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# **A bioenergetic framework for aboveground terrestrial food webs**

Fernanda S. Valdovinos<sup>1</sup>, Kayla R.S. Hale<sup>1,2</sup>, Sabine Dritz<sup>1</sup>, Paul R. Glaum<sup>1</sup>,  
Kevin S. McCann<sup>3</sup>, Sophia M. Simon<sup>1</sup>, Elisa Thébault<sup>4</sup>, William C. Wetzel<sup>5</sup>, Kate  
L. Wootton<sup>6</sup>, Justin D. Yeakel<sup>7</sup>

1 Dept. of Environmental Science and Policy, University of California, Davis,  
CA.

2 Dept. of Ecology and Evolutionary Biology, University of Michigan, Ann  
Arbor, MI.

3 Dept. of Integrative Biology, University of Guelph, Canada.

4 Sorbonne Université, UPEC, Université Paris Cité, CNRS, IRD, INRAE Inst. of  
Ecology and Environmental Sciences of Paris, Paris, France.

5 Depts. of Integrative Biology and Entomology, Michigan State Univ., East  
Lansing, MI.

6 BioFrontiers Institute at the University of Colorado, Boulder.

7 Dept. of Life & Environmental Sciences, University of California, Merced,  
CA.

*ORCID*s: Valdovinos, <https://orcid.org/0000-0002-5270-5286>; Hale,  
<https://orcid.org/0000-0002-2627-9623>; Glaum, <https://orcid.org/0000-0002-7451-8369>; McCann, <https://orcid.org/0000-0001-6031-7913>; Dritz,  
<https://orcid.org/0000-0002-5125-919X>; Simon <https://orcid.org/0000-0002-1114-3707>; Thébault, <https://orcid.org/0000-0002-9669-5227>; Wetzel,  
<https://orcid.org/0000-0001-5390-6824>; Wootton, <https://orcid.org/0000-0002-9033-8210>; Yeakel, <https://orcid.org/0000-0002-6597-3511>

Corresponding author: Valdovinos, F. S. (fvaldovinos@ucdavis.edu)

31 **Keywords**

32 Fast-slow continuum, plant defenses, tissue-specialist herbivores, plant  
33 mutualists, consumer-resource, stage structure.

34

35 **Abstract**

36 Bioenergetic approaches have been greatly influential for understanding  
37 community functioning and stability and predicting effects of environmental  
38 changes on biodiversity. These approaches use allometric relationships to  
39 establish species' trophic interactions and consumption rates, and have been  
40 most successfully applied to aquatic ecosystems. Terrestrial ecosystems,  
41 where body mass is less predictive of plant-consumer interactions, present  
42 inherent challenges that these models have yet to meet. Here, we discuss  
43 the processes governing terrestrial plant-consumer interactions and develop  
44 a bioenergetic framework integrating those processes. Our framework  
45 integrates bioenergetics specific to terrestrial plants and their consumers  
46 within a food-web approach. It also considers mutualistic interactions,  
47 advancing understanding of terrestrial food webs and predictions of their  
48 responses to environmental changes.  
49

## 50 **Ecology needs a terrestrial bioenergetic approach**

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

64 Terrestrial plant-consumer interactions are mostly determined by traits  
65 external to body mass — a problematic characteristic to apply to many plant  
66 species — such as **phytochemistry** [14–16] and morphology of physical  
67 structures such as flowers [17–19]. These characteristics, rather than body  
68 size, matter most to consumers that range from leaf galling arthropods to  
69 large mammal grazing, as well as mutualists consuming floral rewards and  
70 fruits [20]. Terrestrial plants also exhibit large variation in tissue growth and  
71 turnover to build structures that not only attract and repel herbivores and  
72 mutualists [21], but that serve to fight gravity in a race for space and light,

73 relationships that defy traditional bioenergetic approaches. Consequently,  
74 our understanding of community stability and ecosystem functioning that is  
75 obtained through the use of bioenergetic models is by definition biased  
76 toward aquatic systems, where trophic interactions and consumption rates  
77 tend to scale with organismal body mass [10,12]. Additionally, food web  
78 theory has traditionally emphasized the consumer perspective, reflected in,  
79 for example, the greater detail in the functional responses of consumers  
80 compared to those of primary producers, or the focus on consumer adaptive  
81 foraging rather than the adaptive response of resources against consumption  
82 [22]. These emphases have resulted in over-simplistic models of plant  
83 growth and the trait-mediated responses of plants to herbivore attack  
84 [1,5,6], potentially biasing our understanding of food web dynamics from the  
85 bottom up.

86       This complexity of aboveground terrestrial plant-consumer interactions  
87 requires a deeper consideration of their unique processes giving rise to  
88 communities. We review the literature on the bioenergetics of plant-animal  
89 interactions, and discuss extensions to traditional food web frameworks.  
90 These extensions integrate advances in network analyses, bioenergetics, and  
91 the biological mechanisms underlying interactions between plants, their  
92 consumers and mutualists.

