basal metabolic rate (BMR)** of some consumers [28,52]. However, we know of no studies testing the link between cost of n-3 LC-PUFA synthesis and BMR on the evolutionary scale across species. McNab [53] showed that across 533 bird species, mass-specific BMR decreases from species feeding on nectar and nuts, to omnivores, to insectivores to species feeding on vertebrates. While the McNab [53] study was not designed to test the effect of the n-3 LC-PUFA synthesis on BMR, its results are in line with the assumption that BMR might be higher in species adapted to n-3 LC-PUFA-deficient diets. The BMR of consumers is often positively related to key functional effect traits such as food intake rate [54] and excretion rate [55]. High BMR also reduces the amount of energy that can be invested in somatic and gonadal growth, especially under food limited conditions [56]. Reduced growth rate and elevated excretion rate could also influence organismal stoichiometry of consumers by increasing C:N and C:P ratios [57]. Altogether, through its effect

Glossary

Basal metabolic rate (BMR): energy throughput of a resting endothermic animal within its thermoneutral zone, in the absence of any spontaneous activity, digestive or growth costs, and physiological or psychological stress. For ectotherms, the term standard metabolic rate is equivalent, but it is specific for a given temperature.

Eco-evo-devo dynamics: integration of ecological, evolutionary, and developmental processes that highlights the importance of ecological pressures that shape phenotypes of organisms, and the influence that these phenotypic changes have on community structure and ecosystem functioning.

Ecological keystone genes: genes that have large and disproportionate effects (relative to all genes or alleles in the environment) on community structure and ecosystem processes by altering the functional response and effect traits of organisms.

Functional effect traits: the characteristics of an individual that affect ecosystem functioning. Traits such as consumption rate, excretion rate, or organismal stoichiometry define the per-capita ecological impacts of an organism.

Functional response traits: the characteristics of an individual that result from its response to environmental conditions. Traits such as somatic growth, gonadal development, or cognitive capacity define fitness of an individual and have direct consequence for reproduction, mortality, and growth rate of the population. They can influence ecosystem functioning via density-dependent effects.

Information processing capacity of brain: the rate at which a brain can process sensory cues and transform them into a memory or behavioral response.

Internal synthesis: enzymatic synthesis of vital biomolecules from precursors that are more readily available in the diet of the consumer.

Membrane lipids: lipids forming the lamellar lipid phases of cell membranes containing a hydrophilic polar head group, a central group (glycerol or sphingosine), and hydrophobic long hydrocarbon chains.

Omega-3 long-chain polyunsaturated fatty acid

(n-3 LC-PUFA): Fatty acids with 20 or more carbons in their acyl chain, with

on BMR of consumers, n-3 LC-PUFA synthesis has the potential to alter trophic interactions and fluxes of element nutrients in the ecosystem.

Foraging morphology and behavior affect intake of n-3 LC-PUFA

As food sources rich in n-3 LC-PUFA are heterogeneously distributed within and across food webs [7,30,58], their acquisition requires specific morphological and behavioral foraging adaptations. For example, among insectivorous birds, aerial predators such as tree swallows (*Tachycineta bicolor*) regularly prey on n-3 LC-PUFA-rich aquatic insects around riparian areas [59], but species from other avian feeding guilds (e.g., leaf gleaners) do not use this dietary source of n-3 LC-PUFA even when aquatic insects are readily available [10]. Many aquatic consumers have developed specific behavioral adaptations to facultatively forage for fish eggs during the spawning period of species producing large egg numbers, for example, red drum (*Sciaenops ocellatus*) [8] and brown trout (*Salmo trutta*) [60]. This behavioral adaptation provides substantial boost of dietary n-3 LC-PUFA to consumers that otherwise have limited access to n-3 LC-PUFA-rich food sources [8].

Studies of sympatric radiations of arctic charr (*Salvelinus alpinus*) and whitefish (*Coregonus* spp.) colonizing fishless post-glacial lakes demonstrate that pelagic morphological and behavioral phenotypes of these species colonize these lakes first [61] or rapidly evolve from littoral phenotypes [62,63]. This suggests that these fishes may be under strong pressure to quickly colonize the pelagic food web with access to n-3 LC-PUFA-rich prey to satisfy their physiological demands. By contrast, phenotypes utilizing habitats with lower n-3 LC-PUFA availability (e.g., dwarf littoral or profundal phenotypes) usually evolve later [61,64]. This evolutionary pattern could be driven by the combination of competition for prey [65], predation pressure [66], and limited capacity of these fish species to synthesize n-3 LC-PUFAs. By contrast, high capacity to synthesize n-3 LC-PUFA internally might be an important driver of preference for littoral habitat in species, such as brown trout [67] or European perch (*Perca fluviatilis*) [65] that expand to the pelagic part of the lake only under strong competition and predation pressure in the littoral habitat [66].

We suggest that the link between the behavioral and morphologic foraging traits and n-3 LC-PUFA content in food sources is central for eco-devo-devo dynamics, because behavioral and morphologic traits have high developmental plasticity [66,68]. This plasticity can rapidly translate into reduced gene flow between phenotypes and evolutionary diversification of genotypes [12,69]. This diversification of consumers along the n-3 LC-PUFA synthesis–acquisition trade-off can impose new predation pressure on freshly colonized parts of the food web and influence community structure and ecosystem functioning [70,71]. Furthermore, it has been shown that shifts in community structure and prey phenotype can feed back to affect foraging morphology and behavior of predators [72,73].

Dietary n-3 LC-PUFA and rapid changes in brain functioning

Omega-3 LC-PUFAs, particularly DHA, are indispensable for optimal functioning of neural tissues in all vertebrates and in some invertebrates [27] (Box 1). Deprivation of n-3 LC-PUFA has negative effects on brain growth and neuron proliferation in laboratory studies on freshwater fishes [74], marine fishes [75], amphibians [76], passerine birds [77], and rodents [78]. The number of neurons and their connections in the whole brain is the best available determinant of the brain **information processing capacity** [79], yet the effect of DHA on neuron numbers in the whole brain has not been studied. Therefore, brain size remains a useful proxy of cognition in ecological studies.

Despite the large number of laboratory studies, there is only recent evidence suggesting that dietary n-3 LC-PUFAs plays a key role in the brain growth of wild consumers feeding on natural

multiple double bonds between carbon atoms, the first of which is located between the third and fourth carbons from the terminal methyl end.

