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Review

# A bioenergetic framework for aboveground terrestrial food webs

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**Bioenergetic approaches have been greatly influential for understanding community functioning and stability and predicting effects of environmental changes on biodiversity. These approaches use allometric relationships to establish species' trophic interactions and consumption rates and have been successfully applied to aquatic ecosystems. Terrestrial ecosystems, where body mass is less predictive of plant–consumer interactions, present inherent challenges that these models have yet to meet. Here, we discuss the processes governing terrestrial plant–consumer interactions and develop a bioenergetic framework integrating those processes. Our framework integrates bioenergetics specific to terrestrial plants and their consumers within a food web approach while also considering mutualistic interactions. Such a framework is poised to advance our understanding of terrestrial food webs and to predict their responses to environmental changes.**

## Highlights

Bioenergetic food web approaches have fueled a major body of ecological research, but their use of body size for inferring trophic interactions and consumption rates is not sufficient for terrestrial systems.

Terrestrial plants exhibit large variation in tissue growth and turnover not included in bioenergetic models, and their biotic interactions are driven by defenses, different chemical composition of their tissues, and herbivory on different tissues.

Plant growth rate represents a key axis of variation for plant biotic interactions, from fast with low investment in storage and defense to slow with high investment in storage and defense.

Incorporating the continuum of plant growth strategies can serve as a fulcrum for a new bioenergetic food web approach that predicts the network structure and stability of terrestrial food webs and their biodiversity–ecosystem functioning relationships.

## Ecology needs a terrestrial bioenergetic approach

**Bioenergetic food web approaches** (see Glossary) [1,2] have fueled an industry of ecological research [3–10]. However, the inherent focus on body size has resulted in an approach less suitable for exploring empirical patterns in terrestrial systems [11,12], especially plant–consumer (herbivore, mutualist) interactions, which are often determined by factors other than body size [3,10,12]. With the increased use of bioenergetic approaches to understand complex outcomes of global change [4,6,7,9,13], there is increasing need for a holistic bioenergetic framework that addresses the challenges introduced in terrestrial aboveground ecosystems. Here, we review previous efforts to capture the mechanistic processes governing aboveground plant–consumer interactions, and develop a conceptual and mathematical guide for integrating these processes into a framework that is established on bioenergetic constraints.

Terrestrial plant–consumer interactions are mostly determined by traits external to body mass – a problematic characteristic to apply to many plant species – such as phytochemistry [14–16] and morphology of physical structures such as flowers [17–19]. These characteristics, rather than body size, matter most to consumers that range from leaf galling arthropods to large grazing mammals, as well as mutualists consuming floral rewards and fruits [20]. Terrestrial plants also exhibit large variation in tissue growth and turnover to build structures that not only attract and repel herbivores and mutualists [21] but also serve to fight gravity in a race for space and light, relationships that defy traditional bioenergetic approaches. Consequently, our understanding of community stability and ecosystem functioning that is obtained through the use of bioenergetic models is biased toward aquatic systems, where trophic interactions and consumption rates tend to scale with organismal body mass [10,12]. Additionally, food web theory has traditionally emphasized the consumer perspective, reflected in, for example, the greater detail in the

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functional responses of consumers than in those of primary producers or the focus on consumer adaptive foraging rather than the adaptive response of resources against consumption [22]. These emphases have resulted in overly simplistic models of plant growth and the trait-mediated responses of plants to herbivore attack [1,5,6], potentially biasing our understanding of food web dynamics from the bottom up.

This complexity of aboveground terrestrial plant–consumer interactions requires a deeper consideration of their unique processes giving rise to communities. We review the **bioenergetics** of plant–animal interactions and discuss extensions to traditional food web frameworks. These extensions integrate recent advances in network analyses, bioenergetics, and the biological mechanisms underlying interactions between plants, their consumers, and mutualists, from which a more holistic perspective of aboveground ecological interactions can be explored and assessed.

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## Terrestrial bioenergetic framework

The dimensional reduction offered by **allometric scaling** has a rich history in ecology, but harnessing it to analyze species interactions was not seriously attempted until the seminal bioenergetic model by Yodzis and Innes [1]. This framework was expanded to communities of interacting species with the Allometric Trophic Network (ATN) model [2,13] (Box 1), which models food web dynamics with a minimal number of parameters, namely the body sizes of the consumer and resource species and a handful of allometric constants [5,6,23,24]. This model has demonstrated particular success with respect to aquatic systems, where the presence or absence of trophic interactions and rates of consumption are assumed to scale allometrically (Box 1 and Figure 1), largely due to the gape limitations that constrain so many aquatic consumer interactions [10,12,25].

A central principle of the perspective we propose (Figure 1) is that plant species can be organized along a **fast–slow growth axis** [26–28], determining plant mass–specific metabolic rates and ultimately the flow of energy from primary production to higher trophic levels via consumption. Fast-growing plants invest in photosynthetic machinery at the expense of defenses and structural tissue [29], which itself is defensive because it is difficult to digest. Because of these investments, fast-growing plants tend to be leafier, more nutritious for consumers (lower C:N,P ratios and higher tissue digestibility), and less resistant but more tolerant to herbivory. This increased **tolerance** arises both because their ability to grow quickly allows them to quickly replace lost tissue and because their lack of investment in structure and defenses lowers the per-unit cost of their tissue [29]. Slow-growing plants, by contrast, invest more heavily in structure and defenses that promote the longevity of their tissues and therefore tend to be larger, woodier, less nutritious for consumers, and more resistant but less tolerant of herbivory. This lack of tolerance arises because each bite of tissue is more valuable and costlier to replace [26–28,30]. A fast–slow plant axis thus affects key parameters governing food web dynamics, including the ingestion ($f_{ji}$) and assimilation ($e_{ji}$) of plant $i$'s biomass by herbivore $j$, foraging effort ($p_{ji}$), attack rate ($a_{ji}$), and handling time ($h_{ji}$) (Box 1) [14–16,31].

