



Review

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The meaning of functional trait composition of food webs for ecosystem functioning

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There is a growing interest in using trait-based approaches to characterize the functional structure of animal communities. Quantitative methods have been derived mostly for plant ecology, but it is now common to characterize the functional composition of various systems such as soils, coral reefs, pelagic food webs or terrestrial vertebrate communities. With the ever-increasing availability of distribution and trait data, a quantitative method to represent the different roles of animals in a community promise to find generalities that will facilitate cross-system comparisons. There is, however, currently no theory relating the functional composition of food webs to their dynamics and properties. The intuitive interpretation that more functional diversity leads to higher resource exploitation and better ecosystem functioning was brought from plant ecology and does not apply readily to food webs. Here we appraise whether there are interpretable metrics to describe the functional composition of food webs that could foster a better understanding of their structure and functioning. We first distinguish the various roles that traits have on food web topology, resource extraction (bottom-up effects), trophic regulation (top-down effects), and the ability to keep energy and materials within the community. We then discuss positive effects of functional trait diversity on food webs, such as niche construction and bottom-up effects. We follow with a discussion on the negative effects of functional diversity, such as enhanced competition (both exploitation and apparent) and top-down control. Our review reveals that most of our current understanding of the impact of functional trait diversity on food web properties and functioning comes from an over-simplistic representation of network structure with well-defined levels. We, therefore, conclude with propositions for new research avenues for both theoreticians and empiricists.

1. Introduction

The investigation of functional traits has been proposed as a means to find generalities in the structure and dynamics of ecological communities, beyond the mere study of pairwise interactions [1]. It is prohibitive to study and document all potential pairwise interactions, as their number increases in proportion to the square of species richness. Instead, traits are common currencies, allowing comparisons across communities and regional pools [2,3]. Trait-based approaches are commonly used to explore and understand the diversity of forms and functions within an ecosystem, and they have been used to approximate some aspects of ecosystem functioning [4]. While they were originally developed for plants (e.g. [5,6]), there are now more and more studies investigating the functional composition of animal communities [7], including birds,

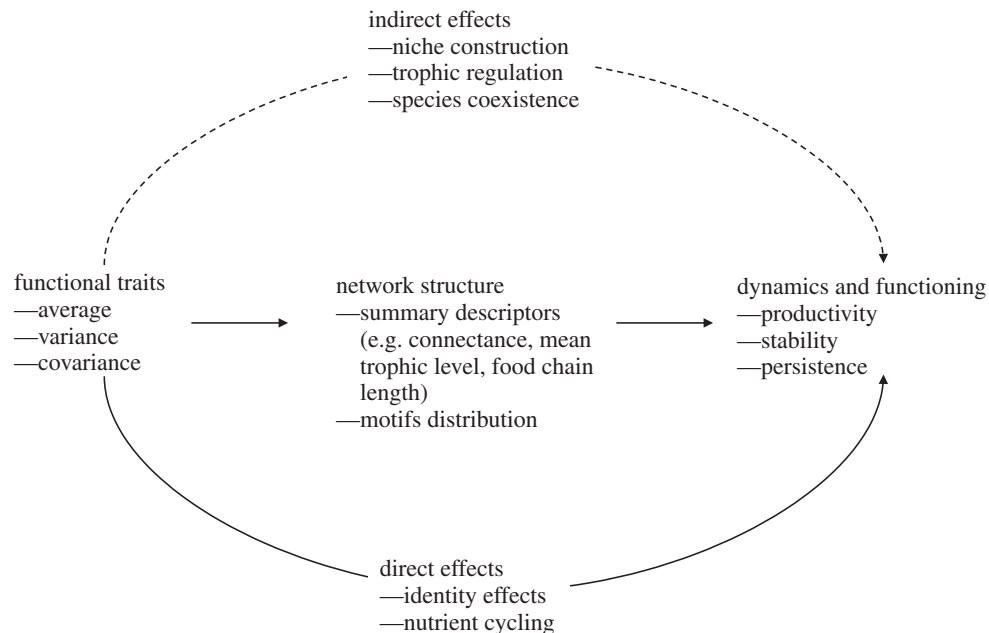


Figure 1. Conceptual relationship between functional composition, food web structure, and dynamics. The functional composition of the community has a direct effect on food webs via identity effects and an indirect effect via its impact on network structure.

mammals, arthropods, fishes, marine invertebrates, reptiles and amphibians (e.g. [8–12]). A quantitative approach to represent the different roles of animals in a community promises to find generalities and will definitely facilitate cross-system comparisons. It is not so clear, however, how the current trait-based approaches apply to food webs, and more generally to interaction networks.

The difficulty arising with animals is their involvement in complex interaction networks, making it hard to measure and understand the role of functional structure and diversity. The theory developed for plants is applicable for a single trophic group driven by competition [13], ignoring the complexity arising with animals involved in a more diverse array of interactions such as herbivory, predation, parasitism, seed dispersal and pollination. The study of plant community structure from functional traits is commonly based on the quantification of the average trait value of a community weighted by relative abundance (community-weighted mean, CWM). CWM is meant to represent the most dominant traits of the community [14], while its associated variance (CWV) represents how variable is the trait in the community [15]. The functional structure of a community is often described to understand the role of key traits and how they relate to environmental gradients [16], and to identify causal links on ecosystem properties and functions [17,18]. Functional trait diversity is also often used to assess complementarity and redundancy among species, which ultimately should give insights on the assembly mechanisms in play [19]. Both CWM and CWV, therefore, nicely relate to the mechanisms driving a positive relationship between the diversity and productivity of plant communities [20]. The sampling effect is based on the hypothesis that some dominant species, because of their traits (such as leaf traits [21]), drive ecosystem functioning [22] and that they are more likely to be found in a diverse community. The complementarity effect, on the other hand, proposes the increase of resource use efficiency with the diversity of ecological strategies (e.g. diversity of rooting depth). The CWM and the CWV, therefore, represent the sampling and the complementarity effects, respectively [23]. While the biodiversity and ecosystem

functioning (BEF) theory is clearly established for plants [24] and well supported by experiments [25], it was found not so easy to generalize for food webs because of the complex interactions that could either reverse expectations or simply blur any relationship [26]. Trophic regulation and the complexity of food web topologies including omnivory, intra-guild predation, cannibalism and loops prevent such generalization.

