



# Recent Advances in the Integrative Nutrition of Arthropods

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## Abstract

In this review we highlight recent advances in four areas in which nutrition shapes the relationships between organisms: between plants and herbivores, between hosts and their microbiota, between individuals within groups and societies, and between species within food webs. We demonstrate that taking an explicitly multidimensional view of nutrition and employing the logic of the geometric framework for nutrition provide novel insights and offer a means of integration across different levels of organization, from individuals to ecosystems.

## INTRODUCTION

The past two decades have seen what amounts to a revolution in nutritional biology that has arisen from the study of terrestrial arthropods and has influenced fields far beyond entomology, including, to name but a few, human food animal production systems (e.g., 119), domestic pet nutrition (e.g., 67), conservation of endangered species (e.g., 55), human obesity and metabolic disease (e.g., 60), and the nutritional determinants of life span and aging (e.g., 133). The origins of this revolution lie in the pioneering work of entomologists such as Painter (99), Fraenkel (57), Dadd (40), Waldbauer (143), Dethier (46), Scriber & Slansky (123), and Bernays & Chapman (13), among others (see 114 for a brief thematic history). Their work provided much of the material and the bedrock for building a unifying, integrative framework, called the geometric framework for nutrition (GF) (10, 111, 125, 126). GF models the ways in which nutrients and other food components, such as plant secondary metabolites (113) and cell wall components (81, 25), interact in their effects on food choice; food intake; and the development, health, and evolutionary fitness of individual organisms. They can also be used to model how the independent and interactive effects of food components on organismal responses scale up to influence group dynamics, population growth, and species assemblages (126). The power of GF is that it allows the nutrient requirements, the behavior and physiology of the organism, and the environment to be represented and interrelated within the same, multidimensional model.

The logic, structure, derivation, and application of GF have been the subject of several comprehensive reviews in recent years (10, 114, 126), and it is not our intention to repeat that material here. Rather, we focus on four research areas in the field of insect (and spider) nutritional ecology that have advanced rapidly over the past three to five years and that together extend the boundaries and integrative scope of GF. In so doing, they have extended the contribution of terrestrial arthropods to understanding the impact of nutrition on individual organisms, populations, communities, and ecosystems.

The four focal areas are not the only applications of GF that have advanced rapidly in recent years (see 126), but they have been selected to illustrate how this approach has extended its integrative reach to unify progressively more inclusive biological interactions. First, we ask how the nutritional responses of insect herbivores, measured in the laboratory using synthetic diets and controlled environmental conditions, translate in the real world of plants. Second, we explore the complex network of interactions within individuals between diet, nutritional state, immune function, gut microbiota, and pathogens, and show how insects dynamically adjust their feeding behavior and food selection to optimize these interactions for survival and reproduction. Third, we consider how nutrition mediates interactions between individuals to shape the structure and behavior of insect groups and societies—and how these higher-level responses in turn feed back onto the nutritional responses of individuals. Last, we consider the impact of nutritional regulatory responses of individuals on trophic interactions and the structure of food webs within ecosystems.

## UNDERSTANDING PLANT QUALITY

Terrestrial eukaryotic biodiversity is dominated by plants and the animals that eat them, the majority of which are insects. A complex suite of factors influence which leaves are eaten by herbivores (1, 18, 126). Much is known from laboratory studies using synthetic diets about the nutritional needs of insect herbivores, the consequences of ingesting suboptimal diets, and the behavioral and physiological flexibility herbivorous insects demonstrate to achieve nutrient balance in heterogeneous environments (e.g., 10, 30, 31, 137). However, we are only beginning

to understand how the chemical and biomechanical properties of leaves combine with abiotic factors such as temperature to determine the quality of plants as food for insect herbivores, with most work having been done on those with chewing mouthparts. Determining the nutritional quality of a plant for an herbivore is not as simple as grinding up and measuring the chemical composition of plant tissue. Among other reasons, chemicals measured within plant tissues are not readily or equally available for digestion and assimilation, and nutritional requirements of insects are dynamic, changing with age, activity, temperature, and other factors (127).

Taking into account both of these issues within an explicitly multinutrient framework has yielded a more nuanced understanding of the meaning of plant quality and the extent to which insects are able to manipulate their nutritional outcomes through demonstrating plasticity in behavior and physiology. Here we do not dwell on changes in nutritional requirements per se, which have been reviewed in detail elsewhere (e.g., 126, 127). Rather, we focus on how the availability of nutrients in plants varies and can be exploited by insect herbivores to meet their changing nutritional requirements.