## Plant structural complexity

Plants have evolved different tissue types to address their simultaneous needs to acquire water and nutrients, photosynthesize, and reproduce [32], and diverse guilds of herbivores have in turn evolved to consume and at times specialize on them (Figure 2). These tissues include leaves, stems, wood, roots, underground storage organs, seeds, nectar, pollen, and sap/phloem, all of which vary in terms of plant investment, nutritional value, and the cost (or benefit) to the plant if the tissue is consumed [32] (Figure 2). These differences influence both the biomass available to

## Box 1. ATN model

The ATN model consists of two sets of governing equations [2,13], one for primary producers (Equation I) and another for consumers (Equation II):

$$\frac{dB_i}{dt} = \overbrace{r_i B_i D_i(\boldsymbol{B})}^{\text{Autotrophic growth gain}} - \overbrace{x_i B_i}^{\text{Maintenance loss}} - \overbrace{\sum_j \frac{1}{f_{ji} e_{ji}} x_j y_j B_j F_{ji}(\boldsymbol{B})}^{\text{Herbivory loss}} \quad [\text{I}]$$

$$\frac{dB_j}{dt} = \overbrace{x_j B_j \sum_k y_j F_{ji}(\boldsymbol{B})}^{\text{Resources consumption gain}} - \overbrace{x_j B_j}^{\text{Maintenance loss}} - \overbrace{\sum_k \frac{1}{f_{kj} e_{kj}} x_k y_k B_k F_{kj}(\boldsymbol{B})}^{\text{Predation loss}} \quad [\text{II}]$$

where $\boldsymbol{B}$ is vector of biomasses for every species in the food web and $B_i$ is biomass of species $i$. $B_i$ of producer species $i$ changes over time according to the balance between gains from autotrophic growth and losses due to metabolic maintenance and herbivory by consumer species $j$. Autotrophic growth is determined by the producer's intrinsic growth rate ($r_i$), metabolic rate ($x_i$), and logistic growth: $D_i(B) = 1 - (\sum_{i=\text{producers}} B_i)/K$, with $K$ as carrying capacity of all primary producers. Biomass loss to herbivory increases with mass-specific metabolic rate ($x_j$) and maximum consumption rate ($y_j$) of consumer species $j$, and decreases with ingestion ($f_{ji}$) and assimilation ($e_{ji}$) efficiencies by consumer $j$ on producer $i$. $B_j$ of consumer species $j$ (Equation II) changes over time according to the balance between biomass gains by resource consumption and biomass loss from metabolic maintenance and predation. Functional response $F_{ji}(\boldsymbol{B})$ determines the consumption rate of each consumer species $j$ on each resource species $i$, defined as follows:

$$F_{ji}(\boldsymbol{B}) = \frac{p_{ji}(\boldsymbol{B}) a_{ji} h_{ji} B_i^q}{1 + c_j B_j + \sum_{i=\text{resources}} p_{ji}(\boldsymbol{B}) a_{ji} h_{ji} B_i^q} \quad [\text{III}]$$

where $p_{ji}(\boldsymbol{B})$, $a_{ji}$, and $h_{ji}$ are, respectively, the foraging effort, attack rate, and handling time of consumer $j$ on resource $i$, $c_j$ is the intraspecific foraging interference of consumer $j$, and $q$ controls the shape of Equation III.

Parameters in Equations I–III are constrained by average body masses of individuals of the consumer ($M_j$) and resource species ($M_i$), as:

$$r_i = \frac{R_i}{R_{ref}} = \left(\frac{M_i}{M_{ref}}\right)^{-0.25} \quad x_i = \frac{X_i}{R_{ref}} = \frac{a_x}{a_r}\left(\frac{M_i}{M_{ref}}\right)^{-0.25} \quad y_j = \frac{Y_j}{X_j} = \frac{a_y}{a_x}$$
$$a_{ji} = a_0 M_j^{0.25} M_i^{0.25} L_{ji} \quad h_{ji} = \frac{e_{ji}}{a_y} M_j^{0.25} \quad [\text{IV}]$$

where $a_0$, $a_r$, $a_x$, and $a_y$ are allometric constants specific to species' metabolic categories (producer, invertebrate, ectotherm vertebrate, or endotherm vertebrate) and $L_{ji}$ quantifies potential feeding efficiency, given the energetically optimum body size ratio. Subscript *ref* denotes the reference producer species, the smallest in the system. Primary production ($R_i$), metabolism ($X_j$), and maximum consumption ($Y_j$) in Equation IV follow negative power laws with each species' average body mass as: $R_i = a_r M_i^{-0.25}$, $X_i = a_x M_i^{-0.25}$, $Y_j = a_j M_i^{-0.25}$. We propose to consider plant growth traits ($T_i$) on a 'fast–slow' axis to determine parameters ($R_i$), ($X_i$), which then can be used with animal body mass to calculate ($a_{ji}$), ($e_{ji}$), ($f_{ji}$), ($h_{ji}$), and ($p_{ji}$) (see Figure 1 and see Appendix S1 in the supplemental information online).