It is not straightforward to appreciate the role of food web functional trait structure and diversity for ecosystem functioning. Traits are involved both directly and indirectly in the processes of shaping ecological communities and driving their dynamics (figure 1). First, traits have a direct effect on ecosystem functioning through the traditional mechanisms of resource use complementarity and identity effects. The presence of top predators, for instance, has been recognized for a long time as being essential for ecosystem functioning [27]. Their extinctions due to human actions have often resulted in dramatic shifts of ecosystem properties. As an example, in the marine ecosystem, sharks play a key role through top-down control on lower trophic levels. The loss of this trophic regulation could have drastic consequences on ecosystem functioning such as declines in fish production, sudden increase of some populations, decrease in stability, and nutrient losses [28]. Secondly, traits have an indirect effect via their impact on the structure of the food web, and thereby on trophic cascades. Further, predators can change the composition of the lower trophic level and thereby influence nutrient cycling processes [29]. There are some hints as to how the topology of ecological networks might impact ecosystem functioning (for instance via the mechanism of trophic complementarity [30]), but we are yet to fully understand this relationship.

The objective of this paper is to provide a conceptual framework to guide the interpretation of functional trait structure and diversity in food webs. We first propose a terminology for the investigation of the functional structure and diversity of food webs. We briefly review the types of traits that are typically used in studies of animal communities. We then review how functional structure and diversity of animal communities

have been studied, and contrast these studies to the investigation of plant communities. Next, we describe how traits have been used to understand pairwise interactions between animals, and assess the implication of functional diversity on food web structure. Finally, we explore the implications of trait diversity for ecosystem functioning. Our framework highlights major gaps in knowledge, and we consequently end with a discussion of the most promising and exciting research avenues opened by the investigation of the functional structure and diversity of food webs.

2. Classifying traits in food webs

We focus on three categories of traits that are essential to food web structure and dynamics. These categories are not exclusive, as some traits—such as body size or movement ability—can be found in multiple categories. We provide definitions, and support this classification with the interpretation of a classical food web model in box 1 and examples of traits that are commonly studied in table 1.

‘Topological traits’ determine whether a given predator species can feed on the given prey species. Topological traits could be further divided into two subcategories [39,40]: ‘foraging traits’ determine the type of preys a predator will look for. For instance, the shape of mouthparts of several arthropods such as ground beetles will tell us much about their optimal prey type [41]. Such traits are often regrouped into broad categories such as herbivores, filter feeders or carnivores. By contrast, ‘vulnerability traits’ determine the type of predators for a given prey species. They include traits providing resistance to predation, such as particular morphological attributes (e.g. spines) or chemical defense. A trophic interaction is the result of a match between foraging and vulnerability traits (see the section below on trait-matching models). Topological traits could include physiological characteristics of a species, morphological, behavioural (e.g. hiding strategies) and microhabitat preferences (e.g. foraging location in canopy trees). They should be precise and measurable attributes of the species, rather than the common representation into feeding guilds (e.g. [42]). Topological traits also encompass any characteristic of species related to phenology and use of space. The occurrence of an interaction requires a match between the time of the activity, its location, and the occurrence of both predators and preys.

‘Consumption traits’ determine the rate at which trophic interactions harm the prey population and benefit the predator. They determine the functional and numerical responses of the prey and the predator, respectively (see extensive discussions of the related traits in [33,34]). These traits are less documented and more difficult to measure (table 1). There are several steps in the process of a trophic interaction and all of them correspond to specific traits (these are more formally interpreted mathematically in box 1). First, the attack rate (which is the result of foraging speed) is influenced by both predator and prey characteristics, such as movement, the capacity to hide, temporal match of activities, spatial distribution of the prey, etc. Further, prey density and the capacity of the predator to handle individuals also influence the rate of interactions. Handling time is impacted by prey characteristics, such as digestibility—for instance, mussels and gastropods are harder to digest than crustaceans because of their shell. The handling time is also impacted by the characteristics of the predator, for instance, the recovery time between

attacks, specialized morphological characteristics to process preys, or the time needed to digest them. Secondly, resource assimilation efficiency determines the fraction of the prey biomass that is ingested by the predator and converted into biomass. Again, both predator and prey characteristics will determine this quantity, as some preys have a larger proportion of edible biomass (e.g. relative weight of bones, lignified tissues in plants), and predators cannot process all of the prey (e.g. parasitoid larvae do not consume the entire biomass of their host). The resource assimilation efficiency is an important characteristic for indirect trophic interactions between scavengers and their resources. Finally, it is also a characteristic of the predator determining the fraction of the consumed prey biomass that is converted into its own biomass and into offspring. Several traits are related to it, such as fecundity and the stoichiometry of the predator [43].

‘Life history traits’ are characteristics of preys and predators affecting their demography, and consequently, equilibrium abundances. Life history traits are not involved directly in the trophic interaction, they do not influence the *per capita* rate at which the interaction happens. However, they affect population dynamics and could thus indirectly determine population size and the per population effect of one species on another. The R^* principle [44], for instance, states that the equilibrium abundance of a resource is determined by the ratio of mortality and attack rates of the consumer. Examples include the rate of ontogenic development, age at sexual maturity, duration of the larval stage, fecundity, or natural mortality rate (examples with references are provided in table 1).