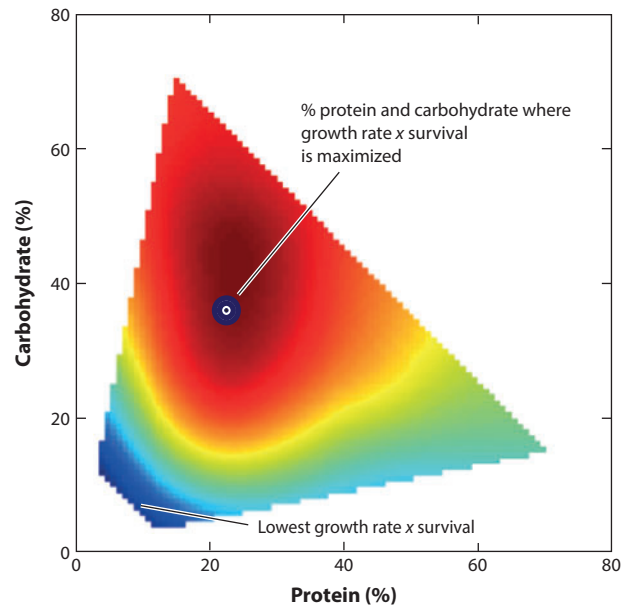
### Nutrient Acquisition From Plants

The mechanisms herbivores use to supply their demand for nutrients include (a) food choice, (b) food intake, (c) nutrient acquisition from ingested food (nutrient digestion and absorption), and (d) postabsorptive processing. A key point is that the rates and efficiencies at which different nutrients (e.g., protein and carbohydrate) are absorbed from ingested food may differ, providing various opportunities for the insect to adjust the ratio of nutrients absorbed from food to meet requirements (112). When insects ingest synthetic diets, which lack cellular structure, the majority of ingested nutrients are absorbed, so the relationship between nutrient intake and performance (e.g., **Figure 1**) does not include a substantial influence of differences in availability of ingested nutrients to digestion and absorption (96). This is also the case when the cellular structure of leaves is removed by grinding, rendering nutrients readily available for digestion and absorption (28, 29) (**Figure 2**).

The extent to which plant cell walls constitute a physical barrier to the extraction of nutrients has been the subject of much debate (reviewed in 25). It is clear, however, that the size of particles produced by chewing food exerts a significant influence on the relative rates and efficiencies at which different nutrients are obtained and hence on nutrient balance (25, 28, 29). This raises a key question, Which plant and animal traits influence fragment size during chewing?

Plant leaves are tough and thus highly resistant to the propagation of fractures. Leaf toughness is influenced by many factors, including the amount, composition, and organization of the cell wall and the tissues it forms; the orientation of the vascular bundles; and leaf thickness, cuticle, and turgidity (117). To overcome leaf toughness, the chewing mouthparts of herbivorous insects consist of hard mandibles with distinctive incisor and molar regions, which share convergent features with the pattern of venation of host plant leaves (21, 25). However, the mechanisms influencing the fragmentation of leaves are complex and poorly understood, as virtually no studies have investigated the mechanical processes involved (21, 25).

Ontogenetic development imposes constraints on feeding; the efficiency with which ingested nutrients are absorbed declines with age/size, because smaller insects have commensurately smaller mandibles and can thus fracture relatively more cells than larger insects can (25). This decline in digestive efficiency with ontogeny can be complex. For example, the pattern differs for protein and carbohydrate; the digestive efficiency of protein declines linearly and the pattern for carbohydrate is specific to the species of plant ingested (25, 28) (**Figure 2**).



**Figure 1**

Performance (growth rate times survival) of the Australian plague locust, *Chortoicetes terminifera*, when confined to one of 43 diets that differed in the ratio of protein to carbohydrate. The bull's-eye shows the ratio of protein to carbohydrate ingested when nymphs were allowed to self-compose the protein and carbohydrate composition of their diet over the final nymphal stadium (see References 127 and 129 for the logic of these experiments). The performance peak obtained from the single no-choice diets correlates with the self-composed percentage of protein and carbohydrate. Therefore, diet quality is a function of both the ratio and density of protein and carbohydrate in a food source.