93

## 94 **Terrestrial bioenergetic framework**

95           The dimensional reduction offered by allometric scaling has a rich  
96 history in ecology, but harnessing it to analyze species interactions was not  
97 seriously examined until the seminal bioenergetic model by Yodzis and Innes  
98 [1]. This framework was expanded to communities of interacting species with  
99 the Allometric Trophic Network (ATN) model [2,13] (see Box 1), which models  
100 food web dynamics with a minimal number of parameters, namely, the body  
101 sizes of the consumer and resource species and a handful of allometric  
102 constants [5,6,23,24]. This model has demonstrated particular success with  
103 respect to aquatic systems, where the presence/absence of trophic  
104 interactions and rates of consumption are assumed to scale allometrically  
105 (see Box 1, Figure 1), largely due to the gape limitations that constrain so  
106 many aquatic consumer interactions [10,12,25].

107           A central tenant of the new perspective we propose (Figure 1) is the  
108 notion that plant species can be organized along a fast-slow growth axis [26-  
109 28], determining plant mass-specific metabolic rates and ultimately the flow  
110 of energy from primary production to higher trophic levels via consumption.  
111 Fast-growing plants invest in photosynthetic machinery at the expense of  
112 defenses and structural tissue [29], which itself is defensive because it is  
113 difficult to digest. Because of these investments, fast growing plants tend to  
114 be leafier, more nutritious for consumers (lower C:N,P ratios and higher  
115 tissue digestibility), and less **resistant** but more **tolerant** to herbivory. This  
116 increased tolerance arises both because their ability to grow quickly allows  
117 them to quickly replace lost tissue and because their lack of investment in

118 structure and defenses lowers the per unit cost of their tissue [29]. Slow-  
119 growing plants, in contrast, invest more heavily in structure and defenses  
120 that promote the longevity of their tissues and therefore tend to be larger,  
121 woodier, less nutritious for consumers, and more resistant but less tolerant  
122 of herbivory. This lack of tolerance arises because each bite of tissue is more  
123 valuable and more costly to replace [26–28,30]. A fast-slow plant axis thus  
124 affects key parameters governing food web dynamics, including herbivore  
125 ingestion ( $f_{ji}$ ) and assimilation ( $e_{ji}$ ) of plant biomass, foraging effort ( $p_{ji}(B)$ ),  
126 attack rate ( $a_{ji}$ ), and handling time ( $h_{ji}$ ) (see Box 1) [14–16,31].

127

## 128 **Plant structural complexity**

129       Plants have evolved different tissue types to address their  
130 simultaneous needs to acquire water and nutrients, photosynthesize, and  
131 reproduce [32], and diverse guilds of herbivores have in turn evolved to  
132 consume and at times specialize on them (Figure 2). These tissues include  
133 leaves, stems, wood, roots, underground storage organs, seeds, nectar,  
134 pollen, and sap/phloem, all of which vary in terms of plant investment,  
135 nutritional value, and the cost (or benefit) to the plant if the tissue is  
136 consumed [32] (Figure 2). These differences influence both the biomass  
137 available to herbivores and the effect of biomass loss on plant maintenance,  
138 growth, and reproduction [14–16,31]. Plants are indeterminate growers, such  
139 that their allocation to different organs or tissues are often plastic in  
140 response to both internal and external factors [32]. Internal factors include



141 life stages and phenology [33], whether the plant has a fast or slow growth  
142 strategy [27,28], and how resistant or tolerant the plant is to herbivory  
143 [30,34]. In contrast, external factors include the effects of environmental  
144 pressures (e.g. water and nutrient availability [35,36]), competition with  
145 other plants [37], and herbivory [38]. For example, in resource-poor  
146 environments, plants may exhibit slower growth rates, altering energetic  
147 allocation to different organs [32] in response to the total energy available to  
148 the ecosystem. As a result, profiles of organ proportions differ across  
149 environments or seasons [39,40], potentially driving substantial changes in  
150 the herbivore community [31].

151         The effects of plant structural complexity can be integrated into a  
152 bioenergetic food web framework by incorporating the chemical and physical  
153 constraints governing the interactions between herbivores and particular  
154 plant tissues — as opposed to interactions with plant species or functional  
155 groups (Figure 2A). This can be accomplished using either fixed (Figure 2B)  
156 or dynamic pool (Figure 2C) approaches. The fixed pool approach assumes  
157 the plant biomass is composed of fixed fractions of each tissue, with  
158 herbivore groups limited to feeding on that fraction of biomass. Alternative  
159 tissues vary in their nutrient composition and thus provide different yields to  
160 herbivores. This fixed pool approach incorporates the topological complexity  
161 of different animal guilds feeding on different plant tissues without  
162 increasing the complexity of the dynamic models. In contrast, the dynamic  
163 pool approach allows dynamic allocations to growth and maintenance for

164 each tissue [21,41,42] at the cost of additional model complexity. Dynamic  
165 pools allows for feedbacks between consumption and production of each  
166 tissue, such that adaptive foraging behaviors among herbivores [22,41–43],  
167 in response to the relative availability, cost, and benefit from different  
168 tissues, may promote coexistence even when diets are similar.