In summary, topological traits determine the pairwise interactions in a food web, the consumption traits impact the *per capita* interaction strength, in both directions, and finally, the life history traits will be involved in the per population interaction strength. All these traits will combine to set trophic regulation [45], species composition and population size of both prey and predator at equilibrium (box 1), community stability in face of a disturbance [46–48], and the direct and indirect effects of perturbations [49]. Note that we have thus far kept aside traits that are involved in species-specific responses to environmental variation (e.g. optimal temperature, habitat requirements), as they are not directly involved in the trophic interactions and food web dynamics. They should nonetheless be kept in mind, as they influence the co-distribution of predators and preys over environmental gradients and consequently the occurrence of an interaction [50], they could condition interaction rates [51], as well as temporal dynamics. We also ignored trait-mediated interactions, which are well known to impact community dynamics and ecosystem functioning [52]. Some interactions impact the expression of species traits, and indirectly affect other interactions [51]. Trait-mediated interactions are susceptible to affect all three categories of traits we described here.

The trait-based conceptual framework for plant ecology is based on a different classification of traits. Lavorel & Garnier [13] distinguished ‘effect traits’, determining the effect species have on ecosystem dynamics and properties, from ‘response traits’, which determine the response of species to the environment. The framework has been successfully used to analyse how environmental gradients and disturbances shape the functional structure of plant communities (e.g. [16,53]), and how effect traits can be used to link biodiversity, ecosystem functioning and even ecosystem services [54,55]. It has also been

Box 1. Interpretation of functional traits in a food web model.

We illustrate how the different categories of traits influence food web dynamics directly and indirectly. A tri-trophic diamond food web model (figure B1) is commonly used to study coexistence [31] and stability [32]. The model represents with ordinary differential equations the dynamics of a producer compartment P , herbivores H_1 and H_2 , and a top carnivore C . For simplicity, the dynamics of the producer follows a logistic equation with intrinsic growth rate r and carrying capacity K . Consumers harm the resource population at a given rate, and only a fraction of the resource ingested is converted into consumer biomass. The dynamics could be described by the following set of differential equations:

$$\left. \begin{aligned} \frac{dP}{dt} &= rP \left(1 - \frac{P}{K}\right) - \sum f_i(P)H_iP, \\ \frac{dH_i}{dt} &= e_{iP}f_i(P)H_iP - g(H_i)H_iC - m_{H_i}H_i, \\ \text{and } \frac{dC}{dt} &= \sum e_{CH_i}g(H_i)H_iC - m_C C. \end{aligned} \right\} \quad (2.1)$$

The definition of the different fluxes illustrates how the classification of traits we propose in the main text impacts directly on the dynamics of this system. The herbivores consume the plant at rate $f_i(P)H_iP$ and only a fraction e_{iP} of that flux is converted into biomass. Similarly, the carnivore consumes the herbivores at rate $g(H_i)$. The functions $f_i(P)$ and $g_i(H_i)$ vary across systems, types of interactions and pairs of species (see Jeschke *et al.* [33] and Jeschke [34] for an extensive discussion on the topic). In a type II functional response, for instance, such as $a_{ij}/(1 + a_{ij}b_{ij}R_j)$, the maximal attack rate a_{ij} is a single parameter embedding foraging characteristics of the consumer (e.g. its mobility) and the vulnerability of the resource (e.g. defensive traits). Similarly, the handling time b_{ij} is a consumption trait that depends on the characteristics of both the consumer (its capacity to catch and process resources) and the resource (mainly its digestibility). For the same reasons, the assimilation efficiency depends on both consumer and resource traits. The natural mortality rate m_i is a life history trait that depends only on the characteristics of the consumer, not its prey. Resource selection impacts on network structure and will be found in the variation of the attack rates. For instance, a preference for one of the herbivores by the carnivore would be reflected by a higher a_{CH_i} or a better conversion efficiency e_{CH_i} .

Solving the system at equilibrium also illustrates how the different traits affect the abundance of the different species indirectly. The analytical solution to the equilibrium densities of the four species web is tedious to write down and not so useful for this example, but the tri-trophic chain $P-H_1-C$ is nonetheless instructive. At equilibrium we get:

$$\left. \begin{aligned} \hat{P} &= K \left(1 - \frac{f_i(\hat{P})\hat{H}_i}{r}\right), \\ \hat{H}_i &= \frac{m_C}{g(\hat{H}_i)e_{C_i}}, \\ \text{and } \hat{C} &= m_{H_i} - f_i(\hat{P})e_{H_iP}\hat{P}, \end{aligned} \right\} \quad (2.2)$$

which shows that the equilibrium abundances of the different species depends on all types of traits. The *per capita* effect of the carnivore on the herbivore is simply the functional response gH_i , and inversely the *per capita* effect of the herbivore on the carnivore is $-g\hat{H}_ie_{CH_i}$. Similarly, the per population effects are, respectively, $g\hat{H}_i\hat{C}$ and $-e_{CH_i}g(\hat{H}_i)\hat{H}_i$. This simple example shows that while *per capita* effects only depend on the set of traits of the species pair, per population effects also depend on the entire distribution of traits of the community because indirect interactions propagate through the food chain and affect all species. As an example, the traits of the plant will affect the per population effect of the carnivore on the herbivore because the more productive is the plant community (high r and K), the larger will be the carnivore population, and consequently, the total amount of herbivore consumed at equilibrium. Accordingly, we expect that the entire distribution of traits (mean, variance, covariance and higher moments) will impact net interactions between all pairs of species in a food web.

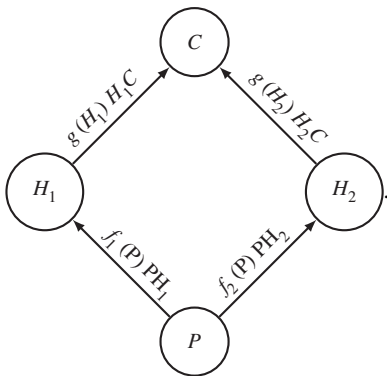


Figure B1. Schematic representation of the modelled food web (note that only the outgoing flux is represented for clarity, the assimilation efficiency is not included).