### Altering Nutrient Rates and Ratios Through Behavioral, Physiological, and Morphological Plasticity

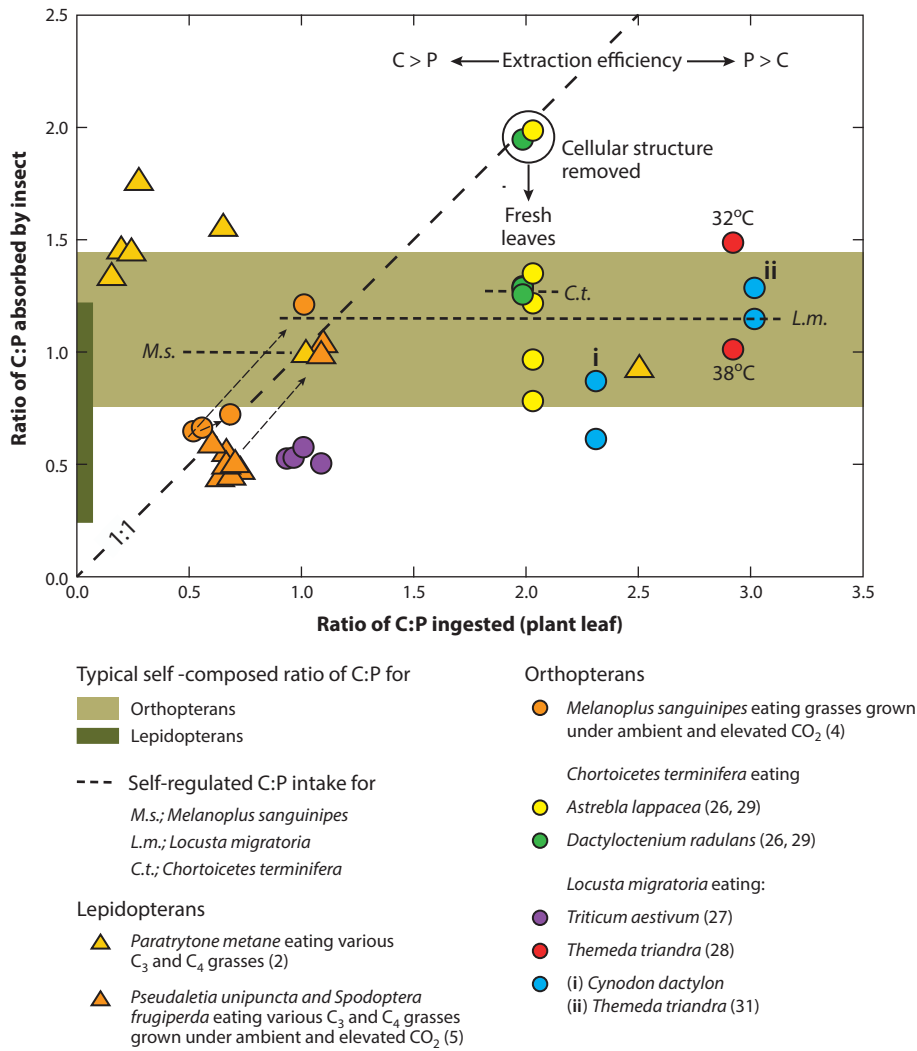
Although insects, like mammals, chew differently in response to many factors, such as food texture (12, 25), once a meal has been ingested, five mechanisms, identified from detailed studies of grasshoppers, can be employed to vary the amount and/or ratio of protein to carbohydrate (P:C) absorbed. First, as discussed in more detail below, thermoregulatory behavior can be used to adaptively alter nutritional outcomes (27). Second, adjusting gut passage time, e.g., by changing the interval between meals, can have profound impacts on P:C absorption (112). Third, drinking can lead to changed P:C absorption; for example, access to free water resulted in a 45% increase in carbohydrate extracted by last instar *Chortoicetes terminifera* nymphs consuming the grass *Astrebala lappacea* (28). Fourth, the differential release of digestive enzymes in response to an experimentally imposed nutritional (P:C) imbalance was used by *Locusta migratoria* nymphs to alter the P:C ratio absorbed from two C<sub>4</sub> grasses (30). Fifth, changes to the mass of the digestive tract resulting from chronic exposure to diets with different P:C ratios (26, 109) were associated with larger meal sizes and increased rates of nutrient absorption in *L. migratoria* (26).

### Using Thermoregulatory Behavior to Regulate Nutrient Balance

Typically, as temperatures rise, an insect's development rate increases (to a maximum and then declines with morbidity), and additional food is required to fuel growth because metabolic wastage

is greater at higher temperatures (82, 96). When *L. migratoria* nymphs were challenged with either short-term or chronic food shortage, they selected lower temperatures within a thermal gradient, thereby reducing metabolic costs and maintaining size at maturity, albeit at the cost of slower rates of development (31).

When insects ingest plants, the relationship between host plant, temperature, and life-history outcomes can be complex (47, 85, 153). For example, inconsistent changes in growth and body size as they relate to temperature and diet have been demonstrated for many herbivorous insects (e.g., 27, 47, 144). One study showed that *Manduca sexta* was larger on a poor-quality host and smaller on a good-quality host when reared at a higher temperature, yet dry-mass-based gravimetric measures of digestion and metabolic efficiency failed to reveal why this difference occurred (47). The same patterns were observed for *L. migratoria* fed either the perennial grass *Themeda triandra* or lower-quality grass seedlings of wheat (*Triticum aestivum*). When the amounts of protein and carbohydrate extracted from the two host plants were determined, differences in body



size were fully explainable (27). At 38°C *L. migratoria* extracted a nutrient ratio high in protein and low in carbohydrate from *T. triandra*, and at 32°C the reverse occurred (27). *L. migratoria* redressed nutritional imbalances and altered the P:C ratio extracted from *T. triandra* using postingestive thermoregulation (27) (**Figure 2**). This relationship between temperature and host plant was specific to plant species, as temperature affected the rate but not the P:C ratio absorbed by *L. migratoria* nymphs fed *T. aestivum* (27) (**Figure 2**).