169

## 170 **Herbivore ingestion and assimilation of plant biomass**

171 The proportion of plant biomass ( $B_i$ ) available for consumption by  
172 herbivores (that is, the fraction ingested,  $B_i/f_{ji}$ , see Box 1) is constrained by  
173 plant and herbivore traits. Indeed, much plant-herbivore research (especially  
174 for insects) examines how plant defenses, including the vast diversity of  
175 **phytochemicals** and physical traits such as toughness and spinescence,  
176 influence  $f_{ji}$  and rates of herbivory in general. We review literature on  
177 constitutive and inducible defenses in Box 2 and propose to integrate those  
178 defenses in our framework as affecting herbivores' consumption parameters  
179 ( $a_{ji}, e_{ji}, f_{ji}, h_{ji}, p_{ji}$ ) (see Boxes 1 and 2). For ground-based mammals (e.g.,  
180 ungulates), the proportion of plant biomass available will also depend on the  
181 relative height of the plant and the herbivore, because these herbivores can  
182 only access tissue within a vertical range roughly spanning ground level to  
183 shoulder-height [44]. While plant height might place a physical limit on  
184 access, these mammals tend to partition their diets across a relatively low-  
185 dimensional plant trait access correlating with nutritional quality [45]. Key to

186 understanding plant-herbivore interactions is that not all green tissue is  
187 equally available — physically or biochemically — to herbivores.

188         Once plant biomass is ingested, plant-consumer interactions are  
189 constrained by the efficiency with which herbivores can transform ingested  
190 food into new biomass. That is, the assimilation efficiency ( $e_{ji}$  in Eq. 1 of Box  
191 1). We propose expressing this efficiency as yield from the perspective of  
192 bulk requirements of consumer-resource interactions [46]. The consumer  
193 yield (grams of consumer produced per grams of resource consumed) is  
194 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  
195 the energy density of resource  $i$  (Joules/g) and  $E_{L_j}$  represents the lifetime  
196 energetic requirements of a consumer  $j$  that reaches maturity (Joules). The  
197 resource removed by the consumer is then proportional to the efficiency  
198  $e_{ji} = d_{ji} B_i / Y_{ji}$ , where  $d_{ji}$  is the proportion of digested plant biomass, which must  
199 be a function of both plant biochemistry and the herbivore's digestive  
200 abilities (see Box 2 and Online Supplemental Information Appendix S1).  
201 Herbivores exhibit species-specific behaviors designed to optimize  $e_{ji}$  within  
202 particular communities and habitats [47], the result of unique evolutionary  
203 trajectories driven by local fitness gradients [48].

204

## 205 **Adaptive behavior of plants and herbivores**

206         Both consumers and resources interact dynamically, adapting the  
207 energy allocated to searching for and consuming, attracting, and/or  
208 defending against those species with which they interact. Following [22], we

209 define adaptive behavior as the fitness-enhancing changes in individuals'  
210 feeding-related traits due to variation in their trophic environment. This  
211 includes adaptive foraging of consumers, as well as the adaptive responses  
212 of resources, which we define as changes in resource behavior and other  
213 traits in response to consumers and environmental cues. Box 3 details a  
214 method by which herbivore adaptive foraging and plant adaptive responses  
215 can be introduced into a comprehensive bioenergetic ATN framework.

216         Herbivores adaptively forage in a multi-scale manner [49] by first  
217 searching the landscape for a promising foraging habitat, and then locating  
218 particular plant individuals using multiple sensory modalities [50], after  
219 which a decision to eat them or keep searching is made [48]. Insects use a  
220 diverse array of cues to find their hosts, including habitat context and plant  
221 odor and color, after which many sense tissue quality and make feeding  
222 decisions using specialized chemoreceptors [49,51]. Ovipositing females also  
223 search for places to lay eggs by sensing the leaves with their ovipositor [52].  
224 And while it is clear that herbivores respond to a complex constellation of  
225 plant traits and conditions to maximize profitability, plants demonstrate  
226 equally dynamic responses to both repel and attract their herbivores.

227         Chemical defenses are central to the adaptive response to herbivory  
228 by plants, with many species upregulating the production of toxins following  
229 detection of herbivore damage or other herbivore cues (Box 2). The fast-slow  
230 trait axis ( $T_i$ ) may also affect the response to herbivory of plant species  $i$  by  
231 influencing its average adaptation rate ( $s'_i$ ) or the benefit in per-capita

232 growth rate obtained by its response to herbivore  $j$  ( $\partial G_i / \partial v_{ij}$ ). Plant adaptive  
233 responses also involve mutualistic interactions in terms of attracting the  
234 consumers of their herbivores (i.e., indirect defenses) or attracting  
235 pollinators and seed dispersers. For example, some plants respond to  
236 herbivore cues or attack by releasing volatiles that attract predators or even  
237 reward predators with nectar or pearl bodies (concentrations of protein) [53].  
238 Other plants produce chemicals that, after being ingested by herbivores,  
239 volatilize from their feces and guide predators to them [54]. Inducible  
240 extrafloral nectaries attract ants that then remove herbivores from the plant  
241 [55]. Plants also provide predator shelters (domatia; e.g., leaf pits, swollen  
242 thorns), the production of which can be upregulated following herbivory [56].  
243 Finally, floral rewards and fruits produced by plants to attract pollinators and  
244 seed dispersers, respectively, can also be formalized as adaptive responses.  
245 They are resource traits where investment responds directly to consumers  
246 and environmental cues, though their role is to attract, rather than repel, the  
247 consumer (pollinator, seed disperser) with a potentially positive effect on  
248 plant fitness [17-19].