Vital dietary biomolecules: molecules of biological origin such as structural fatty and amino acids, vitamins, and sterols that play key roles in tissue formation and physiological performance. Dietary biomolecules are acquired from diet, and consumers differ widely in their physiological dependence on them and their capacity to synthesize them internally from precursor molecules.

prey [80], hinting at the large potential influence of variation in the n-3 LC-PUFA content of food sources on cognition of consumers. Brain size is positively associated with the capacity of prey to evade predators [81] and the capacity of predators to capture a broad variety of prey [82]. Therefore, developmental and evolutionary changes in the brains of consumers induced by dietary n-3 LC-PUFA might influence trophic interactions among organisms, shifting the selection pressures in the entire food web [81,82]. However, it is worth noting that relatively large brains with high neuron numbers have evolved among taxa with n-3 LC-PUFA poor plant-based diets (e.g., parrots) as well as among taxa with n-3 LC-PUFA-rich marine fish diet (e.g., tooth whales) [79]. Studies aiming to link food web structure and the evolution of the brain need to consider changes in availability of dietary n-3 LC-PUFA together with the capacity of consumers to

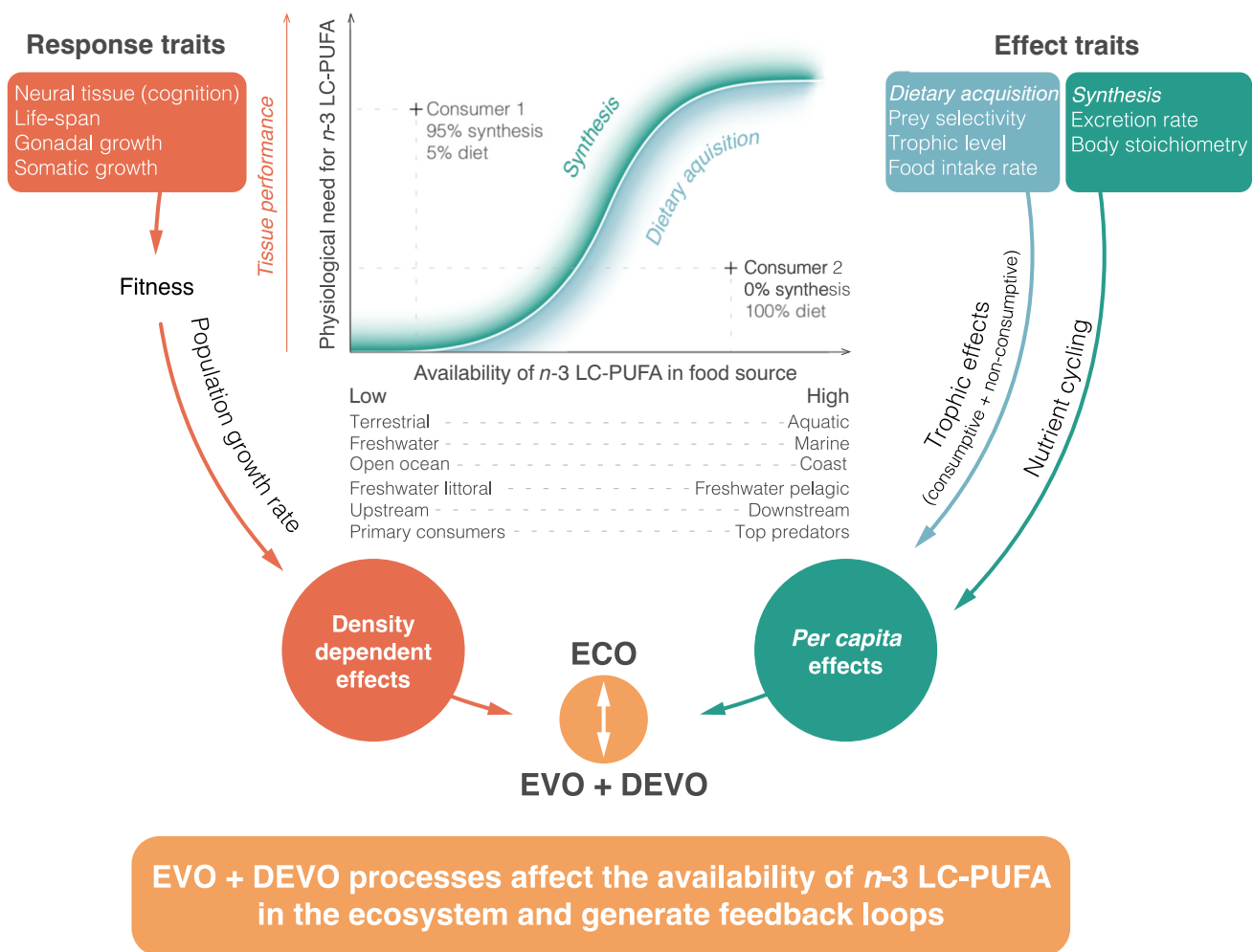


Figure 1. A conceptual overview of how food source availability and a consumer's physiological need for vital dietary biomolecules, specifically for omega-3 long-chain polyunsaturated fatty acid (n-3 LC-PUFA), affect the trade-off between their dietary acquisition and synthesis. Changes in a consumer's functional effect and response traits related to this trade-off feedback to the ecosystem functions (e.g., trophic transfer efficiency, primary production, nutrient turnover rates) that affect the availability of vital dietary biomolecules. We provide a non-exhaustive list of examples of gradients in availability of n-3 LC-PUFA across different environments and spatial scales. Two examples of hypothetical consumers are provided. Consumer 1 is an animal with high physiological need for n-3 LC-PUFA that lives in an environment with relatively low n-3 LC-PUFA availability (e.g., a herbivorous mammal with a large brain). To maintain high performance of their tissues, high fitness, and population growth, these consumers must evolve a relatively high capacity to synthesize n-3 LC-PUFA. By contrast, consumer 2 has low physiological need for n-3 LC-PUFA and lives in an environment with relatively high n-3 LC-PUFA availability (e.g., marine gastropods). Such consumers acquire sufficient amount of n-3 LC-PUFA from their diet and have no need to invest energy in the synthesis of these molecules.

Box 1. Cellular function of n-3 LC-PUFA

The most physiologically important n-3 LC-PUFAs for many consumers are DHA (22:6n-3) and EPA (20:5n-3) and their short-chain precursor ALA (18:3n-3) [27,36]. LC-PUFAs increase the fluidity of cellular membranes due to their high rotation potential given by high number of unsaturated double bonds and chain length [113]. The high rotation potential of DHA has a critical role in signal transfer efficiency in neural tissues of virtually all vertebrates, and a large number of aquatic invertebrates such as copepods, malacostraca, and cephalopods [27,36]. However, many freshwater invertebrates do not have DHA in their membrane lipids and its function is provided by EPA [6]. Furthermore, terrestrial invertebrates contain negligible amount of DHA and EPA and their neural tissue membrane lipid function is realized by ALA [114].

The importance of these fatty acids in the cellular structure of consumers means that these lipids are not primarily oxidized for energy production, but are retained and incorporated into membranes or used for synthesis of n-3 LC-PUFA species required by the consumer (e.g., synthesis of DHA from ALA and EPA by vertebrates) [46]. When consumers acquire more dietary n-3 LC-PUFA than needed to maintain optimal functioning of cellular membranes, they can store them for later use as triacylglycerols (TAGs) [115], retro-convert them to shorter chain (e.g., conversion of DHA and EPA to ALA by terrestrial insects [114] or DHA to EPA in *Daphnia* [116]); or oxidize them to produce energy [117]. Because excess dietary n-3 LC-PUFAs are stored or used as an energy source, an increase of n-3 LC-PUFA in diet above the physiological optimum is unlikely to improve functioning of consumer's cellular membranes and their fitness (Figure 1) [38]. Excessive anthropogenic supply of n-3 LC-PUFAs (e.g., from genetically modified crops; see Figure 2 in main text) to consumers that utilize ALA as dominant membrane lipid (i.e., terrestrial insects) can cause developmental deformities [114], but the negative health effects of excessive n-3 LC-PUFA consumption (i.e., oversaturation) are not known in natural ecosystems. By contrast, dietary intake of n-3 LC-PUFA below the physiological optimum can have severe negative effects on the performance of consumers' tissues and ultimately their fitness (Figure 1) [27,36].