## INTEGRATING NUTRITION AND IMMUNOLOGY

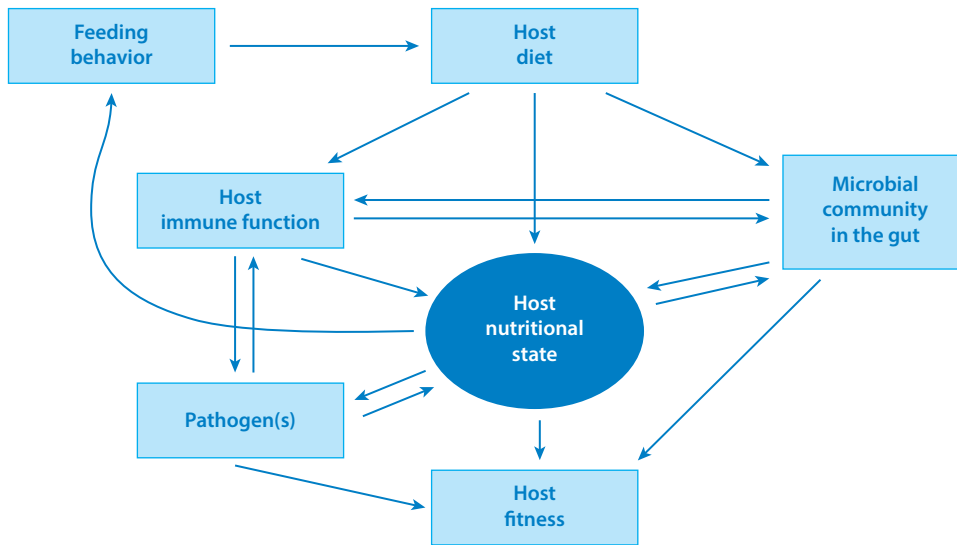
Like free-feeding individuals, parasites too face particular challenges in meeting their nutritional requirements. For example, the nutrition provided by the host influences not only within-host pathogen population dynamics, but also the degree of pathogenicity of the infection through, for instance, effects on immune function (38, 107). The commensal and symbiotic microbial communities inhabiting the host make interpreting nutritional interactions between hosts and parasites significantly more complex. The digestive tract of metazoans is particularly rich in such facultative microbes, where their activity may influence nutrient quality and absorption, as well as provide immunological challenges. Host nutrition can influence the bacterial composition of these symbiotic populations. The challenge remains to unravel the relationships between nutrition, immune function, pathogen population growth, and structure and function of the gut microbiota (**Figure 3**). GF designs offer a powerful approach for studying these interactions, allowing scientists to make quantitative predictions about the effects of nutrition on immunity, health, and disease (103).

## Infection

The availability of nutrients is a fundamental constraint on parasite populations (61). A growing literature shows how resource quantity and quality influence the abundance and development of parasites (9, 42, 50, 120, 141) and directly shape virulent effects of parasitic infections (16, 58, 69, 83,

**Figure 2.**

Comparison of the ratio of carbohydrate (C) to protein (P) from leaves ingested and absorbed (passed across the gut wall) by lepidopterans (▲) and orthopterans (●). Points that fall on the dashed line (labeled 1:1) indicate the herbivore was able to absorb the same C:P ratio it ingested. Points above or below the line indicate the herbivore is digesting C or P more efficiently than P or C, respectively. All of the P and C in leaves was absorbed by *Chortoicetes terminifera* when the effects of plant cellular structure were removed by grinding *Dactyloctenium radulans* and *Astrebla lappacea* leaves (green and yellow circles, respectively) to a fine powder (25). However, when the insects were feeding on fresh leaves the ability to extract C declined with age, especially when they were eating *A. lappacea* (28). After ingestion, *Locusta migratoria* is able to alter the ratio of C:P absorbed using two mechanisms: (a) temperature (red circles) when feeding on *Themeda triandra* (27), and (b) the differential release of digestive enzymes [plant species are *Cynodon dactylon* (i) and *T. triandra* (ii); 30]. Although seedling *Triticum aestivum* is a high-protein resource, it cannot supply sufficient carbohydrate to optimize development and growth of grasshoppers (26, 30), as illustrated by the position of the purple circles, outside of the light olive shading (data from Reference 10). The self-regulated ratio of C:P is represented by the short dashed lines for *C. terminifera* (*C.t.*), *L. migratoria* (*L.m.*), and *Melanoplus sanguinipes* (*M.s.*) (26). Lepidopterans typically self-compose a diet with a lower C:P ratio than orthopterans (the dark olive green bar) (data from Reference 10). Digestive efficiency of P and C was similar for *Pseudaletia unipuncta*, *Spodoptera frugiperda* (▲), and *M. sanguinipes* (●) feeding on C<sub>3</sub> grasses grown under normal and elevated CO<sub>2</sub> conditions (dark orange). Plants grown under elevated CO<sub>2</sub> conditions had a higher C:P ratio, as illustrated by the dashed arrows (3, 4). For the lepidopteran *Paratrytone melane*, C<sub>3</sub> and C<sub>4</sub> grasses (2) can provide a wide range of foods differing their C:P ratio (orange).