249 Frequency dependence can play an important role in plant-herbivore  
250 adaptive responses. For some species of caterpillars, survival is low when  
251 they attack a plant in small groups and high when they attack in larger  
252 groups, apparently because plant responses depend on herbivore density  
253 [57]. For example, herbivores that overcome plant defenses by attacking *en*  
254 *masse*, such as bark beetles, often have aggregation hormones that help

255 them reach high local densities [58]. In other systems, negative density-  
256 dependence drives dynamics. Herbivores avoid damaged plants because: (i)  
257 previously attacked plants are likely to have induced resistance traits [59], (ii)  
258 earlier attacking herbivores are likely to have removed the best quality  
259 tissue [60], (iii) to avoid direct interference interactions with competing  
260 herbivores [61].

261

## 262 **Stage-structure dynamics**

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

277 in plant defenses influences herbivores to prefer particular plant stages over  
278 others [70,71].

279         Ontogeny interacts with phenology to affect plant-herbivore  
280 interactions. In semelparous monocarpic plant species, unique stages are  
281 differentially available across the growing season, potentially creating  
282 distinct phenological windows of interaction between consumers that would  
283 instead be static trophic links without considering ontogeny [72] (compare  
284 Figure S1B with Figure S1C in Supplementary Information). In longer-lived,  
285 multi-season, iteroparous plants, seasonally specific growth for younger  
286 versus older stages can still open up distinct interaction windows (as in  
287 Figure S1C) but with potential cross-generational intraspecific competition.  
288 For example, high adult density limits the survival or maturation rates of  
289 younger stages either by restricted access to necessary nutrients [73] or  
290 increased exposure to soil pathogens [74].

291

## 292 **Structure of terrestrial networks**

293         Our bioenergetic framework advocates for a broader definition of food  
294 web topology that includes both antagonistic and mutualistic trophic  
295 interactions (Figure 2). Food webs typically exclude mutualistic trophic  
296 interactions, which limits the analysis of terrestrial food web dynamics [21].  
297 Of the few networks available [10], many include only a subset of the local  
298 taxa, with uneven levels of taxonomic resolution, often representing the  
299 specialties of the investigators. As a consequence, plants and insects tend to

300 be less resolved than vertebrates [75,76], potentially biasing our  
301 understanding of both structure and dynamics in these systems. Fortunately,  
302 recent advances in DNA barcoding from feces and stomach contents  
303 provides unprecedented opportunity to increase sampling resolution [77].  
304 Despite these challenges, that aquatic and terrestrial food webs reveal clear  
305 differences in topological and biomass structures is well understood (see  
306 panels iv of Figure 1). Aboveground terrestrial food webs have shorter food  
307 chains with more producer biomass and less herbivore biomass and  
308 consumption than aquatic food webs with similar net primary productivity,  
309 presumably due to the greater structural complexity and lower edibility of  
310 terrestrial plant tissues [11, 12]. We suggest that a comprehensive  
311 bioenergetic framework that includes the unique relationships observed  
312 between plants and their consumers (including mutualists) may improve our  
313 understanding of where these differences arise.

314         Generative models of food web topologies [78–80] offer a powerful  
315 means by which food web bioenergetic dynamics can be explored, given the  
316 inherent difficulty of collecting food web data. These phenomenological  
317 models generate topologies with broadly similar properties compared to  
318 empirical food webs [79,80], though typically contain too few herbivore  
319 species, too few plant-herbivore interactions, and accumulate too many  
320 trophic levels [9,80] compared to terrestrial communities. Together these  
321 differences substantially alter predicted biomass dynamics compared to  
322 empirical terrestrial topologies [9]. We predict these deviations will be



323 magnified when the traditionally unresolved plant taxa are better resolved  
324 and when the consumption of different plant tissues is incorporated (Figure  
325 2).

326 To better accommodate these deviations, we propose a terrestrial  
327 extension to a class of topological models that use an empirically-  
328 measurable body size axis. These models, inspired by the **Allometric Diet**  
329 **Breadth Model**, specify an energetically optimal body mass ratio ( $\lambda$ ) at  
330 which animals can most efficiently feed on a resource [3,25]. Animals can  
331 feed on a range of resource sizes, but efficiency decreases away from the  
332 optimum until effectively no interaction occurs. Therefore, species' traits  
333 determine both the presence and rate of feeding interactions (Box 1). We  
334 propose that plant trait values ( $T_i$ ) on a fast-slow axis determine the feeding  
335 efficiency of herbivores on plant tissues (Figure 1). Such a trait axis contains  
336 high dimensional information on the nutritiousness (stoichiometry) and  
337 defendedness of plant leaves. Herbivores of a given metabolic class (e.g.,  
338 ectotherm invertebrates, endotherm vertebrates) likely have maximum  
339 feeding efficiency on optimally-matched plant traits ( $M_j/T_i$ ) but can tolerate a  
340 range of plant traits with diminishing feeding efficiency and yield (i.e., Eq. 4  
341 is dependent on  $T_i$ , see also Online Supplemental Information Appendix S1).  
342 For example, larger-bodied herbivores can handle taller and less nutritious  
343 forage - 'slower' plants in our framework - than can smaller-bodied  
344 herbivores, due to lower mass-specific metabolic needs and greater digestive  
345 capacity and efficiency [81]. Though empirical evidence connecting this