herbivores and the effect of biomass loss on plant maintenance, growth, and reproduction [14–16,31]. Plant growth is indeterminate, such that their allocation to different organs or tissues are often plastic in response to both internal and external factors [32]. Internal factors include life stages and phenology [33], whether the plant has a fast or slow growth strategy [27,28], and how resistant or tolerant the plant is to herbivory [30,34]. By contrast, external factors include the effects of environmental pressures (e.g., temperature, water, nutrient availability [35,36]), competition with other plants [37], and herbivory [38]. For example, in resource-poor environments, plants may exhibit slower growth rates, altering energetic allocation to different organs [32] in response to the total energy available to the ecosystem. As a result, profiles of organ proportions differ across environments or seasons [39,40], potentially driving substantial changes in the herbivore community [31].

## Glossary

**Allometric Diet Breadth Model:** a topological model for food webs in which species are ordered along an axis by their body size. Consumers can potentially forage on all species within an allometrically optimal range of body sizes that allows maximum energy intake, given the constraints of handling time. As a result, consumers tend to feed on species smaller than themselves, and larger consumers tend to have larger feeding ranges.

**Allometric scaling:** body mass–dependent relationships with respect to anatomical, physiological, and/or ecological characteristics that often follow power laws.

**Bioenergetic food web approach:** approach that bridges the perspectives of metabolic ecology and food web ecology by using allometric relationships to establish rate laws governing population dynamics and the structure of species interactions.

**Bioenergetics:** the set of rate laws governing the direction and flow of energy/biomass from one biological compartment to another in a web of interactions among biological entities.

**Fast–slow growth axis:** a plant trait axis that can be used to estimate plant–consumer interactions and their bioenergetic rates. 'Fast' plants tend to grow and reproduce quickly, invest more in leaves, and be more tolerant and less resistant to herbivory. 'Slow' plants tend toward the opposite characteristics, investing more in structure and defense.

**Phytochemicals:** plant compounds thought to function primarily in interactions with the biotic and/or abiotic environment instead of basic metabolic processes.

**Resistance:** ability to prevent or reduce herbivory.

**Tolerance:** ability to maintain fitness despite damage from herbivores.

**Topology:** network structure composed of nodes representing species and links representing interactions between species.