Table 1. Classification of common traits used in studies of animal functional diversity. References for terrestrial communities are [7,10,35] and references for marine communities include [8,36–38] and references therein.

type of trait	fishes	marine invertebrates	birds	mammals	amphibians	reptiles	invertebrates
topological	body length	maximum size	body mass	body mass	body length	body length	body mass
	body mass	maximum growth rate	body shape	body shape	body shape	body shape	body shape
	gut length	body design	plumage colour		skin colour	skin colour	aposematic colour
	median paired fin length	living habit	diet type	diet type	diet type	diet type	substrate mimicry
	pectoral fins surface to caudal fin surface	living location/environmental position	foraging behaviour	foraging behaviour	foraging behaviour	foraging behaviour	diet type
	pectoral fin shape	exposure potential	nesting behaviour	nesting behaviour	poisonous skin	nesting behaviour	foraging behaviour
	peduncle throttling	degree of attachment to substrate	feeding behaviour	nesting behaviour	nesting behaviour	feeding behaviour	sociality
	caudal fin shape	degree of flexibility	activity time	feeding habitat	feeding habitat	activity time	specific weapons
	body shape	strength of attachment to substrate	wing morphology	activity time	activity time	swimming traits	toxicity/resistance
	eye position	resource capture method	social behaviour	social behaviour	swimming traits		mouthparts size
consumption	skin coloration	movement method					mouthparts strength
	swimming traits	mobility					escape strategy
	body size	defence strategy					adhesion strength
	physical protection—spines, bony carapaces	water column migration					palatability
	chemical defense						cognitive ability
	fish body mass	body design	metabolic rate	metabolic rate	metabolic rate	metabolic rate	metabolic rate
	visual acuity: maximum eye diameter relative to head size	degree of flexibility	body mass	body mass	body mass	body mass	body mass
	barbel length	resource capture method	diet type	diet type	diet type	diet type	diet type
	oral gape surface/shape	food type	bill morphology	gape width	gape width	gape width	mouthparts size
	vertical position of oral gape	movement method	wing morphology				mouthparts strength
shape of teeth	mobility	feet morphology	feet morphology	feet morphology	feet morphology	defence strategy	
density and maximal length of gill rakers	defence strategy	tarsus/leg length	tarsus/leg length	tarsus/leg length	tarsus/leg length	escape strategy	
maximal length of gill rakers	water column migration	social behaviour	social behaviour	social behaviour	social behaviour	toxicity/resistance	
		competitive ability	competitive ability	competitive ability	competitive ability	sociality	
		local movement	local movement	local movement	local movement	competitive ability	

(Continued.)

Table 1. (Continued.)

type of trait	fishes	marine invertebrates	birds	mammals	amphibians	reptiles	invertebrates
life history	egg size		reproductive effort	reproductive effort	reproductive effort	reproductive effort	egg size
	number of eggs	maximum growth rate	reproductive behaviour	reproductive behaviour	reproductive behaviour	reproductive behaviour	egg number
larval life history		reproductive method	metabolism	metabolism	metabolism	metabolism	length of larval stage
	type of reproduction sites	time to maturity	fecundity	fecundity	fecundity	fecundity	number of larval stages
parental care		fecundity					
		propagule dispersal	digestive physiology	digestive physiology	digestive physiology	digestive physiology	dispersal
			relative brain size	relative brain size	relative brain size	relative brain size	temperature requirements
			social behaviour	social behaviour			larval diet type
			migratory status	migratory status			competitive ability
			home range size	home range size	home range size	home range size	survival rate
			dispersal strategy	dispersal strategy	dispersal strategy	dispersal strategy	metabolism
			competitive ability	competitive ability	competitive ability	competitive ability	resistance to starvation
			survival rate	survival rate	survival rate	survival rate	resistance to desiccation
							reproduction system
							sociality

applied directly to animal communities (e.g. [56]). Plant ecologists have recently recognized that other compartments of the interaction network might influence the link between biodiversity and ecosystem functioning. Plant–pollination or plant–herbivory are two examples of interactions that can influence indirectly the relationship between response traits and the environment, as well as effect traits and ecosystem functioning. To address this issue, the framework was extended to measure the functional linkages that cascade through the primary producers to the consumers [7]. The general idea is to link response traits at a given trophic level to effect traits at another. As an example, the corolla length and flower colour of a grassland community would be considered as effect traits because they influence the pollinator community. In turn, body size and proboscis length of the pollinators would be considered response traits. The problem with this classification is that it remains strongly influenced by a plant-centred perspective, where the primary producers are structuring the community, and causal relationships are from the bottom to the top of the food web. But a predator harms a prey, just as the prey sustains the needs of the predator, and consequently, it is simply impossible to determine effect and response traits in such an interaction. In addition, consumption and life history traits can be viewed as effect traits, as they influence the *per capita* and the per population effects one species has on another, respectively. Our classification thereby appears more appropriate to food webs than the more traditional effect/response dichotomy. The classification of some response traits, however, stays relevant when used to describe attributes related to abiotic or habitat preferences.

3. Quantifying the functional structure and diversity of food webs

The functional composition of a community is the multivariate distribution of traits across co-occurring organisms. It is characterized by the different moments of the distribution of each trait (mean, variance, skewness, etc.), and the covariance among them. The functional structure is characterized by the average for each trait, which could be weighted by abundance (CWM). The ordination of CWMs for all traits allows a visual representation of the central aspects of the multivariate trait structure. The functional diversity represents the dispersion of the traits around their mean. There are also several techniques to quantify the dispersion of traits around the central moments of the distribution [57], the more direct being the CWV. The relevant question is, therefore, should we measure functional diversity of food webs in the same way we do for plants?