**Figure 3**

The network of interactions between nutrition, immunity, parasites, and gut microbiota. Diet affects host nutritional state and immune status, both of which interact with microbial symbionts, commensals, and pathogens to affect the fitness of all partners. Because nutrient feedbacks modulate host feeding behavior, the potential exists for the host to adjust its diet to optimize its microbial interactions and increase resistance to infection. Alternatively, parasites and pathogens might subvert host feeding behavior to their nutritional advantage (figure from Reference 103).

124, 139). Typically, access to elevated quantity and/or quality of resources by parasites enhances the production of infective propagules. Because key aspects of host-parasite interactions often hinge on resources consumed by the host, variation in host nutrition may directly influence disease dynamics. For instance, in many terrestrial systems, host plant type altered parasite transmission rate (42, 79). However, just as the determinants of plant quality are complex (see above), the mechanisms that link resource quality to disease are multifaceted, so generalities relating host nutrition to infection are difficult to derive.

## Immunity

Foods contain myriad components that affect insect physiology and immune function. Recent advances in functional genomics and molecular biology have greatly expanded our understanding of the details of the immune mechanisms that enable arthropods to defend themselves against infections (84, 132, 146). There is clear evidence of cross-regulation between metabolism and innate immunity. For example, antimicrobial peptide genes in uninfected *Drosophila melanogaster* can be activated in response to varying energy status of cells and tissues through a direct interaction with the nutrient sensor FOXO (7). Key questions are whether different immune components share similar or different nutritional requirements, and whether they compete for limiting host-derived resources (37, 97). Recent studies have used GF to quantify the effects of macronutrients on innate immunity in insects. Such studies have shown that, in caterpillars (*Spodoptera littoralis*), the dietary P:C ratio influences resistance to infection (80), mainly through its effects on immunity traits such as hemolymph antimicrobial activity and phenoloxidase activity. However, component immunity traits differed in their level of activation according to diet composition (107), suggesting



either a physiological trade-off between these traits or different nutritional optima for these traits. Cotter et al. (38) confirmed the latter hypothesis, showing that no single diet composition can simultaneously optimize all immune system components in either naïve or immune-challenged caterpillars; rather, immunological traits were maximized at different dietary compositions (P:C). It logically follows that hosts could adjust their dietary choices to achieve a nutrient balance that best meets a particular immune challenge and/or compensates for the cost associated with the activation of specific immune traits.

Recent work suggests that infected hosts can regulate dietary macronutrient intake (self-medicate) to circumvent the negative effects of infection (38, 80, 102, 107, 108), as they are also able to do through the use of plant secondary metabolites (14, 113, 131). Identifying the nutrients and, critically, the nutritional interactions that modulate immunity remains a central challenge for the field of nutritional immunology (103, 104).

### Gut Microbiota

Hosts also share their resources with numerous opportunistic commensals that contribute to their physiology (48) and have a central role in the infection process (24). Gut microbiota can affect levels of infection through direct interaction with parasites by producing inhibitory bioactive compounds or by constraining parasite development through the immune system (145). Host nutrition can explain variation in persistence, abundance, and species composition of gut bacterial communities within invertebrates (20, 34) and vertebrates (41, 86, 116, 152). For instance, the natural *Drosophila*-associated microbiota appears to be shaped predominantly by the food substrate and, to a lesser extent, by the host species itself (135). These observations were made primarily after compiling data in meta-analyses and in this respect have limitations; however, experimental manipulations of dietary composition have shown that dietary macronutrients have an important impact on the bacterial composition and abundance of gut microbiota in mammals (54).

Different diet compositions might promote specific bacterial strains by providing them with favorable nutritional conditions. Diet also influences the physical and chemical milieus of the gut (30, 56, 134) and hence may constrain the strains of bacteria that can survive in the gut ecosystem. In addition, foods can act as vectors of bacteria, and different types of foods provide the host with diverse bacterial inoculates. Blum et al. (15) have shown that the establishment and maintenance of the *D. melanogaster* microbiota depends on the ingestion of bacteria. Replenishment represents a strategy by which animals can sustain a gut microbial community. More studies are needed to provide a detailed and comprehensive assessment of how diet shapes gut microbiota and, more particularly, to quantify the effects of multiple nutrients on gut bacterial communities as well as the subsequent effects on host immunity and disease dynamics.