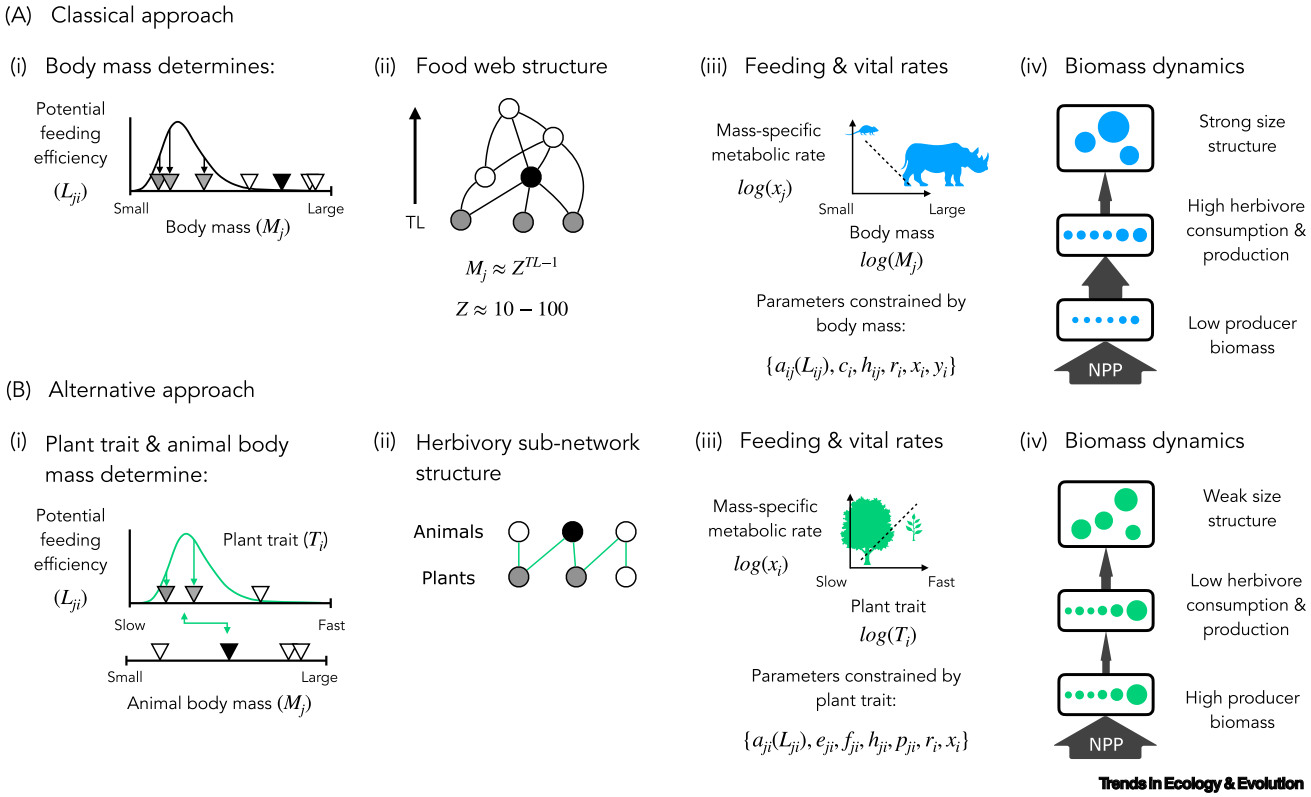


Figure 1. Terrestrial alternative to bioenergetic models. (A) The classical approach determines food web structure and dynamics from allometric patterns based on each species' average adult body mass ($M_j$) and metabolic class (Box 1). (i) Species' potential feeding efficiency $L_{ji}$ depends on their body mass relative to their resources. Consumers can feed on resources within a range of sizes around an energetically optimum body mass ratio. (ii) This enforces strong size structure with producers (trophic level [$TL$] = 1) of similar size and consumers approximately $Z$ = 10–100× larger than their resources. (iii) Growth and consumption rates are also calculated from body masses, allowing (iv) high consumption and production by herbivores typical of aquatic ecosystems. (B) Our framework uses plant traits ($T_i$) representing the 'fast–slow' axis to determine the structure and dynamics of herbivory interactions. Fast-growing plants are smaller, leafier, with more palatable leaves, whereas slow-growing plants are larger, woodier, with less nutritious and more defended leaves. (i) Animals' potential feeding efficiency $L_{ji}$ on plants depends on the match between their body mass for a given metabolic class and $T_i$. (ii) This creates herbivory subnetworks with weaker size structure. (iii) Plant growth ($r_i$, $x_i$) and herbivory [$a_{ji}(L_{ji})$, $e_{ji}$, $f_{ji}$, $h_{ji}$, $p_{ji}$] can also be calculated using plant traits. (iv) Allowing variation in plant size and stoichiometry breaks the dependence of herbivore attack rate on consumer/resource body size ratio. This results in lower herbivore consumption and production than aquatic ecosystems with similar net primary productivity (NPP) due to less nutritious and more defended plant tissues.

The effects of plant structural complexity can be integrated into a bioenergetic food web framework by incorporating the chemical and physical constraints governing the interactions between herbivores and particular plant tissues (Figure 2A). This can be accomplished using either fixed (Figure 2B) or dynamic (Figure 2C) pool approaches. The fixed pool approach assumes the plant biomass is composed of fixed fractions of each tissue, with herbivore groups limited to feeding on that fraction of biomass. Alternative tissues vary in their nutrient composition and thus provide different yields to herbivores. This fixed pool approach incorporates the topological complexity of different animal guilds feeding on different plant tissues without increasing the complexity of dynamic models. By contrast, the dynamic pool approach allows dynamic allocations to growth and maintenance for each tissue [21,41,42] at the cost of additional model complexity. Dynamic pools allow feedback between consumption and production of each tissue, such that adaptive foraging behaviors among herbivores [22,41–43] – in response to the relative availability, cost, and benefit from different tissues – may promote coexistence even when diets are similar.