There are several tools to quantify the functional composition of communities, some redundant and others emphasizing particular aspects of the multivariate distribution. First analyses of functional diversity were based on expert classification, with functional diversity quantified from the number of functional groups [58], but many functional diversity indices have been proposed since [59]. A group of indices is based on the computation of pairwise distances between species (e.g. [17,60]). A major breakthrough was the proposition of a decomposition of the functional diversity in three components: the richness, the divergence, and the evenness [61]. The computation of functional volume is also a powerful tool to explore variations in the functional

Box 2. Correlation among traits influences the occurrence of interactions.

We are interested in understanding if a predator species i will feed on a prey species j . It is convenient to treat the problem as a stochastic event resulting from the random draw of two species from the multivariate trait distribution. Species i , therefore, has the trait value T_i with probability $P(T_i)$, and similarly for the species j . The observation of an interaction between these species, L_{ij} , should thus be expressed as a joint probability event:

$$P(L_{ij}, T_i, T_j). \quad (2.3)$$

A trait-matching function describes the probability of observing this interaction, given the traits of the two species [66]:

$$P(L_{ij}|T_i, T_j). \quad (2.4)$$

Now, a correlation between traits indicates that trait T_i is more likely to be observed if T_j is observed. Such correlation can arise because of non-random co-occurrence of species [67,68]). Because the traits are not independent, the joint probability of observing both traits is:

$$P(T_i, T_j) = P(T_i|T_j)P(T_j). \quad (2.5)$$

Finally, the probability of observing the interaction could be decomposed as:

$$P(L_{ij}, T_i, T_j) = P(L_{ij}|T_i, T_j)P(T_i|T_j)P(T_j). \quad (2.6)$$

This last equation shows that the occurrence of the interaction will increase with the conditional probability of observing trait i given the observation of trait j . In other words, the interaction will be more likely to happen if the two traits are more susceptible to be found together than by chance alone.

composition of assemblages through space and time due to biotic (e.g. species invasions) or abiotic (e.g. climate change) perturbations [57]. Computation of functional diversity and dispersion has been widely applied to different types of organisms such as fishes [11], birds [62], plants [63] or insects [64]. This class of methods, however, considers all organisms the same way, and the application to food webs, or more generally to interaction networks, has not been explored in detail. Further, there is currently no method to relate the functional composition (or occupation of the functional space) to network structure.

An important aspect of functional composition that is relevant to food webs but overlooked in these indices is the covariance among traits. Such covariance could arise, for instance, from coevolution of the enemy and the victim in an evolutionary arms race [65]. They could also occur when traits are correlated in the same way to an underlying environmental gradient [16]. Relationships among traits are susceptible to have important implications for the structure of the interaction network and thus indirectly on ecosystem functioning (see box 2 for a formal mathematical argument and figure 2 for an illustration). It could make interactions more or less likely to occur relative to the situation where they are independently distributed. The effect of such correlation depends on

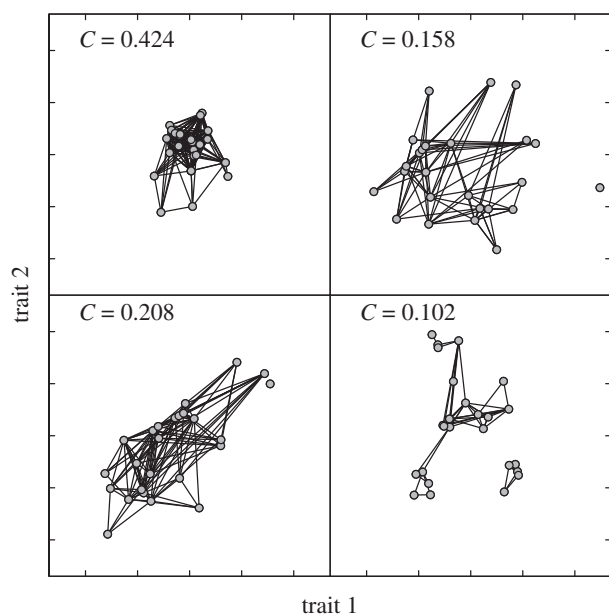


Figure 2. The effect of functional trait structure and diversity on food web topology. The figure illustrates the potential impact of different aspects of the multivariate trait distribution while keeping the trait-matching rules constant: trait variability (top left compared with top right), trait correlation (top left compared with bottom-left) and non-uniform trait distribution (clustering, top left compared with bottom right). Formal proof of the effect of trait correlation is provided in box 2. The simulations are run with a two-dimensional adaptation of the niche model [69]. We generalized the model to several niche axes and flexible distributions of the different traits, but keeping the trait-matching function based on the ordering of niche positions and the existence of a diet optimum. Each point represents the position of a species in a two-dimensional trait space (foraging and vulnerability traits). Each line represents a trophic interaction. The predator has the largest trait value (for both traits) and the prey the smallest. The connectance of the network, C , is indicated on each panel. It emerges from the underlying rules, instead of being predetermined, as in the original model. Niche position for each species is drawn from a bivariate normal distribution with mean trait value of 0. Correlation between niche axes is null for all panels, except for the bottom left panel that has a correlation of 0.8. The standard deviation for each trait is set to 10, except for the top left panel that has standard deviation of 5. A non-uniform distribution of traits is simulated by five niche positions n_i from the bivariate normal with mean 0 and standard deviation of 10, and then after drawing four additional species with niche positions of mean n_i and standard deviation of 3.16. The range r for each axis is obtained by drawing a random number from a uniform distribution between 0 and 30. The centroid o for each axis is obtained by drawing a random number from a uniform distribution between the minimal niche position and $r/2$. Preys of a given predator i are the species whose niche falls within the interval $o_i - r_i/2$ and $o_i + r_i/2$.

the function relating foraging and vulnerability traits to the occurrence of an interaction. We currently have a minimal empirical documentation of the existence of such covariance structure in the distribution of traits. Further, numerical methods to analyse it are currently limited and thus new techniques to characterize this particular aspect of functional composition are required.