### SOCIAL NUTRITION

By acting on the physiology, behavior, and fitness of animals, nutrition influences the ways individuals interact within groups and populations (126). At the most conspicuous level, nutrient distribution defines the foraging areas of individuals and the frequency at which they encounter one another. An individual's decision to eat a food item thus depends not only on its individual nutritional needs but also on its interactions with other conspecifics, including social partners and competitors (59). Arthropods have evolved an impressive spectrum of social interactions, from simple interindividual attraction (36) to division of labor (70), many of which are fashioned by these nutritional trade-offs. German cockroaches (*Blattella germanica*), for instance, are attracted by feeding conspecifics, a behavior that often results in large temporary aggregations at food sources



(88). In the leafcutter ant *Atta cephalotes*, hundreds of thousands of individuals work together to cultivate a mutualistic fungus, which is essential to convert plant biomass into digestible food for the larvae (101). Investigating the connections between nutritional processes at the individual and collective levels is a promising approach to illuminate the mechanisms and evolution of social interactions organized around nutrient acquisition (87).

### Mass Migration

At the most basic level of social phenomena, variations in the spatiotemporal distribution of nutrients have direct repercussions on population dynamics. Spectacular examples are the mass migrations of desert locusts (*Schistocerca gregaria*) and Mormon crickets (*Anabrus simplex*), which form marching bands extending over kilometers (140). During population outbreaks, locusts and crickets congregate on receding vegetation patches in response to food scarcity. In locusts, prolonged interactions with conspecifics trigger a phenotypic shift from an isolated and cryptic solitary phase to an actively aggregating gregarious phase (100). The gregarizing effect of patchy food distributions (33), which results from insects having to move more between patches to balance their diet, is further enhanced if foods are nutritionally imbalanced or low in nutrient density (45). Aggregation provides antipredatory benefits to individuals (118) but also increases competition and the risk of cannibalism. Measures of the nutritional states of crickets (130) and locusts (6) in crowds revealed that these insects seek protein and mineral salts at concentrations matching those found in the tissues of conspecifics. Cannibalistic interactions trigger a push-pull mechanism in which individuals move to reduce their own risk of being bitten while pursuing animals ahead for a potential meal. This behavior results in an autocatalytic marching activity whereby millions of individuals align and move in large cohesive bands (17). Protein satiation reduces the locomotion and cannibalistic tendency of locusts (6) and crickets (130) and in this way ultimately slows mass movements. In these animals, depletion of specific nutrients thus mediates complex collective dynamics through the synchronization of the nutritional states and behavior of individuals.

### Collective Foraging Decisions

Gregarious foragers often make collective decisions during which most or all group members choose to eat from one food source among several available alternatives (74). In the nomadic forest tent caterpillar (*Malacosoma disstria*), for instance, colony members travel en masse along pheromone trails in search of fresh leaves. Small variations in their nutritional state have critical consequences for the outcome of the collective foraging decisions. Individual caterpillars fed a protein-deficient diet tend to take shorter and more frequent meals, which increases their propensity for exploration (32). Consequently, colonies are more likely to abandon a food source and explore novel areas if that food source contains little protein (92). Manipulation of the nutritional state of caterpillars showed that the most protein-deficient individuals in a colony tend to initiate the collective departure and lead the trail toward new feeding sites, whereas protein-satiated individuals tend to follow (93). Variations in nutritional state among caterpillars thus regulate the emergence of temporary roles, which is essential for colonies to probe multiple food sources and make efficient collective decisions (74).

### Colony-Level Nutrition

In eusocial insects characterized by a division of labor (ants, some bees and wasps, and termites), nutritional homeostasis is achieved collectively through the coordinated action of colony members

taking different roles in the assessment, collection, processing, and storage of foods (70). Foragers need to satisfy their own nutritional requirements, principally for carbohydrates as a source of energy, in addition to the needs of other colony members, including the growing larvae and the reproductive females, which have high protein requirements. Foragers solve this challenge by adjusting their nutrient collection at the colony level, optimizing colony growth and survival (23, 35, 49). In the green-head ant, *Rhytidoponera metallica*, the foragers are indirectly informed about the colony's nutritional state by the larvae (49). If ants are constrained to an imbalanced diet that is higher than optimal in protein relative to carbohydrate, the excess protein not consumed by the colony is deposited outside the nest as "pelleted discard," the presence of which influences future decisions of foragers (49). Therefore, in addition to being a nutrient-balancing superorganism at the level of food collection, the colony is also a collective nutrient-processing, storage, and waste disposal system.