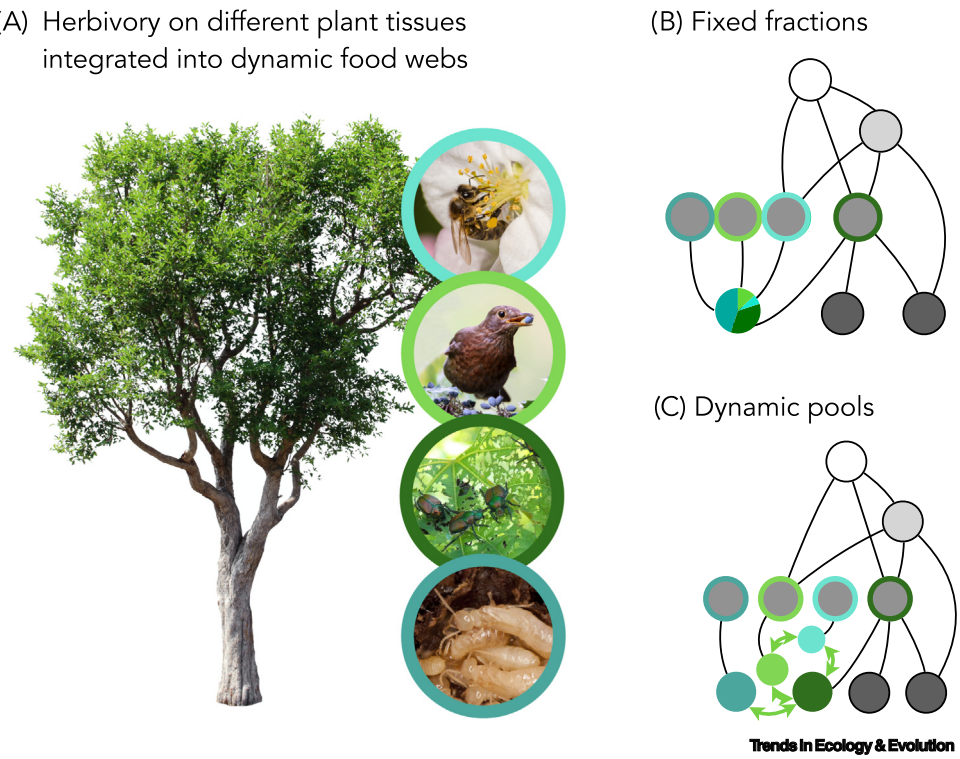


Figure 2. Approaches to herbivory in aboveground terrestrial food webs. (A) The structural complexity of terrestrial plants supports many groups of herbivores feeding on different plant tissues, including (photos from top to bottom): nectar and pollen, fruits and seeds, leaves, and bark and wood. Plant and herbivore growth and reproduction strongly depend on these different trophic interactions, which indirectly affect the full food web dynamics. Despite the importance of these different interactions, the traditional approach to food webs has focused only on antagonistic herbivory (e.g., folivory), excluding 'mutualistic' feeding by pollinators and seed dispersers. We propose two new approaches to incorporate the network complexity of different animal guilds feeding on different plant tissues by assuming plant biomass as (B) composed of fixed fractions of each tissue, with herbivore groups limited to feeding on a specific fraction, and (C) partitioned into coupled pools, allowing dynamic plant allocations to growth or maintenance for each tissue, feedbacks between consumption and production of each tissue, and herbivore adaptive foraging. In both approaches, the structure of herbivory interactions on different plant tissues can be derived from the matching between plant and animal traits (Figure 1). Illustrative food webs show grayscale nodes lighter in color with increasing trophic level. Colored nodes indicate different plant tissues matching the photo borders for different types of herbivory. Links represent bioenergetic couplings due to feeding (gray) or dynamic feedbacks between the production and maintenance of different tissues (green).

## Herbivore ingestion and assimilation of plant biomass

The proportion of plant biomass ($B_i$) available for consumption by herbivores (i.e., the fraction ingested, $B_i/f_{ji}$; see Box 1) is constrained by plant and herbivore traits. Indeed, much plant-herbivore research (especially for insects) examines how plant defenses, including the vast diversity of **phytochemicals** and physical traits such as toughness and spinescence, influence $f_{ji}$, and rates of herbivory in general. We review literature on constitutive and inducible defenses in Box 2 and propose to integrate those defenses in our framework as affecting herbivores' consumption parameters ($a_{ji}$, $e_{ji}$, $f_{ji}$, $h_{ji}$, $p_{ji}$) (Boxes 1 and 2). For ground-based mammals (e.g., ungulates), the proportion of plant biomass available will also depend on the relative height of the plant and the herbivore, because these herbivores can only access tissue within a vertical range roughly spanning ground level to shoulder height [44]. While plant height might place a physical limit on access, these mammals tend to partition their diets across a relatively low-dimensional plant trait axis correlating with nutritional quality [45]. Key to understanding plant–herbivore interactions is that not all green tissue is equally available – physically or biochemically – to herbivores.

Box 2. Plant defense

Plant defenses are organized in two major categories: constitutive and inducible [59]. Constitutive defenses are always expressed and more common in environments where herbivore pressure is consistently high and with low resource availability, in which it is challenging to replace lost tissue. Inducible defenses develop in response to environmental cues or to herbivory, with plants responding to chemical cues [91]. For example, when many species in the pine family (Pinaceae) are attacked by herbivores, they induce production of resin and phenolic compounds that resist herbivores, and these induced responses are stronger in faster-growing, low-latitude, and low-elevation species than in the slower-growing species found at higher latitudes and elevations [92]. These responses can be transgenerational [93] but commonly happen throughout the lifespan of an individual, even at the scale of hours [94]. We propose to include both types of defenses as affecting herbivores' consumption parameters ($a_{ji}$, $h_{ji}$, $e_{ji}$, $p_{ji}$) (see Box 1). For instance, high levels of defenses are expected to decrease $e_{ji}$ (section 3) and $p_{ji}$ (section 4), whereas inducible responses should strongly determine plant adaptive response $v_{ij}$ (Box 3), especially for fast-growing plants.

There are two main defensive pathways for plant inducible defenses: the jasmonic acid pathway, which responds to chewers, such as caterpillars, and the salicylic acid pathway, which responds to pathogens and sucking insects, such as aphids [14]. For example, many milkweeds (*Asclepias* spp.) increase production of toxic cardenolides and exudation of sticky latex in response to feeding by monarch caterpillars (*Danaus plexippus*), which can reduce monarch survival and performance [15]. Research shows clear constraints in some plant species to induction of defenses between these two pathways [14]. When a chewing herbivore attacks, the jasmonic acid pathway is upregulated, and the plant suppresses the salicylic acid pathway, so it becomes more susceptible to the attack of phloem suckers or pathogens.

Plant chemical receptors and metabolic pathways responding to chemical cues are so sophisticated that they can even sense an insect walking on them before biting [95]. For trees or highly sectorial plants (e.g., shrubs), localized responses can lead individuals to be defensive mosaics, which are likely adaptive in the face of heterogeneous herbivore attack [96,97]. Communication via volatiles or belowground mycorrhizal connections can lead plant responses to herbivore attack to include large patches of plants [91]. Plants change their odors when attacked, and neighboring plants can respond in a process of plant–plant communication or eavesdropping [91].

Once plant biomass is ingested, plant–consumer interactions are constrained by the efficiency with which herbivores can transform ingested food into new biomass. That is, the assimilation efficiency ($e_{ji}$ in Equation I in Box 1). This efficiency can be expressed as yield from the perspective of bulk requirements of consumer–resource interactions [46]. The consumer yield (grams of consumer produced per grams of resource consumed) is given by $Y_{ji} = M_j E_{D_i} / E_{L_j}$, where $M_j$ is the body mass of consumer $j$ (g), $E_{D_i}$ is the energy density of resource $i$ (joules/g), and $E_{L_j}$ represents the lifetime energetic requirements of a consumer $j$ that reaches maturity (joules). The resource removed by the consumer is then proportional to the efficiency $e_{ji} = \frac{d_{ji} B_i}{Y_{ji}}$, where $d_{ji}$ is the proportion of digested plant biomass, which must be a function of both plant biochemistry and the herbivore's digestive abilities (see Box 2 and Appendix S1 in the online supplemental information). Herbivores exhibit species-specific behaviors designed to optimize $e_{ji}$ within particular communities and habitats [47], the result of unique evolutionary trajectories driven by local fitness gradients [48].