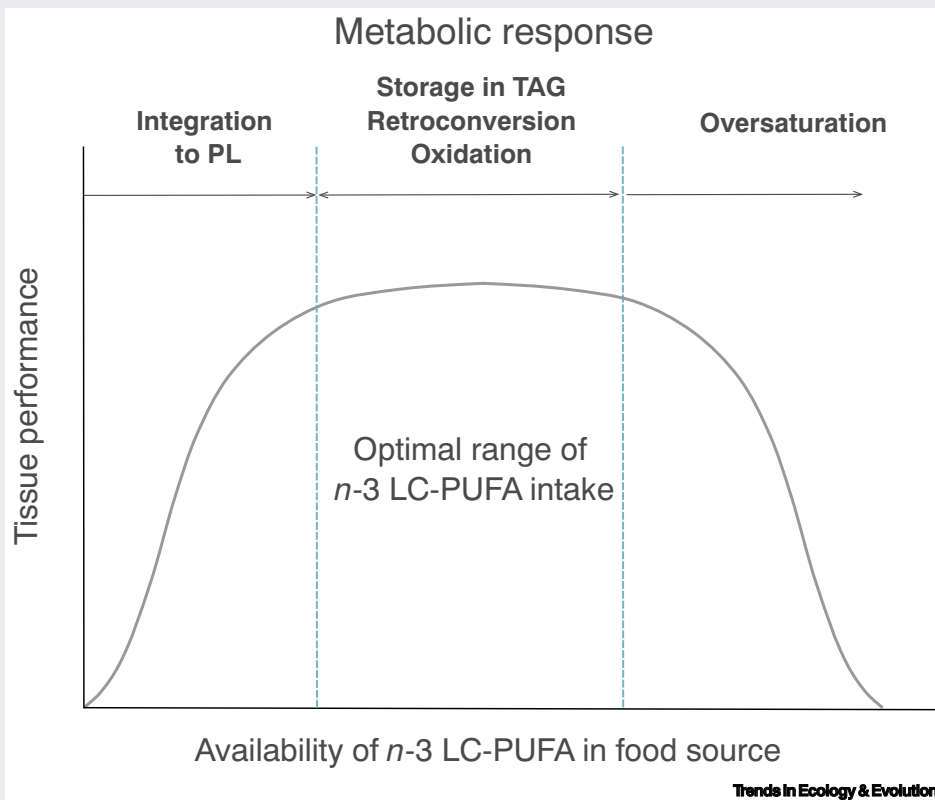


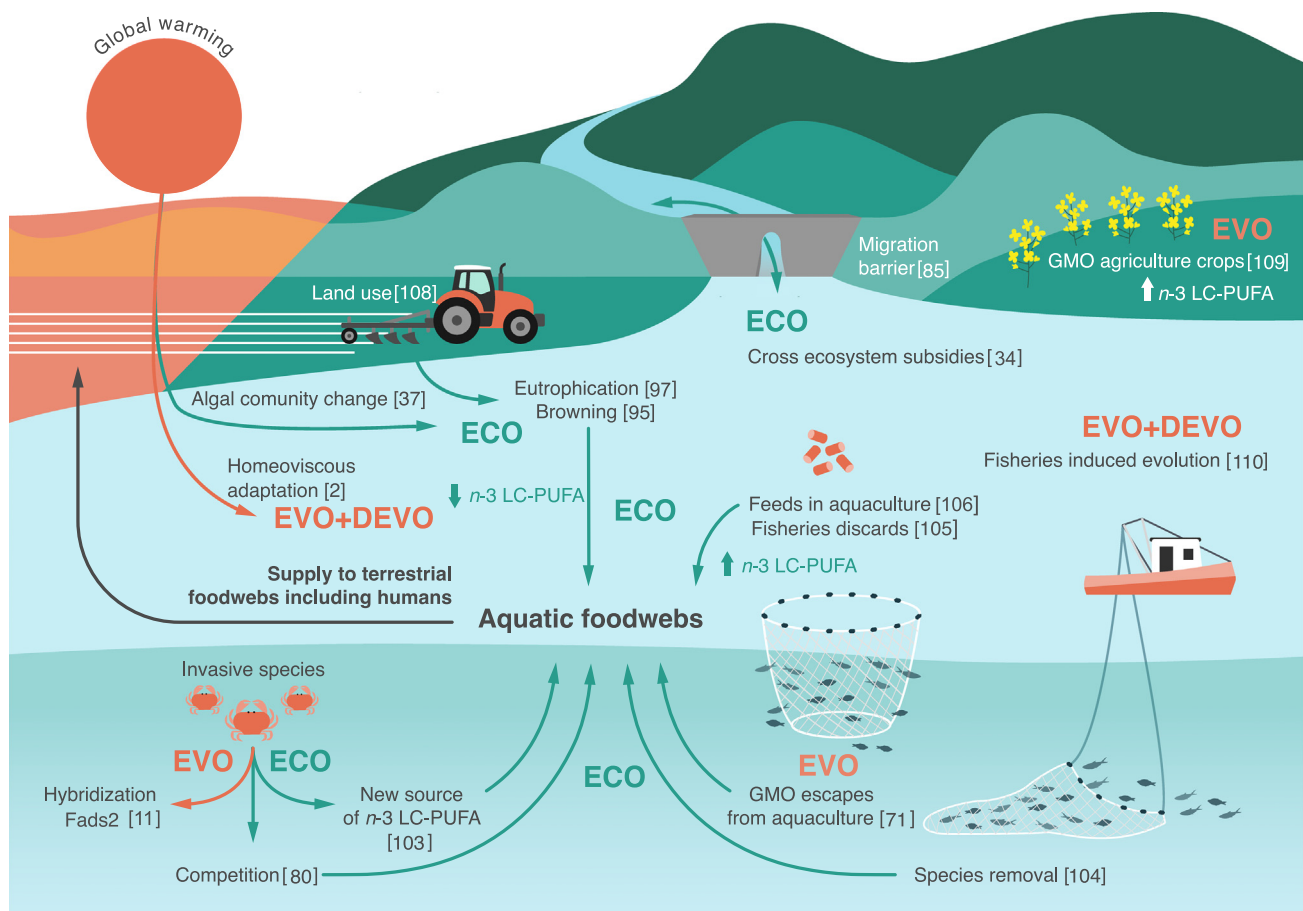
Figure 1. Hypothesized association between dietary intake of n-3 LC-PUFA and tissue performance, which is critical for fitness of consumers.

synthesize them. The availability of n-3 LC-PUFA in food webs can limit the potential for developmental and evolutionary changes of brain information-processing capacity. This is because a scarcity of dietary n-3 LC-PUFA in species with low capacity for their synthesis likely prevents a

rapid increase in brain size and neuron numbers under a selection pressure [83] and can thus limit the construction of novel or altered behavioral patterns in response to new ecological challenges.