Representing the spatial variation of functional structure and diversity of food webs is of great interest as it can reveal the effects of environmental filtering between regions or along gradients. However, despite the large availability of trait data, this is not a common practice in ecology. Although several studies have analysed how environment and biotic interactions may influence functional structure and diversity, this is usually

carried out at small spatial scales and for some specific groups [70]. Few attempts have been made to analyse the covariation of diversity across groups and plants. Macroecologists have mapped the spatial variation of some traits (e.g. maximal body size) for various groups [71,72], but the covariation among groups is currently overlooked. The observation of systematic variation in functional structure and diversity of different groups is susceptible to be instructive for understanding network assembly. For instance, it is known that high floral diversity usually stimulates a diversity of functional groups of pollinators [73]. Most published studies, however, have either analysed covariation between different biodiversity facets within a given group (e.g. birds, [74]) or covariation of a given facet (e.g. phylogenetic diversity) across different groups [75,76]. However, as far as we are aware, there is no systematic analysis of large-scale functional diversity between different groups of animals or/and with plants. We argue that it should give some insights on the link between functional structure and diversity and food webs.

A promising avenue in the study of functional structure and diversity is the measure of the contribution of a given species to the functional diversity of a community. There are various methods to measure the functional distinctiveness of a given species in respect to the others [77]. Unlike phylogenetic distinctiveness, which emphasizes the evolutionary heritage of a species, the functional distinctiveness rather emphasizes how a given species uses a different set of resources, behaves differently or uniquely affects ecosystem functioning. It has important implications when it comes to food webs as functionally distinct species are likely to be particularly important for the stability of the entire food web and act as unique hubs gluing the network together [78]. A recent meta-analysis has also shown that functionally distinct species are usually geographically rare or of low abundance, for both plants and animals [79]. Functional distinctiveness could reveal unique species that have specific diet or strong identity effects.

4. Relating trait structure to network topology

How do we move from a given trait distribution to a network? There is currently no clear answer to this question, but the many theoretical models of food web structure do provide some preliminary intuition. The first one proposed, the cascade model [80], ranks species along an abstract axis, and any predator interacts with a given probability with all species with an inferior position along this axis. The niche model of food web structure [69] is similarly based on a single niche axis, and also considers that predators feed on preys whose niche falls within a range around an optimum. The minimum potential niche model [81] extends this approach to multiple niche axes. The nested hierarchy model is based on similar rules, with the addition of phylogenetic constraints [82]. All of these models have in common that species could be ordered according to their position along a niche axis, which for the purpose of generality, is never associated with a particular trait. It was recently shown, however, that most ecological networks could be summarized with only a few of such axes, which could easily match to some functional traits [50].

All of these theoretical models of network structure have been fitted to empirical data and compared with each other [81,83], opening the way for the development of trait-matching

models of interactions [84]. Indirect methods of inference of ecological interactions based from traits were developed first. For instance, Rohr *et al.* [40] represents the structure of interaction networks using latent traits (basically the niche position and optimum), which could be later related to functional traits and to phylogenies. Williams *et al.* [83] did similarly by fitting a probabilistic version of the niche model to empirical data, evaluating the niche, the optimum and the range for each species, and then by regressing these parameters to body size. Direct methods of trait-matching were proposed after. The niche model was fitted directly with the assumption that body size is the main niche axis and that the predator–prey body size relationship represents the optimal niche of a species [85]. This method was successfully extended to other types of interactions, such as plant–herbivores where traits such as leaf dry matter content and incisive strength are good predictors of interactions [66]. Crea *et al.* [86] considered multinomial regression to model interaction probability based on plant and pollinator traits and abundance. A totally different approach, derived from multivariate statistics and ordination techniques [87], also confirmed that physiological and morphological traits are driving the diet of marine mammals. At the end, despite some important differences in the statistical approach used to evaluate trait-matching functions, we find that a common denominator of all of these methods is the classification of traits involved in trophic interactions as foraging and vulnerability traits (see above and the detailed table in [84]).

However, while trait-matching constraints are fundamental to establish potential interactions between pairs of species, their realization also requires that species encounter each other. Abundance and prevalence consequently have a fundamental importance to food web structure [51]. Neutral models of trophic structure are exclusively based on the law of mass action; they propose that the frequency of an interaction happening and the strength of that interaction should be proportional to the product of abundances between pairs of species [88]. In other words, they hypothesize that consumers do not select their resources; they only take them in the proportion they find them. Not surprisingly, rare species interact with much fewer species than abundant ones, and predominantly with the most abundant ones. Neutral models can fit well empirical data, even for interactions that are hypothesized to be strongly driven by trait-matching constraints [89,90]. An important point to remember for the purpose of our framework is that traits, in particular life history ones, involved in the determination of abundance could also indirectly impact both the topology of food webs and the intensity of the interactions.

The key question, now that it is established that traits impact the occurrence of pairwise interactions, is how do we move from the entire trait distribution to the network structure? The mean of the different traits, their variance and their covariance are all moments of the multivariate distribution that will all affect the network structure. We illustrate in figure 2 with an adaptation of the niche model [69] that increasing functional diversity in a food web whose interactions are determined by trait-matching constraints could significantly impact on its emerging properties. The niche model is based on the match between the niche position of the prey (a vulnerability trait) and the centroid of the diet of the predator (a foraging trait). The distribution of the foraging and vulnerability traits in the niche model were originally fixed by hypothesis, but

the figure 2 illustrates that more flexible distributions with a variation of the average, the variance and the covariance could alter the properties of the resulting network. Increasing the variance (figure 2, top left to top right) of both traits could decrease the connectance and impact the way the links are distributed. Similarly, a correlation between traits (figure 2, bottom left) or their clustering (figure 2, bottom right) can also significantly impact the network structure. These properties are, in turn, expected to impact the dynamics, stability, persistence and functioning of food webs. This figure is only a specific example, and further investigations will be required to clarify the roles that the different moments of the multivariate trait distribution have on network structure, both in theory and in empirical systems.