## Adaptive behavior of plants and herbivores

Both consumers and resources interact dynamically, adapting the energy allocated to searching for and consuming, attracting, and/or defending against those species with which they interact. Following [22], we define adaptive behavior as the fitness-enhancing changes in individuals' feeding-related traits due to variation in their trophic environment. This includes adaptive foraging of consumers, as well as the adaptive responses of resources, which we define as changes in resource behavior and other traits in response to consumer pressure and environmental cues. Box 3 details a method by which herbivore adaptive foraging and plant adaptive responses can be introduced into a comprehensive bioenergetic ATN framework.

Herbivores adaptively forage in a multiscale manner [49] by first searching the landscape for a promising foraging habitat and then locating particular plant individuals using multiple sensory

### Box 3. Adding plant-herbivore adaptive behavior to our bioenergetic framework

Herbivore adaptive foraging and plant defenses can be incorporated into the functional response of the ATN model (Equation III of Box 1) as follows:

$$F_{ji}(\boldsymbol{B}) = \frac{p_{ji}(\boldsymbol{B})(1-v_{ij})a_{ji}h_{ji}B_i^q}{1 + c_jB_j + \sum_{l=resources} p_{jl}(\boldsymbol{B})(1-v_{lj})a_{jl}h_{jl}B_l^q} \quad [I]$$

where $p_{ji}$ is the foraging effort consumer $j$ assigns to resource $i$ and $v_{ij}$ is the antipredator effort resource $i$ assigns against consumer $j$, respectively. Note that in some versions of the ATN (e.g., [2]), $p_{ji} = \omega_{ji}$ denoting fixed consumer preference (unitless), whereas here it denotes variable foraging effort (also unitless [13]). These efforts define the fraction of individuals' energy or time allocated to consuming a particular resource species and avoiding a particular consumer species, respectively [22]. The higher the foraging effort invested in a particular resource, the higher the capture efficiency is of that resource and the larger Equation I is. The higher the antipredator effort of a resource against a consumer, the lower the capture efficiency of that consumer and the smaller Equation I is. Adaptive foraging and inducible defenses are incorporated into Equation I by allowing $p_{ji}$ and $v_{jk}$, respectively, to adapt over time:

$$\frac{dp_{ji}}{dt} = s_j\left(\frac{\partial G_j}{\partial p_{ji}} - \gamma_j\right) \quad [II]$$

$$\frac{dv_{jk}}{dt} = s'_j\left(\frac{\partial G_j}{\partial v_{jk}} - \gamma_j\right) \quad [III]$$

Parameters $s_j$ and $s'_j$ are the rates by which species $j$ changes its foraging and antipredator efforts, respectively. Function $G_j = \frac{1}{B_j}\frac{dB_j}{dt}$ is $j$'s per-capita (per-biomass in this case) growth rate. If $s_j < 1$ or $s'_j < 1$, changes in foraging and antipredator efforts are slower than population dynamics, and the shift of strategies reflects evolutionary changes, whereas $s_j > 1$ or $s'_j > 1$ represents faster changes acquired through behavioral responses [98]. These efforts increase when they increase the per-biomass growth rate more than the average per-biomass growth rate obtained from assigning the effort to other consumers or resources, $\gamma_j$, defined as follows:

$$\gamma_j = \sum_{l\ \epsilon\ resources} p_{jl}\frac{\partial G_j}{\partial p_{jl}} + \sum_{k\ \epsilon\ consumers} v_{jk}\frac{\partial G_j}{\partial v_{jk}} \quad [IV]$$

If a species only adaptively forages, then $v_{jk} = 0$, Equation III is zero, and $\gamma_j$ in Equation II will only contain the first sum of Equation IV. If a species only adaptively defends, then $p_{ji} = 0$, Equation II is zero, and $\gamma_j$ in Equation III only contains the second sum. Optimization of Equations II and III is constrained by allocation costs [99], representing the impossibility of individuals infinitely and simultaneously assigning energy or time to every task, expressed as follows:

$$\sum_{l\ \epsilon\ resources} p_{jl} + \sum_{k\ \epsilon\ consumers} v_{jk} = 1 \quad [V]$$

modalities [50], after which a decision to eat or keep searching is made [48]. Insects use a diverse array of cues to find their hosts, including habitat context and plant odor and color, after which many sense tissue quality and make feeding decisions using specialized chemoreceptors [49,51]. Ovipositing females also search for places to lay eggs by sensing the leaves with their ovipositor [52]. Although it is clear that herbivores respond to a complex constellation of plant traits and conditions to maximize profitability, plants demonstrate equally dynamic responses to both repel and attract their herbivores.