346 pattern to herbivory network structure is sparse, some observations suggest  
347 this to be a good first hypothesis. For example, mammals of similar body  
348 sizes tend to have similar diets [82], and resource partitioning among African  
349 savanna grazers is well-explained by their body sizes [83]. Within a  
350 taxonomically diverse leaf-chewing community, smaller insect herbivores  
351 preferred younger, less defended, and more nutritious leaves of *Ficus wassa*  
352 than larger species [84].

353         Different trait axes may be appropriate for different plant tissues,  
354 allowing different sub-networks for specific types of herbivory such as  
355 nectarivory (Figure 2). Therefore, we propose generating similar sub-  
356 networks for different types of terrestrial feeding interactions using animal  
357 body size as the trait axis for carnivory and the matching of the plant trait  
358 and animal body size axes for herbivory. These sub-networks can then be  
359 interlinked into multiplex topologies following plausible assembly rules (e.g.,  
360 [21,78,79,85]).

361

## 362 **Community stability and ecosystem functions**

363         The weakening and diversification of consumer-resource interactions  
364 are well-known to stabilize food web dynamics [86]. We suggest that  
365 introducing a more accurate accounting of plant and herbivore communities  
366 and their associated constraints in food web structure and function will  
367 fundamentally alter the distribution of interaction strengths relative to  
368 current bioenergetic approaches. Specifically, incorporating plant defenses

369 and herbivory on different plant tissues (as we propose in Figs. 1 and 2 and  
370 Box 2) will diversify and weaken energy flows from plants to herbivores and,  
371 therefore, stabilize terrestrial in comparison to aquatic food webs. Further,  
372 weakening interactions generally will tend to reduce the strength of trophic  
373 cascades by constraining vertical energy flow through the food web [86,87].  
374 Intriguingly, empirical evidence from terrestrial ecosystems are consistent  
375 with weak-skewed interactions [87].

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

392

## 393 **Concluding Remarks**

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

404

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411

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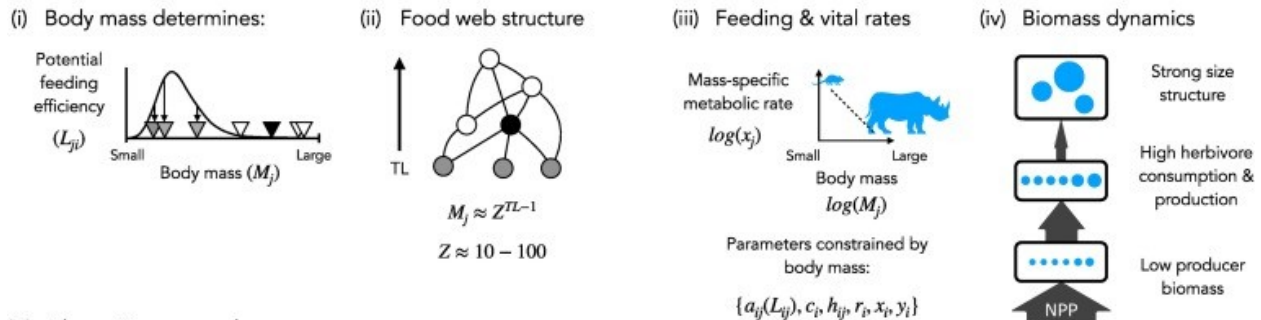
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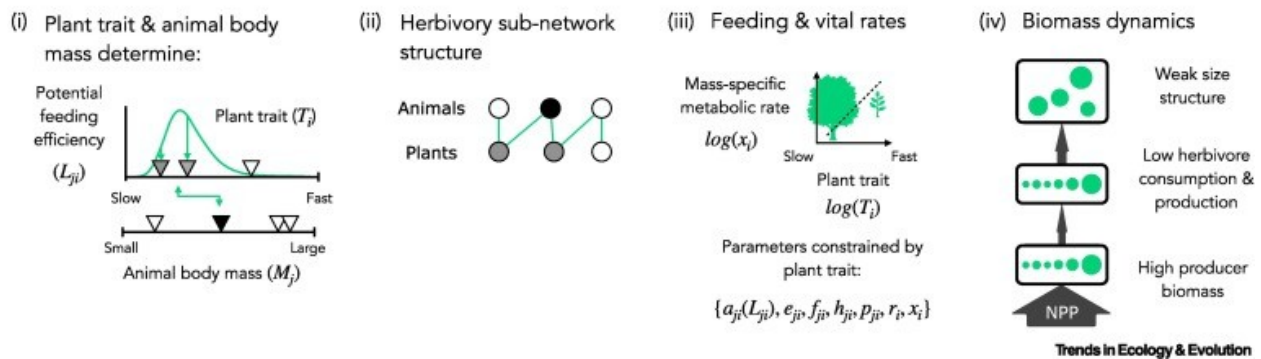