Life history of consumers drives the flux of n-3 LC-PUFA

Consumers that migrate from n-3 LC-PUFA-rich to n-3 LC-PUFA-poor food webs are critical for transporting these molecules across ecosystems [34,35]. Examples of such transfers include subsidies of marine-derived nutrients rich in N, P, and n-3 LC-PUFA to coastal streams and lakes by anadromous fishes [84,85], or the movement of emergent aquatic insects [35,59] and amphibians [34] from freshwater to terrestrial ecosystems. Changes in magnitude and phenology of these cross-ecosystem fluxes may induce selection pressure on consumers in n-3 LC-PUFA-poor food webs that depend on this supply [9,86]. For example, it has been shown that the earlier emergence of aquatic insects that are rich in n-3 LC-PUFA, caused by climate change, is associated with a shift in timing of reproduction of insectivorous birds depending on these subsidies [9]. However, bird reproduction is not keeping pace with the peak of aquatic insect emergence, which may be contributing to lower fitness and population declines in these insectivorous birds [9,52,59]. Delivery of marine-derived nutrients rich in n-3 LC-PUFA by anadromous fishes to nursery



Trends in Ecology & Evolution

Figure 2. Overview of the anthropogenic factors impacting the fluxes of omega-3 long-chain polyunsaturated fatty acid (n-3 LC-PUFA) in food webs (indicated as ECO effects) and factors impacting the position of consumers along the n-3 LC-PUFA acquisition-synthesis trade-off (indicated as EVO and DEVO effects). Numbers in brackets represent to the corresponding case studies (see also [2,11,34,37,71,80,85,95,97,103-106,108-110]). Abbreviations: Fads, fatty acyl desaturases 2; GMO, genetically modified organism; n-3 LC-PUFA, omega-3 long-chain polyunsaturated fatty acid.

streams is crucial for stream food webs [85]. Therefore, while the n-3 LC-PUFA eco-evo-devo dynamics has never been explicitly studied in this context, n-3 LC-PUFA may play a critical role in the coastal freshwater food web dynamics. For instance, marine-derived nutrients delivered by eggs and carcasses of spawning Atlantic salmon (*Salmo salar*) increase the biomass of aquatic insect in the nursery streams [87,88], which in turn leads to increased biomass of the salmon juveniles and weakens the selection pressure on their metabolic rates [88], aging rate [89], and genetic diversity [87]. Finally, increased fluxes of marine-derived nutrients also reduce the age and length of the seaward migration of juvenile salmon [87], which can ultimately reduce the number of spawners returning to the nursery stream [90] and decrease the supply of marine-derived nutrients to the following salmon generations. This could subsequently close the negative feedback loop between the flux of n-3 LC-PUFA and phenotypic changes of salmon.

Dietary n-3 LC-PUFAs have a positive effect on growth of gonads [91] and body size [52,92] of wild consumers, life history traits positively related to fecundity. Maternal provisioning of n-3 LC-PUFA is critical for growth, brain development, behavior, and survival of the offspring [93]. Therefore, offspring provisioning might lead to higher selection pressure on females to synthesize n-3 LC-PUFA internally and thus buffer fluctuations in its availability in food webs. For example, in three-spined sticklebacks, *Fads2* copy number duplication occurs on the X chromosome and, thus within populations, females have generally higher number of *Fads2* gene copies (i.e., higher capacity to synthesize n-3 LC-PUFA) than males [12]. In mammals, internal synthesis of n-3 LC-PUFA increases in females during pregnancy and lactation [94]. Overall, evidence suggests that the position of consumers along the n-3 LC-PUFA synthesis–acquisition trade-off and availability of n-3 LC-PUFA in food sources likely have a direct influence on the number of surviving offspring and population growth rate (Figure 1).

Anthropogenic impacts on the n-3 LC-PUFA eco-evo-devo dynamics

Anthropogenic pressures could disrupt n-3 LC-PUFA fluxes through food webs [95–98] and induce evolutionary and developmental changes in consumer phenotype [99,100] (Figure 2). Eutrophication, browning, and climate warming can reduce algal primary production of n-3 LC-PUFA, for example, by homeoviscous adaptation [2] and community assemblage shifts (e.g., toward cyanobacteria) [37] and thus limit n-3 LC-PUFA fluxes to consumers at higher trophic levels [95–97]. In some cases, food webs may buffer the reduced primary production of n-3 LC-PUFA through increased synthesis of n-3 LC-PUFA of consumers at lower trophic levels [101]. However, there is also evidence that n-3 LC-PUFA deficiency induced by eutrophication and climate warming can spill across multiple trophic levels [6,97], and could induce developmental and evolutionary changes even in top consumers, such as fishes [102] or humans [98]. Invasion of new species may also alter the flux of n-3 LC-PUFA through the food web. For example, when an invasive species becomes a novel source of n-3 LC-PUFA for native consumers [103] or limits the access of native consumers to n-3 LC-PUFA-rich food sources via competition [80]. Reduced population density or extinction of harvested species in fisheries can limit the flux of n-3 LC-PUFA through food webs [104]. By contrast, discards from industrial fisheries [105] and outfall of feeds from cage aquaculture [106] can become a significant anthropogenic supply of n-3 LC-PUFA to consumers in n-3 LC-PUFA-poor food webs. Disruption of migration routes (e.g., by dams and roads) and habitat degradation (e.g., pond and wetland drainage) can cause profound reduction of n-3 LC-PUFA subsidies from freshwater to terrestrial [107,108] and from marine to freshwater [85].

Genetic modifications in aquaculture fishes aimed at increasing somatic growth and the capacity to synthesize and retain n-3 LC-PUFA [100] can magnify the ecological impacts of individuals escaping from aquaculture into natural ecosystems due to their altered physiology and behavior

[71]. Crops genetically modified to produce n-3 LC-PUFA can negatively influence consumers in terrestrial food webs as many terrestrial invertebrates are not adapted to consume n-3 LC-PUFA-rich diets [109]. Harvest-induced evolution, especially in the context of industrial fisheries, alters the physiological traits of consumers [110], and therefore it is foreseeable that this may also alter their capacity to synthesize n-3 LC-PUFA internally and acquire n-3 LC-PUFA from diet, but this remains to be tested. Similarly, genetic introgression of native consumers with non-native lineages and species introduced by humans may affect the capacity of native consumers to synthesize or acquire n-3 LC-PUFA from diet [11,111].

Box 2. Tracing pathways of vital dietary biomolecules

Stable isotope analysis (SIA) is the main analytical method for tracing sources of dietary energy and vital biomolecules, usually using $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^2\text{H}$ [118]. The central assumption of SIA is that the isotopes in bulk tissues of consumers reflect the isotopes in their diet (i.e., food and water) plus the metabolic activity of the consumer, which results in an increase of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^2\text{H}$ values, that is, fractionation (Figure 1). Origin of individual biomolecules can be further traced by compound-specific SIA (CSIA) [119,120]. This is an important method as the main food sources of energy and vital biomolecules may not be the same [119]. Essential compounds, that is, vital biomolecules that cannot be synthesized *de novo* by the consumer, closely reflect the isotopic value of their diet. By contrast, non-essential compounds, that is, biomolecules that can be synthesized by consumer, show high isotopic fractionation (Figure 1).

CSIA has been used to determine, for example, the critical minimal threshold content of n-3 LC-PUFA in diet that triggers internal synthesis by consumers [101], or to estimate the turnover time of these vital biomolecules in tissues [121]. CSIA in combination with genome sequencing and expression analysis of genes key to the internal synthesis (e.g., [13]) can provide a robust insight into physiological capacity to synthesize different vital biomolecules in wild free ranging consumers at intra- and inter-specific level. CSIA can also provide fine-scale information on spatial distribution of consumer's foraging habitats [122] and increase the precision of estimates of a consumer's position within the food web [123].