Chemical defenses are central to the adaptive response to herbivory by plants, with many species upregulating the production of toxins following detection of herbivore damage or other herbivore cues (Box 2). The fast–slow trait axis ($T_i$) may also affect the response to herbivory of plant species $i$ by influencing its average adaptation rate ($s'_i$) or the benefit in per-capita growth rate obtained by its response to herbivore $j$ ($\frac{\partial G_i}{\partial v_{ij}}$). Plant adaptive responses also involve mutualistic interactions in terms of attracting the enemies of their herbivores (i.e., indirect defenses) or attracting pollinators

and seed dispersers. For example, some plants respond to herbivore cues or attack by releasing volatiles that attract predators or even reward predators with nectar or pearl bodies (concentrations of protein) [53]. Other plants produce chemicals that, after being ingested by herbivores, volatilize from their feces and guide predators to them [54]. Inducible extrafloral nectaries attract ants that then remove herbivores from the plant [55]. Plants also provide predator shelters (domatia; e.g., leaf pits, swollen thorns), the production of which can be upregulated following herbivory [56]. Finally, floral rewards and fruits produced by plants to attract pollinators and seed dispersers, respectively, can also be formalized as adaptive responses. They are resource traits where investment responds directly to consumers and environmental cues, though their role is to attract rather than repel the consumer (pollinator, seed disperser) with a potentially positive effect on plant fitness [17–19].

Frequency dependence can play an important role in plant–herbivore adaptive responses. For some species of caterpillars, survival is low when they attack a plant in small groups and high when they attack in larger groups, apparently because plant responses depend on herbivore density [57]. For example, herbivores that overcome plant defenses by attacking *en masse*, such as bark beetles, often have aggregation pheromones that help them reach high local densities [58]. In other systems, negative density dependence drives dynamics. Herbivores avoid damaged plants because (i) previously attacked plants are likely to have induced **resistance** traits [59], (ii) earlier attacking herbivores are likely to have removed the best quality tissue [60], and (iii) these behaviors mitigate direct interference interactions with competing herbivores [61].

## Stage-structure dynamics

Organismal ontogeny can play a significant role in changing species' metabolic rates [62] and interactions [63], especially for plants [64]. Species can either consume or be consumed by different species as they grow and mature [65]. Integrating ontogenetic structure into aquatic food web models has had varied effects on food web dynamics, with some showing increased stability [66] due to trade-offs or emergent facilitation [67] and others showing decreased stability through ontogenetic niche shifts [65]. Terrestrial food web models integrating plant ontogeny remain scarce, though preliminary work indicates the potential for emergent facilitation in certain food web motifs at the autotroph level [68]. The relationship between plant individual growth and defenses [69] can be a way to incorporate plant ontogeny in a more comprehensive bioenergetic framework. Inducible defenses tend to be highest during seedling stages, whereas constitutive defenses take over with individual growth. In turn, this ontogenetic variability in plant defenses influences herbivores to prefer particular plant stages over others [70,71].

Ontogeny interacts with phenology to affect plant–herbivore interactions. In semelparous monocarpic plant species, unique stages are differentially available across the growing season, potentially creating distinct phenological windows of interaction between consumers that would instead be static trophic links without considering ontogeny [72]. In longer-lived, multiseason, iteroparous plants, seasonally specific growth for younger versus older stages can still open up distinct interaction but with potential cross-generational intraspecific competition. For example, high adult density limits the survival or maturation rates of younger stages by either restricted access to necessary nutrients [73] or increased exposure to soil pathogens [74].

## Structure of terrestrial networks

Our bioenergetic framework advocates for a broader definition of food web **topology** that includes both antagonistic and mutualistic trophic interactions (Figure 2). Food webs typically exclude mutualistic trophic interactions, which limits the analysis of terrestrial food web dynamics

[21]. Of the few networks available [10], many include only a subset of the local taxa, with uneven levels of taxonomic resolution, often representing the specialties of the investigators. As a consequence, plants and insects tend to be less resolved than vertebrates [75,76], potentially biasing our understanding of both structure and dynamics in these systems. Fortunately, recent advances in DNA metabarcoding from feces and stomach contents provides unprecedented opportunity to increase sampling resolution [77]. Despite these challenges, that aquatic and terrestrial food webs reveal clear differences in topological and biomass structures is well understood (Figure 1A,Biv). Aboveground terrestrial food webs have shorter food chains with more producer biomass and less herbivore biomass and consumption than aquatic food webs with similar net primary productivity, presumably due to the greater structural complexity and lower edibility of terrestrial plant tissues [11,12]. We suggest that a comprehensive bioenergetic framework that includes the unique relationships observed between plants and their consumers (including mutualists) may improve our understanding of where these differences arise.

Generative models of food web topologies [78–80] offer a powerful means by which food web bioenergetic dynamics can be explored, given the inherent difficulty of collecting food web data. These phenomenological models generate topologies with broadly similar properties compared with empirical food webs [79,80], though they typically contain too few herbivore species, too few plant–herbivore interactions, and accumulate too many trophic levels [9,80] compared with terrestrial communities. Together these differences substantially alter predicted biomass dynamics compared with empirical terrestrial topologies [9]. We predict these deviations will be magnified when the traditionally unresolved plant taxa are better resolved and when the consumption of different plant tissues is incorporated (Figure 2).