### Reproductive Division of Labor

In addition to mediating a range of collective-level behaviors, nutrition influences the structure of social groups by affecting reproductive skews, in which only a subset of individuals reproduce (breeders) while others provide alloparental care to the brood (helpers). Cooperatively breeding spiders of the genus *Stegodyphus* form colonies of several hundred individuals in which less than half of the females reproduce (89). These spiders share large webs and occasionally feed on the same prey items, thus setting the stage for intense competition. The largest females tend to win contest competitions and monopolize limited nutritional resources required for growth and reproduction (148). Experimental manipulations of prey nutritional composition given to *S. dumicola* colonies showed that the amount of lipid available in the food is positively correlated with the number of reproductive females in the colony, thus suggesting a direct effect of nutrient limitation on reproductive skews in species with a flexible social structure (121). Variation in access to nutrients also has critical consequences for the reproductive division of labor in eusocial insects, such as the western honey bee (*Apis mellifera*), in which differential nourishment of larvae by the workers induces modifications of gene expression that channel the development of females into future reproductive queens or sterile workers (77).

## THE GEOMETRY OF TROPHIC INTERACTIONS

Beyond plant-herbivore interactions, sociality, and the ecosystem within the organism, nutrition fundamentally shapes trophic interactions within food webs and, hence, shapes species assemblages and ecosystems (11, 43, 114, 126). Given that animals have regulatory mechanisms for nutrient intake and utilization (114, 115, 126), data on the multidimensional nutritional requirements of animals at different trophic levels and on the nutrient content of available food may help predict trophic interactions and their potential consequences for community and ecosystem dynamics (8, 78, 94, 128).

### Food Chain Length

Food chain length is one attribute of food webs that may be influenced by nutrient-based diet choice (62, 53, 114, 151). Why food chains are relatively short and constant in length has been a subject of research and debate for decades (105, 122). Food chain length is determined by the sequential number of predators, because all food webs have one primary producer and one herbivore level (that may be populated by a diversity of species) (106). Hence, prey choice by

predators (i.e., whether they choose to feed on prey at higher versus lower trophic levels) is an important determinant of food chain length (62, 106, 114). The trophic level of prey on which predators feed can be influenced by the nutrient requirements of predators relative to the nutrient content of prey at different trophic levels (44, 114, 126).

The balance of nutrients consumed by predators can have large effects on their growth, survival, and reproduction, and at least some predators balance their macronutrient intake to maximize fitness (5, 75, 76, 91, 150). In one of the most extensive quantitative studies of how nutrient intake affects fitness of a predator, Jensen et al. (75) showed that the lipid-to-protein ratio at which ground beetles (*Anchomenus dorsalis*) maximized egg production was 0.8:1 on an energy basis. When given a choice among diets, beetles regulated their intake to approach this same ratio (75). In other studies of predatory arthropods, increasing intake of another nonprotein source of energy, carbohydrates, increased growth, survival, and reproduction of a wide range of species (73, 142). Moreover, many predatory arthropods, including spiders, seek sources of carbohydrates (73, 142). In parallel to the research on arthropods, research on vertebrate predators has uncovered the importance of nonprotein energy, especially lipid, for predator diet regulation and population dynamics in nature (68, 90, 138). Hence, whereas the dietary requirements of predators have long been assumed to be strongly protein biased, growing evidence suggests that nonprotein energy (i.e., lipid and carbohydrates) may be an important component in the diets of predators and one that is actively regulated (44, 52, 53, 114, 150).

Carbohydrates are available at higher concentrations at lower trophic levels, but it was not until the work of Fagan, Denno, and colleagues (44, 52, 53) that data were available on how the nutrient composition of arthropods changes with trophic position. They found that predatory arthropods had higher concentrations of nitrogen and lower ratios of carbon to nitrogen than herbivorous arthropods (44, 52, 53). More recently, an experimental study (110) and a survey of the macronutrient content of arthropods at different trophic levels (151) confirmed that these differences in elemental content reflect differences in macronutrients. Predatory arthropods had relatively higher concentrations of protein and lower concentrations of lipid in their bodies than herbivorous arthropods (151). Given that predators require significant amounts of nonprotein energy in their diet and that nonprotein energy is found in higher concentrations at lower trophic levels (e.g., carbohydrates in plants and higher lipid content in herbivorous arthropods), there may be selection for predators to feed at lower trophic levels to balance their diet. If predators selectively feed at lower trophic levels to balance their diet, then this diet choice may maintain a relatively short overall food chain length (114, 151).

The combination of significant nonprotein energy requirements of predators and higher concentrations of nonprotein energy at lower trophic levels (53, 75, 151), coupled with an ability by predators to regulate their intake and utilization of macronutrients (5, 75, 76, 91, 110, 149), provides the basis for explaining limited food chain length. Further work, including mesocosm experiments and agent-based models (128), are needed to test the relative importance and strength of nutrient-based diet choice for regulating food chain length relative to other important factors, e.g., productivity, disturbance, and ecosystem size (105).