SIA can also be combined with artificial isotopic labeling of vital dietary biomolecules using dietary substrates of known isotopic composition [123]. Labeling enhances the differences in isotopes of biomolecules compared with the natural dietary sources and thus can help to determine finer variability in synthetic capacity of consumers and distinguish among vital biomolecules from dietary sources that do not differ isotopically at the natural abundance level. While isotopic labeling has been primarily used in laboratory studies, it can be also used in open system to trace pathway of vital dietary biomolecules in food webs [124] and within consumers [125].

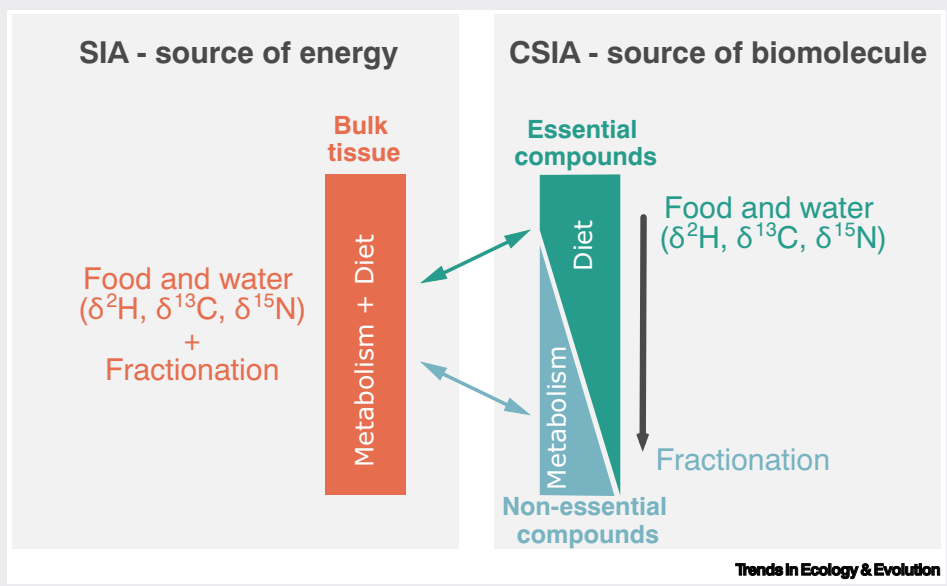


Figure 1. Comparison of information provided by bulk tissue SIA and compound specific CSIA.

Concluding remarks

Emerging research on the ecological, developmental, and evolutionary roles of n-3 LC-PUFA indicates that vital dietary biomolecules likely play critical roles within numerous eco-evo-devo feedbacks. However, to date, most evidence is indirect, and often assumes that documented changes in fluxes of n-3 LC-PUFA-rich subsidies within and across food webs, together with changes in the capacity of consumers to acquire and synthesize n-3 LC-PUFA, are the dominant drivers of such eco-evo-devo dynamics. Moreover, we lack knowledge about the specific ecological and evolutionary role of vital dietary biomolecules in general because most eco-evo-devo dynamic research has focused on fluxes of inorganic nutrients such as carbon, nitrogen, and phosphorus (e.g., [43,57]). We therefore suggest explicitly integrating n-3 LC-PUFA and other vital dietary biomolecules (e.g., vitamins [24], sterols [25], and amino acids [26]) into ecologically relevant experiments [112], eco-evo-devo models [23], and ecosystem management [108] using a range of novel methodological tools (Box 2). This will help improve the conservation of biodiversity and the mitigation of anthropogenic impacts. To meet this goal, we must substantially improve our understanding of the importance of vital dietary biomolecules for ecosystem functioning (e.g., trophic transfer efficiency, primary production, nutrient turnover rates) and for performance of wild consumers (see Outstanding questions).

Acknowledgments

This review is a result of workshop at the online 11.5th International Conference on the Applications of Stable Isotope Techniques to Ecological Studies 2021. We thank Len Wassenaar and all other organizers of the conference for providing us the platform for discussion. We thank the Science Crunchers for help in developing the visuals. Authors were supported by the following research grants: L.Z., Austrian Science Fund (FWF; Project M 2742-BBL); A.B., Agencia Galega de Innovación (grant number ED481B 2018/68); S.S.K., NERC Standard Grant (number NE/T008334/1); C.L., Walter and Andrée de Nottbeck post-doctoral grant; P.N., Czech Science Foundation (grant number 20-28135S); M.M.-R., Agence Nationale de la Recherche and Conseil Régional de Bretagne (grant number ANR-17-EURE-0015); K.S., Deutsche Forschungsgemeinschaft (grant number DFG-GRK 2118/2); C.W.T., European Research Council (grant number H2020-MSCA-IF-2020).

Declaration of interests

No interests are declared.

References

- Ejsmond, M.J. *et al.* (2019) Modeling vitamin B1 transfer to consumers in the aquatic food web. *Sci. Rep.* 9, 10045
- Hixson, S.M. and Arts, M.T. (2016) Climate warming is predicted to reduce omega-3, long-chain, polyunsaturated fatty acid production in phytoplankton. *Glob. Change Biol.* 22, 2744–2755
- Innis, S.M. (2007) Dietary (n-3) fatty acids and brain development. *J. Nutr.* 137, 855–859
- Kraft, C.E. and Angert, E.R. (2017) Competition for vitamin B 1 (thiamin) structures numerous ecological interactions. *Q. Rev. Biol.* 92, 151–168
- Stabler, S.P. (2013) Vitamin B12 deficiency. *N. Engl. J. Med.* 368, 149–160
- Guo, F. *et al.* (2021) Longitudinal variation in the nutritional quality of basal food sources and its effect on invertebrates and fish in subalpine rivers. *J. Anim. Ecol.* 90, 2678–2691
- Colombo, S.M. *et al.* (2017) A fundamental dichotomy in long-chain polyunsaturated fatty acid abundance between and within marine and terrestrial ecosystems. *Environ. Rev.* 25, 163–174
- Fuiman, L.A. (2018) Egg boon fatty acids reveal effects of a climatic event on a marine food web. *Ecol. Monogr.* 88, 585–599
- Shiple, J.R. *et al.* (2022) Climate change shifts the timing of nutritional flux from aquatic insects. *Curr. Biol.* 32, 1342–1349
- Twining, C.W. *et al.* (2021) Use of fatty acids from aquatic prey varies with foraging strategy. *Front. Ecol. Evol.* 9, 735350
- Hudson, C.M. *et al.* (2021) Fit and fatty freshwater fish: contrasting polyunsaturated fatty acid phenotypes between hybridizing stickleback lineages. *Oikos* 2022, 1–14
- Ishikawa, A. *et al.* (2021) Copy number variation of a fatty acid desaturase gene *Fads2* associated with ecological divergence in freshwater stickleback populations. *Biol. Lett.* 17, 20210204
- Ishikawa, A. *et al.* (1979) (2019) A key metabolic gene for recurrent freshwater colonization and radiation in fishes. *Science* 364, 886–889
- Husnik, F. (2018) Host–symbiont–pathogen interactions in blood-feeding parasites: nutrition, immune cross-talk and gene exchange. *Parasitology* 145, 1294–1303
- Crenier, C. *et al.* (2017) Minor food sources can play a major role in secondary production in detritus-based ecosystems. *Freshw. Biol.* 62, 1155–1167
- Cohen, A.A. *et al.* (2017) Co-existence of multiple trade-off currencies shapes evolutionary outcomes. *PLoS One* 12, e0189124
- Maklakov, A.A. and Chapman, T. (2019) Evolution of ageing as a tangle of trade-offs: energy versus function. *Proc. R. Soc. B* 286, 20191604
- Lahti, D.C. *et al.* (2009) Relaxed selection in the wild. *Trends Ecol. Evol.* 24, 487–496
- Ellers, J. *et al.* (2012) Ecological interactions drive evolutionary loss of traits. *Ecol. Lett.* 15, 1071–1082
- Olsen, L. *et al.* (2021) Lipid metabolism in adaptation to extreme nutritional challenges. *Dev. Cell* 56, 1417–1429