5. Impacts of trait diversity on ecosystem functioning

Completing the loop from the distribution of traits to network structure and ecosystem functioning is far from trivial. Fortunately, layered food webs can give some preliminary insights. First studies on the impact of trophic interactions on the relationship between biodiversity and ecosystem functioning were mostly restricted to the investigation of extreme cases where networks were composed of either generalists or specialists, but nothing in between [91]. It was proposed recently that ‘trophic complementarity’ is a mechanism driving the shape of the BEF relationship [30] in networks of intermediate complexity. The principle is simple; it mirrors the one of resource-use complementarity. Species in a given layer of a food web interact by both exploitative and apparent competition through shared resources and predators. The contribution of a given species to ecosystem functioning is expected to increase with its trophic complementarity. It is defined as the overlap of interactions between pairs of species (across resources and predators). According to the models described above relating traits to interactions, species sharing similar traits are also expected to share similar interactions. We thus intuit that there should be a positive relationship between functional distinctiveness and trophic complementarity. A key question at this stage is how traits responsible for trophic interactions are independent of the ones determining resource use. If they were uncorrelated, it would imply that quantifying trophic complementarity would be as important as functional complementarity in predicting ecosystem functioning and even coexistence. The BEF relationship in food webs has been discussed [26] and some experiments have provided evidence of a positive relationship ([92], but see [93]), but only species richness has been investigated thus far, not functional diversity.

We note at least two hypotheses by which functional diversity of the food web could promote ecosystem functioning. First, increasing functional diversity at one layer could provide niches for above layers, such as plant diversity sustaining a diverse herbivore community (e.g. [94]). In other words, diversity could beget diversity, simply because the higher trophic layers do require a diversity of preys at the lower level to establish and persist [67]. Such ‘niche construction’ is based on the assumption of a sequential build-up of the food web, where bottom-up processes dominate. It predicts a positive correlation between functional diversity at the different trophic levels. High plant functional diversity should promote the diversity of herbivores, which in turn would promote diversity

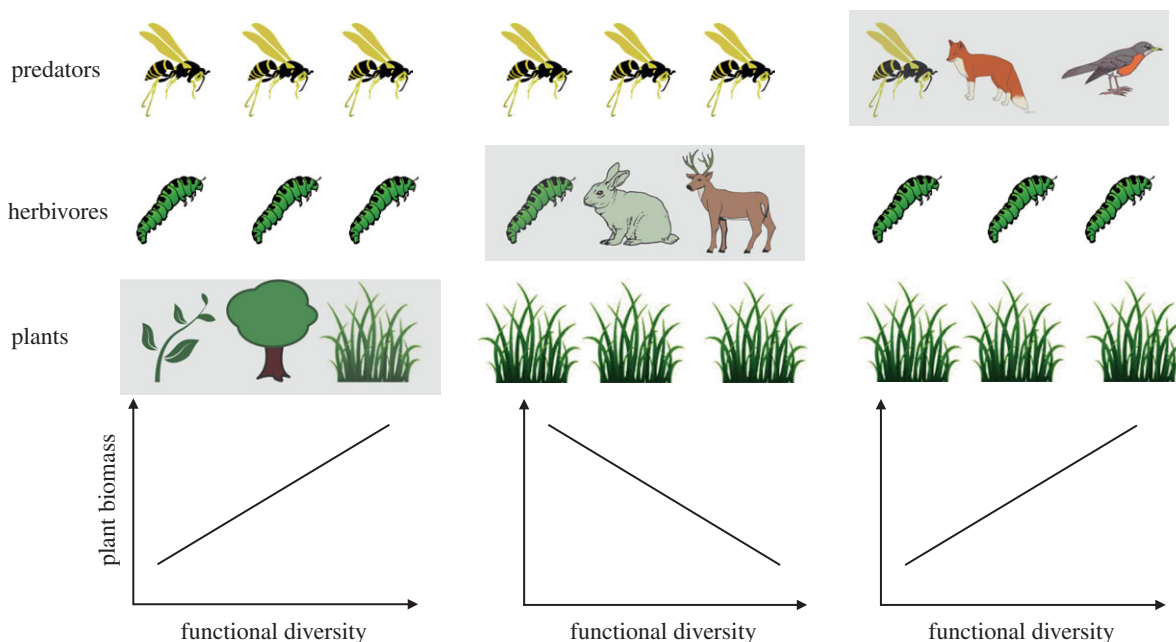


Figure 3. Cartoon representation of the effect of trait diversity in layered and top-down control food webs. The figure represents hypothesized relationships between functional diversity and plant biomass in BEF experiments where the functional diversity is varied at different trophic levels (indicated by shading). (Online version in colour.)

of predators [95]. It is important, however, to understand the role of trophic regulation in this relationship to adequately distinguish the cause and the effect. A strong top-down control, as imposed by functional diversity of the top layer, could either promote diversity through keystone predation [96] or via reduced apparent competition [31]. Functional diversity could also have a positive effect on nutrient retention and cycling within the food web [29]. Primary productivity will be promoted by a tight nutrient cycling loop and thus the diversity of feeding modes, including scavengers and detritivores, will ensure that primary and secondary production remains local and is not exported out of the system [97]. Further, a diversity of stoichiometry in the various organisms, as long as exudates, could promote the efficiency of detritivores [98].