648 **Figure 1.**

(A) Classical approach



(B) Alternative approach



649

650 **Figure 1. Terrestrial alternative to bioenergetic models. (A)**

651 classical approach determines food web structure and dynamics from

652 allometric patterns based on each species' average adult body mass ( $M_j$ )653 and metabolic class (Box 1). **(i)** Species' potential feeding  $L_{ji}$  efficiency

654 depends on their body mass relative to their resources. Consumers can feed

655 on resources within a range of sizes around an energetically optimum body

656 mass ratio. **(ii)** This enforces strong size structure with producers (trophic657 level  $[TL] = 1$ ) of similar size and consumers approximately  $Z = 10-100\times$ 658 larger than their resources. **(iii)** Growth and consumption rates are also659 calculated from body masses, allowing **(iv)** high consumption and production660 by herbivores typical of aquatic ecosystems. **(B)** Our framework uses plant661 traits ( $T_i$ ) representing the "fast-slow" axis to determine the structure and

662 dynamics of herbivory interactions. Fast-growing plants are smaller, leafier,

663 with more palatable leaves; while slow-growing plants are larger, woodier,

664 with less nutritious and more defended leaves. **(i)** Animals' potential feeding

665  $L_{ji}$  efficiency on plants depends on the match between their body mass for a  
 666 given metabolic class and  $T_i$ . **(ii)** This creates herbivory sub-networks with  
 667 weaker size structure. **(iii)** Plant growth ( $r_i, x_i$ ) and herbivory (  
 668  $a_{ji}(L_{ji}), e_{ji}, f_{ji}, h_{ji}, p_{ji}$ ) can also be calculated using plant traits. **(iv)** Allowing  
 669 variation in plant size and stoichiometry breaks the dependence of herbivore  
 670 attack rate on consumer-resource body size ratio. This results in lower  
 671 herbivore consumption and production than aquatic ecosystems with similar  
 672 net primary productivity (NPP) due to less nutritious and more defended  
 673 plant tissues.

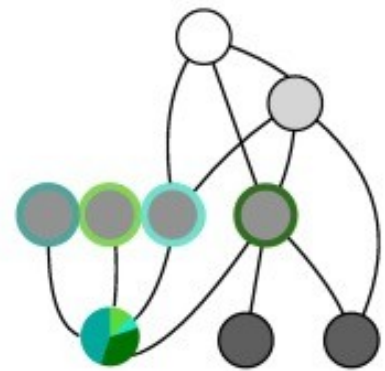
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675 **Figure 2.**

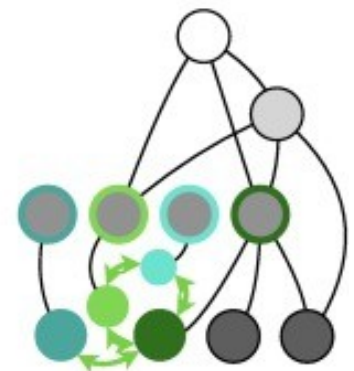
(A) Herbivory on different plant tissues integrated into dynamic food webs



(B) Fixed fractions



(C) Dynamic pools



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676

677 **Figure 2. Approaches to herbivory in aboveground terrestrial food**  
 678 **webs.** The structural complexity of terrestrial plants supports many groups

679 of herbivores feeding on different plant tissues, including (photos from top to  
680 bottom): nectar and pollen, fruits and seeds, leaves, and bark and wood.  
681 Plant and herbivore growth and reproduction strongly depend on these  
682 different trophic interactions, which indirectly affects the full food web  
683 dynamics. Despite the importance of these different interactions, the  
684 traditional approach to food webs has focused only on antagonistic herbivory  
685 (e.g., folivory), excluding “mutualistic” feeding by pollinators and seed  
686 dispersers. We propose two new approaches to incorporate the network  
687 complexity of different animal guilds feeding on different plant tissues by  
688 assuming plant biomass as: **(A)** composed of fixed fractions of each tissue,  
689 with herbivore groups limited to feeding on a specific fraction, and **(B)**  
690 partitioned into coupled pools, allowing dynamic plant allocations to growth  
691 or maintenance for each tissue, feedbacks between consumption and  
692 production of each tissue, and herbivore adaptive foraging. In both  
693 approaches, the structure of herbivory interactions on different plant tissues  
694 can be derived from the matching between plant and animal traits (Fig. 1).  
695 Illustrative food webs show grayscale nodes lighter in color with increasing  
696 trophic level. Colored nodes indicate different plant tissues matching the  
697 photo borders for different types of herbivory. Links represent bioenergetic  
698 couplings, due to feeding (gray) or dynamic feedbacks between the  
699 production and maintenance of different tissues (green).  
700

701

## TEXT BOXES

702 **Box 1 - Allometric Trophic Network (ATN) model**

703 Consists of two sets of governing equations [2,13], one for primary  
704 producers (Eq. 1) and another for consumers (Eq. 2):