Outstanding questions

How does the evolution of trophic niche affect the capacity of consumers to synthesize vital dietary biomolecules?

What is the energetic cost of synthesis of vital biomolecules? Are there energetic tipping points that delimit when a synthesis strategy or a dietary acquisition strategy is more favorable?

Is there a negative relationship between genes associated with increased capacity of consumers to acquire vital biomolecules from diet and genes for their internal synthesis?

What factors determine the direction (reinforcing vs. balancing) of eco-evo-devo feedbacks dominated by vital dietary biomolecules?

How does the availability of inorganic nutrients affect the trade-off between synthesis and dietary acquisition of vital dietary biomolecules?

How does the availability of n-3 LC-PUFA, in particular DHA, correlate with the rate of brain evolution within and across species?

21. Raffard, A. *et al.* (2019) The community and ecosystem consequences of intraspecific diversity: a meta-analysis. *Biol. Rev.* 94, 648–661
22. Di az, S. and Cabido, M. (2001) Vive la différence: plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.* 16, 646–655
23. Hendry, A.P. (2019) A critique for eco-evolutionary dynamics. *Funct. Ecol.* 33, 84–94
24. Drouin, G. *et al.* (2011) The genetics of vitamin C loss in vertebrates. *Curr. Genom.* 12, 371–378
25. Martin-Creuzburg, D. *et al.* (2009) Colimitation of a freshwater herbivore by sterols and polyunsaturated fatty acids. *Proc. R. Soc. B* 276, 1805–1814
26. Nepi, M. (2014) Beyond nectar sweetness: the hidden ecological role of non-protein amino acids in nectar. *J. Ecol.* 102, 108–115
27. Pilecky, M. *et al.* (2021) Omega-3 PUFA profoundly affect neural, physiological, and behavioural competences – implications for systemic changes in trophic interactions. *Biol. Rev.* 96, 2127–2145
28. McKenzie, D.J. (2001) Effects of dietary fatty acids on the respiratory and cardiovascular physiology of fish. *Comp. Biochem. Physiol. A* 128, 605–619
29. Hulbert, A.J. (2008) Explaining longevity of different animals: is membrane fatty acid composition the missing link? *AGE* 30, 89–97
30. Twining, C.W. *et al.* (2016) Highly unsaturated fatty acids in nature: what we know and what we need to learn. *Oikos* 125, 749–760
31. Nichols, D.S. (2003) Prokaryotes and the input of polyunsaturated fatty acids to the marine food web. *FEMS Microbiol. Lett.* 219, 1–7
32. Veloza, A.J. *et al.* (2006) Trophic modification of essential fatty acids by heterotrophic protists and its effects on the fatty acid composition of the copepod *Acartia tonsa*. *Mar. Biol.* 148, 779–788
33. Kainz, M. *et al.* (2004) Essential fatty acids in the planktonic food web and their ecological role for higher trophic levels. *Limnol. Oceanogr.* 49, 1784–1793
34. Fritz, K.A. *et al.* (2019) Subsidies of long-chain polyunsaturated fatty acids from aquatic to terrestrial environments via amphibian emergence. *Freshw. Biol.* 64, 832–842
35. Mathieu-Resuge, M. *et al.* (2021) Taxonomic composition and lake bathymetry influence fatty acid export via emergent insects. *Freshw. Biol.* 66, 2199–2209
36. Twining, C.W. *et al.* (2021) The evolutionary ecology of fatty-acid variation: implications for consumer adaptation and diversification. *Ecol. Lett.* 24, 1709–1731
37. Galloway, A.W.E. and Winder, M. (2015) Partitioning the relative importance of phylogeny and environmental conditions on phytoplankton fatty acids. *PLoS One* 10, e0130053
38. Winder, M. *et al.* (2017) The land-sea interface: a source of high-quality phytoplankton to support secondary production. *Limnol. Oceanogr.* 62, S258–S271
39. Heissenberger, M. *et al.* (2010) Effect of nutrition on fatty acid profiles of riverine, lacustrine, and aquaculture-raised salmonids of pre-alpine habitats. *Hydrobiologia* 650, 243–254
40. Kainz, M.J. *et al.* (2017) Polyunsaturated fatty acids in fishes increase with total lipids irrespective of feeding sources and trophic position. *Ecosphere* 8, 13
41. Scharnweber, K. *et al.* (2021) Fatty acid accumulation in feeding types of a natural freshwater fish population. *Oecologia* 196, 53–63
42. Skovmand, L.H. *et al.* (2018) Keystone genes. *Trends Ecol. Evol.* 33, 689–700
43. Treseder, K.K. and Vitousek, P.M. (2001) Potential ecosystem-level effects of genetic variation among populations of *Metrosideros polymorpha* from a soil fertility gradient in Hawaii. *Oecologia* 126, 266–275
44. Monroig, Ó. and Kabeya, N. (2018) Desaturases and elongases involved in polyunsaturated fatty acid biosynthesis in aquatic invertebrates: a comprehensive review. *Fish. Sci.* 84, 911–928
45. Kabeya, N. *et al.* (2018) Genes for *de novo* biosynthesis of omega-3 polyunsaturated fatty acids are widespread in animals. *Sci. Adv.* 4, eaar6849
46. Castro, L.F.C. *et al.* (2016) Long-chain polyunsaturated fatty acid biosynthesis in chordates: insights into the evolution of Fads and Elovl gene repertoire. *Prog. Lipid Res.* 62, 25–40
47. Matsushita, Y. *et al.* (2020) Flatfishes colonised freshwater environments by acquisition of various DHA biosynthetic pathways. *Commun. Biol.* 3, 516
48. Moosmann, M. *et al.* (2021) On the evolution of trophic position. *Ecol. Lett.* 24, 2549–2562
49. Závorka, L. *et al.* (2021) Climate change-induced deprivation of dietary essential fatty acids can reduce growth and mitochondrial efficiency of wild juvenile salmon. *Funct. Ecol.* 35, 1960–1971
50. Salin, K. *et al.* (2021) The relationship between membrane fatty acid content and mitochondrial efficiency differs within- and between- omega-3 dietary treatments. *Mar. Environ. Res.* 163, 105205
51. Hulbert, A.J. (2010) Metabolism and longevity: is there a role for membrane fatty acids? *Integr. Comp. Biol.* 50, 808–817
52. Twining, C.W. *et al.* (2016) Omega-3 long-chain polyunsaturated fatty acids support aerial insectivore performance more than food quantity. *Proc. Natl. Acad. Sci. U. S. A.* 113, 10920–10925
53. McNab, B.K. (2009) Ecological factors affect the level and scaling of avian BMR. *Comp. Biochem. Physiol. Part A* 152, 22–45
54. Selman, C. *et al.* (2001) Resting metabolic rate and morphology in mice (*Mus musculus*) selected for high and low food intake. *J. Exp. Biol.* 204, 777–784
55. Vanni, M.J. and McIntyre, P.B. (2016) Predicting nutrient excretion of aquatic animals with metabolic ecology and ecological stoichiometry: a global synthesis. *Ecology* 97, 3460–3471
56. Killen, S.S. *et al.* (2011) Fuel, fasting, fear: routine metabolic rate and food deprivation exert synergistic effects on risk-taking in individual juvenile European sea bass. *J. Anim. Ecol.* 80, 1024–1033
57. Leal, M.C. *et al.* (2017) The ecology and evolution of stoichiometric phenotypes. *Trends Ecol. Evol.* 32, 108–117
58. Hixson, S.M. *et al.* (2015) Production, distribution, and abundance of long-chain omega-3 polyunsaturated fatty acids: a fundamental dichotomy between freshwater and terrestrial ecosystems. *Environ. Rev.* 23, 414–424
59. Twining, C.W. *et al.* (2018) Aquatic insects rich in omega-3 fatty acids drive breeding success in a widespread bird. *Ecol. Lett.* 21, 1812–1820
60. Näslund, J. *et al.* (2015) Eggs from anadromous adults provide marine-derived nutrients to Atlantic salmon and brown trout parr in late autumn – observations from a Swedish coastal stream. *Environ. Biol. Fish* 98, 2305–2313
61. Præbel, K. *et al.* (2013) Ecological speciation in postglacial European whitefish: rapid adaptive radiations into the littoral, pelagic, and profundal lake habitats. *Ecol. Evol.* 3, 4970–4986
62. Bernatchez, L. *et al.* (2010) On the origin of species: insights from the ecological genomics of lake whitefish. *Philos. Trans. R. Soc. Lond. B* 365, 1783–1800
63. Jacobs, A. *et al.* (2020) Parallelism in eco-morphology and gene expression despite variable evolutionary and genomic backgrounds in a Holarctic fish. *PLoS Genet.* 16, e1008658
64. Østbye, K. *et al.* (2020) “And if you gaze long into an abyss, the abyss gazes also into thee”: four morphs of Arctic charr adapting to a depth gradient in Lake Tinnsjøen. *Evol. Appl.* 13, 1240–1261
65. Svanbäck, R. *et al.* (2008) Intraspecific competition drives multiple species resource polymorphism in fish communities. *Oikos* 117, 114–124
66. Skúlason, S. *et al.* (2019) A way forward with eco evo devo: an extended theory of resource polymorphism with postglacial fishes as model systems. *Biol. Rev.* 94, 1786–1808
67. Sánchez-Hernández, J. and Amundsen, P.-A. (2015) Trophic ecology of brown trout (*Salmo trutta* L.) in subarctic lakes. *Ecol. Freshw. Fish* 24, 148–161
68. Adams, C.E. *et al.* (2003) Epigenetic regulation of trophic morphology through feeding behaviour in Arctic charr, *Salvelinus alpinus*. *Biol. J. Linn. Soc.* 78, 43–49
69. Garduno-Paz, M.V. *et al.* (2020) A phenotypically plastic magic trait promoting reproductive isolation in sticklebacks? *Evol. Ecol.* 34, 123–131