Functional diversity could, on the other hand, increase the strength of top-down regulation and consequently have various effects on primary and secondary productivity, depending of the trophic level considered. Increased functional diversity of a given trophic level will increase the regulation of the lower level by enhanced trophic complementarity. Consequently, the diversity of foraging traits of herbivores will promote their ability to exploit the plant level, and the diversity of vulnerability traits will help to reduce the regulation by carnivores and reduce apparent competition (figure 3, left panel). As a consequence, we would expect a negative relationship between functional diversity of herbivores and primary productivity (figure 3, central panel, see experimental support in [99]). Conversely, the diversity of foraging traits of carnivores will help them to control the herbivore layer, thereby releasing the plants from grazing (figure 3, right panel). The key question, still unresolved, is what will happen in between if we add all of the complexity that is typical of unipartite food webs, such as intra-guild predation, omnivory, cannibalism and loops.

What remains to be understood is the importance of functional identity effects in food webs [100]. Functional traits should be used to better quantify their underlying drivers. The interpretation of strong identity effects is often intuited from knowledge of species traits. The trait-based approach

formalizes this interpretation with quantitative analyses, such as the use of functional distinctiveness and CWM. The food web literature has been instrumental in the establishment of the 'keystone species' concept [96]. It is well documented that some predators, because they are highly efficient at controlling some populations, could promote coexistence and have a significant impact on ecosystem structure [27]. Despite the fact that they are often located at the top of the food chain, we have a poor understanding of the traits determining the keystone role of a predator has to be the result of a match between its traits and the ones of the prey species in the food web. The problem of keystone role was addressed with the investigation of the determinants of direct and indirect interactions in modelled food webs [101]. It was found that the best predictors of single species removal effects were essentially the biomass of the removed species (which is a dominance effect) and the network path length between the removed species and the focal one (the shorter the path, the stronger the effect). Predator-prey body mass ratio surprisingly was only a poor predictor of the interaction strength. As all the interactions were, however, determined by a single trait, body size, we do not know to what extent this result is generalizable to more complex functional structures.

Answering the classic question of whether an ecosystem is bottom-up or top-down regulated remains of primary importance to understand the role of functional diversity in food webs. For bottom-up systems, we could intuitively predict that in most situations, increasing functional diversity, whatever is the complexity of the food web, will always be positive because it will promote niche construction and close the nutrient cycle. The challenge is thus found in trophically regulated systems. Identity effects could also occur with functionally distinct species, which could either be beneficial or harmful for food web dynamics. The main problem is that functional diversity of preys could promote their escape from trophic regulation, while the diversity of predators could enhance it, making undetermined the final relationship between functional diversity of the entire food web and ecosystem functioning.

6. What next?

Understanding the relationship between functional diversity and the structure and dynamics of food webs is a key problem to solve in order to predict ecosystem functioning. The investigation of the functional structure and diversity of communities has been mostly restricted to plants, but recent investigations of animal communities are promising. Traits could both directly and indirectly impact food web dynamics. The food web perspective promises a more integrated perspective of the relationship between biodiversity and ecosystem functioning [102]. A trait-based approach suggests that it could be possible to find generalities and circumvent the idiosyncracies commonly arising in food webs. It extends a fundamental principle linking food web ecology and ecosystem functioning [103]: ‘interactions occur between functional units according to a topology that is driven by trait-matching constraints’. Further, it helps representing energy and material fluxes and the multiple types of species interactions [103].

We have identified three broad categories of traits that are relevant to the characterization of food webs: topological traits, consumption traits and life history traits. These traits combine to determine the *per capita* and per population interaction strengths. We have also pointed out that in food webs the characterization of the functional structure should include not only the mean and the variance of the different traits, but also their covariance. Finally, we have emphasized that determining the strength of trophic regulation is of primary importance to understand the role of the functional structure of food web dynamics. The review also highlighted some key gaps in knowledge and pointed to some of the most critical problems to solve. In conclusion, we see the following main steps for a research agenda on functional diversity of food webs:

- (1) *Gathering and integrating interaction data with functional traits* to improve our understanding of trait-matching constraints. While there has been some work on this question already, only the low-hanging fruits have been picked; more specific data will be required to infer the identity and the strength of trophic interactions. New platforms for interaction data, such as ‘mangal’ [104] need to be coupled with platforms for trait data. A key problem to solve is finding and integrating relevant traits across different groups of organisms such as vertebrates, arthropods and plants.
- (2) *Developing theory relating functional composition, network structure and ecosystem functioning*. As described above

and illustrated in figure 1, we only have a partial understanding of the steps going from traits to ecosystem functioning. Investigations of this problem will require data-driven simulation models and to integrate the entire chain of causal relationships.

- (3) *Large-scale analysis of the covariation between functional composition of trophic guilds and network characteristics*. The above review highlighted that a key aspect of functional trait structure and diversity to quantify is the multivariate nature of the problem. The covariation of traits among predators and preys is key to understand the emergent properties at the network level. There is a critical gap in knowledge to solve, as we do not know how functional structures covary among trophic levels; neither do we understand the covariation between functional structure and emerging network properties. There are also some aspects of the trait distribution that are not qualified by current metrics describing functional composition.
- (4) *Understanding the role of a species in a network from its traits*. This question is key to several fields, from conservation, where it could help to identify keystone species, to invasion ecology, where it could help to predict not only the invasibility, but most of all, the direct and indirect impacts of invaders. We now have tools to document species role in complex networks [105]; the next step will be to predict it from traits. Answering this question will require theoretical investigations of pairwise interactions in trait-based food web models, as well as extensive mining of the literature on predator removal experiments.
- (5) *The relationship between identity effects and extinction risks in food webs*. Traits not only determine the role of a species in a food web and its impact on other species, but also its vulnerability to global changes. Understanding their relationship is essential to make the field of network ecology predictive and relevant for biodiversity managers.

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