## Community and Ecosystem Dynamics

Recent examples indicate that taking a nutritionally and organismally explicit (sensu 114) approach to nutritional ecology has provided scientists with a new understanding of community and ecosystem dynamics. For example, the success of invasive ants, their high population densities, and dominance was due at least in part to greater access to mutualist partners and their carbohydrate-rich exudates in the introduced ranges (71, 66, 150). Further, degradation of Eurasian grasslands

by livestock grazing has been linked to increased outbreaks of the locust *Oedaleus asiaticus* because grasses in these highly grazed areas are more closely matched to the low-protein, high-carbohydrate requirements of this locust species (19). In old-field communities, perceived risk of predation from spiders can alter grasshopper macronutrient requirements, with resulting effects on plant community composition and nutrient cycling (63–65). Additional studies using nutrition to connect the dietary requirements of animals with the distribution of nutrients among food items are likely to provide further insight into the mechanisms responsible for large-scale patterns in ecology.

## CONCLUSIONS AND FUTURE DIRECTIONS

In this review we have highlighted four areas in which nutrition shapes the relationships between organisms: between plants and herbivores, between hosts and their microbiota, between individuals within groups and societies, and between species within food webs. We have also shown that taking an explicitly multidimensional view of nutrition and employing the logic of GF provides novel insights and offers a means of integration across different levels of organization, from individuals to ecosystems.

The ability of herbivorous chewing insects to supply their requirements for nutrients is a product of their arsenal of regulatory mechanisms, both behavioral and physiological. Recent work has begun to show that insect herbivores are remarkably effective at achieving a balanced complement of nutrients from plants, even using temperature selection and drinking to adjust the rates and ratios of nutrients obtained from a single plant species. When such behavioral flexibility is added to physiological and developmental plasticity, for example differential release of digestive enzymes and structural changes in the morphology of the gastrointestinal tract, it becomes clear that terms such as good-quality or poor-quality plants do not capture the richness or dynamic nature of nutrient acquisition by herbivores from plants.

A corollary is that efforts to define plant quality by assessing the chemical composition of plant tissues alone may be misleading. At first sight, herbivore performance landscapes derived from studies using synthetic diets, such as shown in **Figure 1**, appear to bear little resemblance to the composition of real plants. However, when the rates and ratios of nutrients actually gained by the insect when eating plants are measured, there is close concordance with predictions for behavior and performance derived from synthetic diet studies.

Studies on social arthropods have highlighted the role of nutrition as a potential organizer of social life across levels of social complexity and taxonomic groups. A promising approach to explore in greater detail how nutritional interactions among individuals mediate collective-level phenomena is to combine manipulative experiments with simulations of individual-based models implementing the concepts of GF (87). This approach, inspired from collective animal behavior studies (39, 136), will provide unprecedented opportunities to build and validate a mechanistic understanding, based on novel empirically testable predictions, of the nutritional factors that cause social behavior. For instance, several authors have suggested that nutritional factors (such as a deficit of specific nutrients) have favored the evolution of eusociality by triggering variation in the reproductive physiology of individuals and encouraging cooperation for finding and processing foods (36, 72, 98, 147). Individual-based models could also be expanded with evolutionary algorithms to test specific scenarios about how the nutritional environment may drive the series of steps that lead to groups with increasing organizational complexity by acting on the behaviors and fitness of individuals. Such models could be used to test how nutrient availability influences multilevel selection, and whether these mechanisms can lead to classical models of social evolution, such as the subsocial (family) and parasocial (gregarious) paths to eusociality (70, 95). Such

modeling should be undertaken in conjunction with experimental analysis of taxa with different degrees of social organization.

Insects provide useful models to improve our understanding of the functioning of the gut microecosystem and its effects on immune function, metabolism, health, and disease (22, 51). The challenge has been to interpret the complex network of influences and dependencies involved (Figure 3). Studies using insects have demonstrated that GF offers a means to unravel this network of interactions. Such work is still in its relative infancy, but it is becoming apparent that the insect host is far from a passive participant, as shown by the capability of hosts to self-medicate by adjusting food choices and diet composition.

Finally, we have presented recent evidence suggesting that GF can also provide novel insights into the interactions between species within ecosystems, including the structuring of foods webs, regulation of food chain length, flow of nutrients through ecosystems, and community and ecosystem dynamics.

## DISCLOSURE STATEMENT

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- 111. First investigation of the interactive effects of P:C ratios and amounts on insect performance.**

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125. First investigation of the interactive effects of P:C ratios and amounts on insect performance.

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128. A framework to scale nutrient interactions from individuals to communities.

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