705

$$706 \quad \frac{dB_i}{dt} = \overbrace{r_i B_i D_i(B)}^{\text{Autotrophic growth gain}} - \overbrace{x_i B_i}^{\text{Maintenance loss}} - \overbrace{\sum_j \frac{1}{f_{ji} e_{ji}} x_j y_j B_j F_{ji}(B)}^{\text{Herbivory loss}} \quad (\text{Eq. 1})$$

$$707 \quad \frac{dB_j}{dt} = \overbrace{x_j B_j \sum_k y_k F_{kj}(B)}^{\text{Resources consumption gain}} - \overbrace{x_j B_j}^{\text{Maintenance loss}} - \overbrace{\sum_k \frac{1}{f_{kj} e_{kj}} x_k y_k B_k F_{kj}(B)}^{\text{Predation loss}} \quad (\text{Eq. 2})$$

708

709 where  $\mathbf{B}$  is vector of biomasses for every species in the food web and  $B_i$  is  
710 biomass of species  $i$ .  $B_i$  of producer species  $i$  changes over time according to  
711 the balance between gains from autotrophic growth and losses due to  
712 metabolic maintenance and herbivory by consumer species  $j$ . Autotrophic  
713 growth is determined by the producer's intrinsic growth rate ( $r_i$ ), metabolic  
714 rate ( $x_i$ ), and logistic growth:  $D_i(B) = 1 - \frac{B_i}{K}$ , with  $K$  as carrying capacity of all  
715 primary producers. Biomass loss to herbivory increases with mass-specific  
716 metabolic rate ( $x_j$ ) and maximum consumption rate ( $y_j$ ) of consumer species  
717  $j$ , and decreases with ingestion ( $f_{ji}$ ) and assimilation ( $e_{ji}$ ) efficiencies by  
718 consumer  $j$  on producer  $i$ .  $B_j$  of consumer species  $j$  (Eq. 2) changes over time  
719 according to the balance between biomass gains by resource consumption  
720 and biomass loss from metabolic maintenance and predation. Functional

721 response  $F_{ji}(B)$  determines the consumption rate of each consumer species  $j$   
 722 on each resource species  $i$ , defined:

$$723 \quad F_{ji}(B) = \frac{p_{ji}(B) a_{ji} h_{ji} B_i^q}{1 + c_j B_j + \sum_{l=\text{resources}} p_{jl}(B) a_{jl} h_{jl} B_l^q} \quad (\text{Eq. 3})$$

724 where  $p_{ji}(B)$ ,  $a_{ji}$ , and  $h_{ji}$  are, respectively, the foraging effort, attack rate, and  
 725 handling time of consumer  $i$  on resource  $j$ ,  $c_j$  is the intra-specific foraging  
 726 interference of consumer  $j$ , and  $q$  controls the shape of Eq. 3.

727 Parameters in Eqs. 1-3 are constrained by average body masses of  
 728 individuals of the consumer ( $M_j$ ) and resource species ( $M_i$ ), as:

$$729 \quad r_i = \frac{R_i}{R_{ref}} \dot{\iota} \left( \frac{M_i}{M_{ref}} \right)^{-0.25} \quad x_i = \frac{X_i}{R_{ref}} \dot{\iota} \frac{a_x}{a_r} \left( \frac{M_i}{M_{ref}} \right)^{-0.25} \quad y_j = \frac{Y_j}{X_j} \dot{\iota} \frac{a_y}{a_x} \quad (\text{Eq. 4})$$

$$731 \quad a_{ji} = a_0 M_j^{0.25} M_i^{0.25} L_{ji} \quad h_{ji} = \frac{e_{ji}}{a_y} M_j^{0.25}$$

732 where  $a_0$ ,  $a_r$ ,  $a_x$ , and  $a_y$  are allometric constants specific to species' metabolic  
 733 categories (producer, invertebrate, ectotherm vertebrate, or endotherm  
 734 vertebrate) and  $L_{ji}$  quantifies potential feeding efficiency given the

735 energetically optimum body size ratio. Subscript *ref* denotes the reference  
 736 producer species, the smallest in the system. Primary production ( $R_i$ ),

737 metabolism ( $X_j$ ), and maximum consumption ( $Y_j$ ) in Eq. 4 follow negative

738 power laws with each species' average body mass as:  $R_i = a_r M_i^{-0.25}$ ,

739  $X_i = a_x M_i^{-0.25}$ ,  $Y_j = a_y M_j^{-0.25}$ . We propose to consider plant growth traits ( $T_i$ ) on a

740 "fast-slow" axis to determine parameters ( $R_i \dot{\iota}$ ,  $X_i$ ) which then can be used

741 with animal body mass to calculate  $(a_{ji})$ ,  $(e_{ji})$ ,  $(f_{ji})$ ,  $(h_{ji})$ , and  $(p_{ji})$  (see Figure 1  
742 and the Online Supplemental Information Appendix S1).