70. Harmon, L.J. *et al.* (2009) Evolutionary diversification in stickleback affects ecosystem functioning. *Nature* 458, 1167–1170
71. Cucherousset, J. *et al.* (2021) Growth-enhanced salmon modify stream ecosystem functioning. *J. Fish Biol.* 99, 1978–1989
72. Brodersen, J. *et al.* (2018) Upward adaptive radiation cascades: predator diversification induced by prey diversification. *Trends Ecol. Evol.* 33, 59–70
73. Post, D.M. and Palkovacs, E.P. (2009) Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play. *Philos. Trans. R. Soc. Lond. B* 364, 1629–1640
74. Lund, I. *et al.* (2014) Dietary LC-PUFA deficiency early in ontogeny induces behavioural changes in pike perch (*Sander lucioperca*) larvae and fry. *Aquaculture* 432, 453–461
75. Ishizaki, Y. *et al.* (2001) The effect of dietary docosahexaenoic acid on schooling behaviour and brain development in larval yellowtail. *J. Fish Biol.* 58, 1691–1703
76. Igarashi, M. *et al.* (2015) Impact of maternal n-3 polyunsaturated fatty acid deficiency on dendritic arbor morphology and connectivity of developing *Xenopus laevis* central neurons *in vivo*. *J. Neurosci.* 35, 6079–6092
77. Hall, Z.J. *et al.* (2014) Site-specific regulation of adult neurogenesis by dietary fatty acid content, vitamin E and flight exercise in European starlings. *Eur. J. Neurosci.* 39, 875–882
78. Kawakita, E. *et al.* (2006) Docosahexaenoic acid promotes neurogenesis *in vitro* and *in vivo*. *Neuroscience* 139, 991–997
79. Kverková, K. *et al.* (2022) The evolution of brain neuron numbers in amniotes. *Proc. Natl. Acad. Sci. U. S. A.* 119, e2121624119
80. Linking omega-3 polyunsaturated fatty acids in natural diet with brain size of wild consumers. *Oecologia* 199, 797–807
81. Kondoh, M. (2010) Linking learning adaptation to trophic interactions: a brain size-based approach. *Funct. Ecol.* 24, 35–43
82. Edmunds, N.B. *et al.* (2016) A role for brain size and cognition in food webs. *Ecol. Lett.* 19, 948–955
83. Mitchell, D.J. *et al.* (2020) Experimental translocations to low predation lead to non-parallel increases in relative brain size. *Biol. Lett.* 16, 20190654
84. Darimont, C.T. *et al.* (2003) Foraging behaviour by gray wolves on salmon streams in coastal British Columbia. *Can. J. Zool.* 81, 349–353
85. Landsman, S.J. *et al.* (2018) Assimilation of marine-derived nutrients from anadromous Rainbow Smelt in an eastern North American riverine food web: evidence from stable-isotope and fatty acid analysis. *Freshw. Sci.* 37, 747–759
86. Twining, C.W. *et al.* (2022) Climate change creates nutritional phenological mismatches. *Trends Ecol. Evol.* 37, 736–739
87. McLennan, D. *et al.* (2019) Stimulating nutrient release from parental carcasses increases the growth, biomass and genetic diversity of juvenile Atlantic salmon. *J. Appl. Ecol.* 56, 1937–1947
88. Auer, S.K. *et al.* (2018) Nutrients from salmon parents alter selection pressures on their offspring. *Ecol. Lett.* 21, 287–295
89. McLennan, D. *et al.* (2021) Habitat restoration weakens negative environmental effects on telomere dynamics. *Mol. Ecol.* Published online May 11, 2021. <https://doi.org/10.1111/mec.15980>
90. Armstrong, J.D. *et al.* (2018) Effects of individual variation in length, condition and run-time on return rates of wild-reared Atlantic salmon *Salmo salar* smolts. *J. Fish Biol.* 92, 569–578
91. Scharnweber, K. and Gårdmark, A. (2020) Feeding specialists on fatty acid-rich prey have higher gonad weights: pay-off in Baltic perch? *Ecosphere* 11, e03234
92. Chaguaceda, F. *et al.* (2020) Regulation of fatty acid composition related to ontogenetic changes and niche differentiation of a common aquatic consumer. *Oecologia* 193, 325–336
93. Hou, Z. and Fuiman, L.A. (2020) Nutritional programming in fishes: insights from mammalian studies. *Rev. Fish Biol. Fish.* 30, 67–92
94. Brenna, J.T. (2011) Animal studies of the functional consequences of suboptimal polyunsaturated fatty acid status during pregnancy, lactation and early post-natal life. *Matern. Child Nutr.* 7, 59–79
95. Wu, P. *et al.* (2021) Elevated temperature and browning increase dietary methylmercury, but decrease essential fatty acids at the base of lake food webs. *Sci. Rep.* 11, 16859
96. Trommer, G. *et al.* (2019) Nitrogen enrichment leads to changing fatty acid composition of phytoplankton and negatively affects zooplankton in a natural lake community. *Sci. Rep.* 9, 16805
97. Keve, O. *et al.* (2021) Increasing temperature and productivity change biomass, trophic pyramids and community-level omega-3 fatty acid content in subarctic lake food webs. *Glob. Change Biol.* 27, 282–296
98. Heilpern, S.A. *et al.* (2021) Declining diversity of wild-caught species puts dietary nutrient supplies at risk. *Sci. Adv.* 7, eabf9967
99. Watson, H. *et al.* (2017) Transcriptome analysis of a wild bird reveals physiological responses to the urban environment. *Sci. Rep.* 7, 44180
100. Osmond, A.T.Y. and Colombo, S.M. (2019) The future of genetic engineering to provide essential dietary nutrients and improve growth performance in aquaculture: advantages and challenges. *J. World Aquacult. Soc.* 50, 490–509
101. Pilecky, M. *et al.* (2022) Hydrogen isotopes ($\delta^2\text{H}$) of polyunsaturated fatty acids track bioconversion by zooplankton. *Funct. Ecol.* 36, 538–549
102. Jacobs, A. *et al.* (2019) Rapid niche expansion by selection on functional genomic variation after ecosystem recovery. *Nat. Ecol. Evol.* 3, 77–86
103. Kolanowski, W. *et al.* (2007) Fatty acid composition of selected fresh water gammarids (Amphipoda, Crustacea): a potentially innovative source of omega-3 LC PUFA. *J. Am. Oil Chem. Soc.* 84, 827–833
104. Závorka, L. *et al.* (2019) Aquatic predators influence flux of essential micronutrients. *Trends Ecol. Evol.* 34, 880–881
105. Heath, M.R. *et al.* (2014) Cascading ecological effects of eliminating fishery discards. *Nat. Commun.* 5, 3893
106. Johnson, L.E. *et al.* (2018) Asymmetric assimilation of an anthropogenic resource subsidy in a freshwater food web. *Food Web.* 15, e00084
107. Beebee, T.J.C. (2013) Effects of road mortality and mitigation measures on amphibian populations. *Conserv. Biol.* 27, 657–668
108. Fehlinger, L. *et al.* (2022) The ecological role of permanent ponds in Europe: a review of dietary linkages to terrestrial ecosystems via emerging insects. *Inland Waters* Published online August 1, 2022. <https://doi.org/10.1080/20442041.2022.2111180>
109. Colombo, S.M. *et al.* (2018) Potential for novel production of omega-3 long-chain fatty acids by genetically engineered oil-seed plants to alter terrestrial ecosystem dynamics. *Agric. Syst.* 164, 31–37
110. Hollins, J. *et al.* (2018) A physiological perspective on fisheries-induced evolution. *Evol. Appl.* 11, 561–576
111. Huxel, G.R. (1999) Rapid displacement of native species by invasive species: effects of hybridization. *Biol. Conserv.* 89, 143–152
112. Galloway, A.W.E. and Budge, S.M. (2020) The critical importance of experimentation in biomarker-based trophic ecology. *Philos. Trans. R. Soc. Lond. B* 375, 20190638
113. Hazel, J.R. and Williams, E.E. (1990) The role of alterations in membrane lipid composition in enabling physiological adaptation of organisms to their physical environment. *Prog. Lipid Res.* 29, 167–227
114. Hixson, S.M. *et al.* (2016) Long-chain omega-3 polyunsaturated fatty acids have developmental effects on the crop pest, the cabbage white butterfly *Pieris rapae*. *PLoS One* 11, e0152264
115. Mathieu-Resuge, M. *et al.* (2020) Specific regulations of gill membrane fatty acids in response to environmental variability reveal fitness differences between two suspension-feeding bivalves (*Nodipecten subnodosus* and *Spondylus crassisquama*). *Conserv. Physiol.* 8, coaa079
116. Martin-Creuzburg, D. *et al.* (2010) Interactions between limiting nutrients: consequences for somatic and population growth of *Daphnia magna*. *Limnol. Oceanogr.* 55, 2597–2607
117. Stanley-Samuelson, W. *et al.* (1988) Fatty acids in insects: composition, metabolism, and biological significance. *Arch. Insect Biochem. Physiol.* 9, 1–33
118. Layman, C. *et al.* (2012) Applying stable isotopes to examine food-web structure: an overview of analytical tools. *Biol. Rev.* 87, 545–562
119. Pilecky, M. *et al.* (2021) Compound-specific stable hydrogen isotope ($\delta^2\text{H}$) analyses of fatty acids: a new method and