To better accommodate these deviations, we propose a terrestrial extension to a class of topological models that use an empirically measurable body size axis. These models, inspired by the **Allometric Diet Breadth Model**, specify an energetically optimal body mass ratio ($M_j/M_i$) at which animals can most efficiently feed on a resource [3,25]. Animals can feed on a range of resource sizes, but efficiency decreases away from the optimum until effectively no interaction occurs. Therefore, species' traits determine both the presence and rate of feeding interactions (Box 1). We propose that plant trait values ($T_i$) on a fast–slow axis determine the feeding efficiency of herbivores on plant tissues (Figure 1). Such a trait axis contains high dimensional information on the nutritional load and investment in defensive properties of plant leaves. Herbivores of a given metabolic class (e.g., ectotherm invertebrates, endotherm vertebrates) likely have maximum feeding efficiency on optimally matched plant traits ($M_j/T_i$) but can tolerate a range of plant traits with diminishing feeding efficiency and yield (i.e., parameters defined in Equation IV in Box 1 may depend on $T_i$; see also Appendix S1 in the supplemental information online). For example, larger-bodied herbivores can handle taller and less nutritious forage – 'slower' plants in our framework – than can smaller-bodied herbivores due to lower mass-specific metabolic needs and greater digestive capacity and efficiency [81]. Though empirical evidence connecting this pattern to herbivory network structure is sparse, some observations suggest this to be a good first hypothesis. For example, mammals of similar body sizes tend to have similar diets [82], whereas resource partitioning among African savanna grazers falls along a relatively low-dimensional plant trait axis [83]. Within a taxonomically diverse leaf-chewing community, smaller insect herbivores preferred younger, less defended, and more nutritious leaves of *Ficus wassa* than larger species [84].

Different trait axes may be appropriate for different plant tissues, allowing different subnetworks for specific types of herbivory such as nectarivory (Figure 2). Therefore, we propose generating similar subnetworks for different types of terrestrial feeding interactions using animal body size as the trait axis for carnivory and the matching of the plant trait and animal body size axes for

herbivory. These subnetworks can then be interlinked into multiplex topologies following plausible assembly rules (e.g., [21,78,79,85]).

## Community stability and ecosystem functions

The weakening and diversification of consumer–resource interactions are well known to stabilize food web dynamics [86]. We suggest that introducing a more accurate accounting of plant and herbivore communities and their associated constraints in food web structure and function will fundamentally alter the distribution of interaction strengths relative to current bioenergetic approaches. Specifically, incorporating plant defenses and herbivory on different plant tissues (as we propose in Figures 1 and 2 and Box 2) will diversify and weaken energy flows from plants to herbivores, stabilizing terrestrial food webs compared with their aquatic counterparts. Furthermore, weakening interactions will tend to reduce the strength of trophic cascades by constraining vertical energy flow through the food web [86,87]. Intriguingly, empirical evidence from terrestrial ecosystems are consistent with weak-skewed interactions [87].

A holistic terrestrial bioenergetic framework may be well positioned to advance our understanding of the relationship between biodiversity and ecosystem functioning. Current efforts have shown that diversity loss can simultaneously affect multiple ecosystem functions and services, such as primary and secondary production, pollination, pest control, and carbon sequestration [88]. A key challenge is now to understand the trade-offs and synergies among these ecosystem functions and services. The classical bioenergetic approach has been used to analyze the processes affecting primary and secondary production, as well as their trade-offs and synergies (e.g., [3,89]). A holistic terrestrial bioenergetic framework may contribute tools to analyze other important ecosystem functions and services, including pollination, seed dispersal, and biological control within plant–herbivore interactions. It may also provide important insight into the mechanisms behind the relationships among ecosystem services such as pollination and pest control, whose combined effects – either synergistic or antagonistic – remain poorly understood [90].

## Concluding remarks

Bioenergetic approaches have promoted productive research in food web ecology because of their ability to model food web dynamics by estimating demographic and consumption rates of interacting species using allometric scaling. Because of these successes, there is a great demand for a more terrestrially focused bioenergetic approach to address key fundamental and applied questions in community ecology (see Outstanding questions). By combining perspectives and approaches unique to terrestrial plant–animal interactions with traditional tools from network ecology, we outline a roadmap aimed to guide the integration of bioenergetics specific to terrestrial plants and their biotic interactions into those of traditional food web models.

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### Declaration of interests

No interests are declared.

### Supplemental information

Supplemental information associated with this article can be found online at https://doi.org/10.1016/j.tree.2022.11.004.

## Outstanding questions

Do terrestrial and aquatic food webs differ in their responses to environmental perturbations? The distributions of biomass and interaction strength across trophic levels differ between terrestrial and aquatic food webs. These two factors are known to affect food web stability and therefore may also determine how terrestrial versus aquatic food webs respond to environmental changes.

Can food webs respond to environmental change in a way that preserves ecosystem functions? Under what conditions? Bioenergetic approaches can help address this question, given their ability to estimate demographic and consumption rates based on allometric scaling as opposed to species taxonomy and to measure functions such as primary and secondary production. Our proposal of a fast–slow plant trait axis will extend this approach to study aboveground terrestrial ecosystems.

What are the effects of plant–animal mutualisms on food web responses to environmental change? Do these effects differ between terrestrial and aquatic ecosystems? Mutualisms benefiting plants may enhance the resilience and resistance of food webs against environmental change by aiding the reproduction and growth of the core production module. The effects of these mutualists may differ between aquatic and aboveground terrestrial ecosystems, given that mutualists in the latter specialize on specific plant tissues with their own intrinsic dynamics, which is not the rule in aquatic ecosystems.

Can variability in plant tissue, ontogeny, and phenology support increased diversity in plant-associated communities, especially allowing coexistence within the herbivore and mutualist guilds? How will species coexistence within those guilds change as species' phenologies shift under climate change?

How are food webs linked across spatial scales and habitat boundaries, especially between aboveground and belowground and between aquatic and terrestrial systems? How do these linkages affect ecosystem stability and function?

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