### 743 **Box 2 - Plant defense**

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

761 There are two main defensive pathways for plant inducible defenses,  
762 the jasmonic acid pathway, which responds to chewers, such as caterpillars,  
763 and the salicylic acid pathway, which responds to pathogens and sucking-



764 insects, such as aphids [14]. For example, many milkweeds (*Asclepias* spp.)  
765 increase production of toxic cardenolides and exudation of sticky latex in  
766 response to feeding by monarch caterpillars (*Danaus plexippus*), which can  
767 reduce monarch survival and performance [15]. Research shows clear  
768 constraints in some plant species to induction of defenses between these  
769 two pathways [14]. When a chewing herbivore attacks, the jasmonic-acid  
770 pathway is upregulated and the plant suppresses the salicylic-acid pathway,  
771 so it becomes more susceptible to the attack of phloem suckers or  
772 pathogens.

773         Plant chemical receptors and metabolic pathways responding to  
774 chemical cues are so sophisticated that they can even sense an insect  
775 walking on them before biting [95]. For trees or highly sectorial plants (e.g.,  
776 shrubs), localized responses can lead individuals to be defensive mosaics,  
777 which are likely adaptive in the face of heterogeneous herbivore attack  
778 [96,97]. Communication via volatiles or below-ground mycorrhizal  
779 connections can lead plant responses to herbivore attack to include large  
780 patches of plants [91]. Plants change their odors when attacked, and  
781 neighboring plants can respond in a process of plant-plant communication or  
782 eavesdropping [91].

783

784 **Box 3 - Adding plant-herbivore adaptive behavior to our**  
 785 **bioenergetic framework**

786 Herbivore adaptive foraging and plant defenses can be incorporated  
 787 into the functional response of the ATN model (Eq. 3 of Box 1) as:

788

789 
$$F_{ji}(B) = \frac{p_{ji}(B)(1-v_{ij})a_{ji}h_{ji}B_i^q}{1+c_jB_j + \sum_{l=\text{resources}} p_{jl}(B)(1-v_{lj})a_{jl}h_{jl}B_l^q} \quad (\text{Eq. 5})$$

790 where  $p_{ji}$  is the foraging effort consumer  $j$  assigns to resource  $i$  and  $v_{ij}$  is the  
 791 anti-predator effort resource  $i$  assigns against consumer  $j$ , respectively. Note  
 792 that in some versions of the ATN (e.g., [2]),  $p_{ji} = \omega_{ji}$  denoting fixed consumer  
 793 preference (unitless), while here it denotes variable foraging effort (also  
 794 unitless, [13]). These efforts define the fraction of individuals' energy or time  
 795 allocated to consuming a particular resource species and avoiding a  
 796 particular consumer species, respectively [22]. The higher the foraging effort  
 797 invested in a particular resource, the higher the capture efficiency is of that  
 798 resource and the larger Eq. 5 is. The higher the anti-predator effort of a  
 799 resource against a consumer, the lower the capture efficiency of that  
 800 consumer and the smaller Eq. 5 is. Adaptive foraging and inducible defenses  
 801 are incorporated into Eq. 5 by allowing  $p_{ji}$  and  $v_{jk}$ , respectively, to adapt over  
 802 time:

803 
$$\frac{d p_{ji}}{dt} = s_j \left( \frac{\partial G_j}{\partial p_{ji}} - \gamma_j \right) \quad (\text{Eq. 6})$$

804 
$$\frac{d v_{jk}}{dt} = s'_j \left( \frac{\partial G_j}{\partial v_{jk}} - \gamma_j \right) \quad (\text{Eq. 7})$$

805

806 Parameters  $s_j$  and  $s'_j$  are the rates by which species  $j$  changes its foraging

807 and anti-predator efforts, respectively. Function  $G_j = \frac{1}{B_j} \frac{dB_j}{dt}$  is  $j$ 's per-capita

808 (per-biomass in this case) growth rate. If  $s_j < 1$  or  $s'_j < 1$ , changes in foraging

809 and anti-predator efforts are slower than population dynamics and the shift

810 of strategies reflects evolutionary changes, whereas  $s_j > 1$  or  $s'_j > 1$

811 represents faster changes acquired through behavioral responses [98].

812 These efforts increase when they increase the per-biomass growth rate more

813 than the average per-biomass growth rate obtained from assigning the effort

814 to other consumers or resources,  $\gamma_j$ , defined as:

815 
$$\gamma_j = \sum_{l \in \text{resources}} p_{jl} \frac{\partial G_j}{\partial p_{jl}} + \sum_{k \in \text{consumers}} v_{jk} \frac{\partial G_j}{\partial v_{jk}} \quad (\text{Eq. 8})$$

816 If a species only adaptively forages, then  $v_{jk} = 0$ , Eq. 7 is zero, and  $\gamma_j$  in Eq. 6

817 will only contain the first sum of Eq. 8. If a species only adaptively defends,

818 then  $p_{jl} = 0$ , Eq. 6 is zero, and  $\gamma_j$  in Eq. 7 only contains the second sum.

819 Optimization of Eqs. 6 and 7 is constrained by allocation costs [99],

820 representing the impossibility of individuals infinitely and simultaneously

821 assigning energy or time to every task, expressed as:

822 
$$\sum_{l \in \text{resources}} p_{jl} + \sum_{k \in \text{consumers}} v_{jk} = 1 \quad (\text{Eq. 9})$$