- perspectives for trophic and movement ecology. *Rapid Commun. Mass Spectrom.* 35, e9135
120. McMahon, K.W. and McCarthy, M.D. (2016) Embracing variability in amino acid $\delta^{15}\text{N}$ fractionation: mechanisms, implications, and applications for trophic ecology. *Ecosphere* 7, e01511
 121. Twining, C.W. *et al.* (2020) Stable isotopes of fatty acids: current and future perspectives for advancing trophic ecology. *Philos. Trans. R. Soc. Lond. B* 375, 20190641
 122. Pilecky, M. *et al.* (2022) Assessment of compound-specific fatty acid $\delta^{13}\text{C}$ and $\delta^2\text{H}$ values to track fish mobility in a small sub-alpine catchment. *Environ. Sci. Technol.* 56, 11051–11060
 123. Lacombe, R.J.S. *et al.* (2020) Turnover of brain DHA in mice is accurately determined by tracer-free natural abundance carbon isotope ratio analysis. *J. Lipid Res.* 61, 116–126
 124. Lyon, D.R. and Ziegler, S.E. (2009) Carbon cycling within epilithic biofilm communities across a nutrient gradient of head-water streams. *Limnol. Oceanogr.* 54, 439–449
 125. Twining, C.W. *et al.* (2018) Conversion efficiency of α -linolenic acid to omega-3 highly unsaturated fatty acids in aerial insectivore chicks. *J. Exp. Biol.* 221, jeb165373