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A bioenergetic framework for aboveground terrestrial food webs

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31 **Keywords**

32 Fast-slow continuum, plant defenses, tissue-specialist herbivores, plant

33 mutualists, consumer-resource, stage structure.

34

Abstract

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 most 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. It also considers mutualistic interactions, advancing understanding of terrestrial food webs and predictions of their responses to environmental changes.

Ecology needs a terrestrial bioenergetic approach

50

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,

4   4

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

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

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 ¿) 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

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 provided a roadmap that will guide the integration of bioenergetics specific to terrestrial plants and their biotic interactions into those of traditional food web models.

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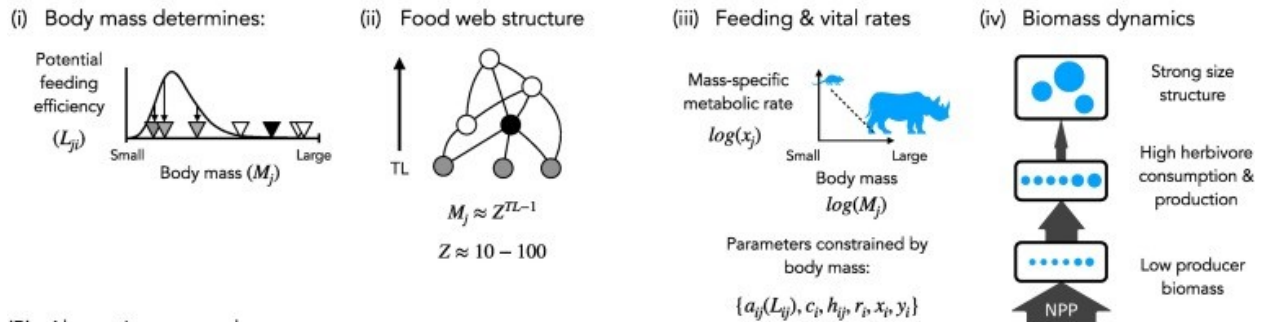641 niche-model food webs. *J. Theor. Biol.* 251, 108–120
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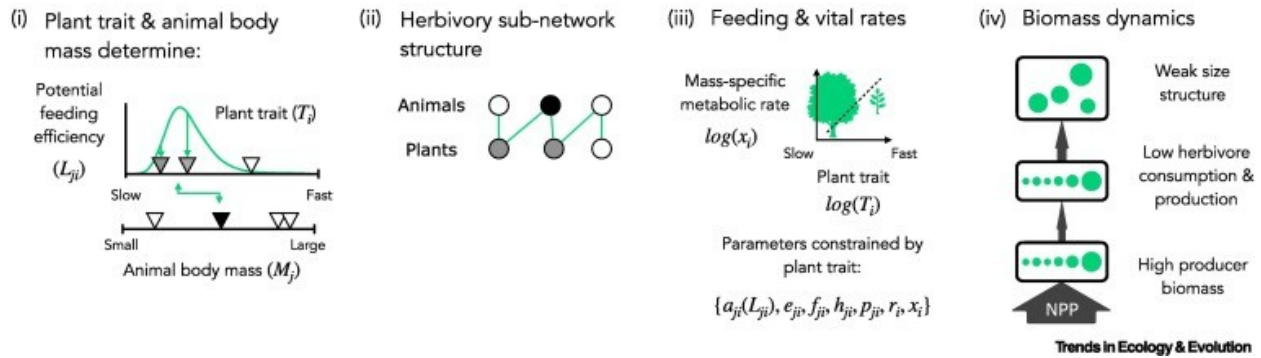644 pp. 177–189
645

648 Figure 1.

(A) Classical approach

(i) Body mass determines:

Potential feeding efficiency (L_{ji})

Small — Large
Body mass (M_j)

(ii) Food web structure

TL

$M_j \approx Z^{TL-1}$

$Z \approx 10 - 100$

(iii) Feeding & vital rates

Mass-specific metabolic rate

$log(x_j)$

Small — Large
Body mass
$log(M_j)$

Parameters constrained by body mass:

$\{a_{ij}(L_{ij}), c_i, h_{ij}, r_i, x_i, y_i\}$

(iv) Biomass dynamics

Strong size structure

High herbivore consumption & production

Low producer biomass

NPP

(B) Alternative approach

(i) Plant trait & animal body mass determine:

Potential feeding efficiency (L_{ji})

Plant trait (T_i)

Slow — Fast

Small — Large
Animal body mass (M_j)

(ii) Herbivory sub-network structure

Animals

Plants

(iii) Feeding & vital rates

Mass-specific metabolic rate

$log(x_i)$

Slow — Fast
Plant trait
$log(T_i)$

Parameters constrained by plant trait:

$\{a_{ji}(L_{ji}), e_{ji}, f_{ji}, h_{ji}, p_{ji}, r_i, x_i\}$

(iv) Biomass dynamics

Weak size structure

Low herbivore consumption & production

High producer biomass

NPP

Trends in Ecology & Evolution

649

650 Figure 1. Terrestrial alternative to bioenergetic models. (A) The
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 (trophic
657 level [TL] = 1) of similar size and consumers approximately Z = 10-100x
658 larger than their resources. **(iii)** Growth and consumption rates are also
659 calculated from body masses, allowing **(iv)** high consumption and production
660 by herbivores typical of aquatic ecosystems. **(B)** Our framework uses plant
661 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
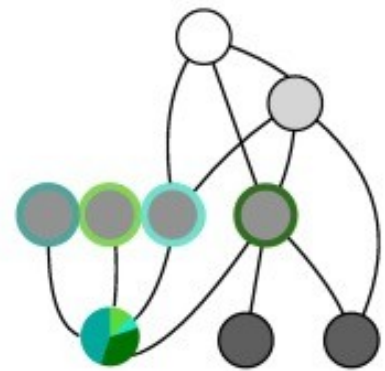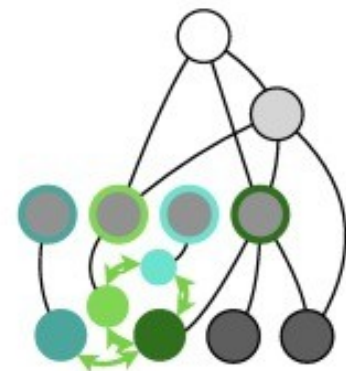673 plant tissues.
674
675 **Figure 2.**

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

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

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

$$\frac{d\,B_j}{dt}=\overbrace{x_j\,B_j\sum_k y_j\,F_{ji}(B)}^{\substack{Resources\\consumption\,gain}}-\overbrace{x_j\,B_j}^{\substack{Maintenance\\loss}}-\overbrace{\sum_k\frac{1}{f_{kj}e_{kj}}x_k\,y_k\,B_k\,F_{kj}(B)}^{\substack{Predation\\loss}}\qquad \text{(Eq. 2)}$$

708

709   where **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: $D_i(B)=1-¿¿$, 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
$$F_{ji}(B)=\frac{p_{ji}(B)a_{ji}h_{ji}B_i^q}{1+c_jB_j+\displaystyle\sum_{l=resources}p_{jl}(B)a_{jl}h_{jl}B_l^q}$$
(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

730
$$r_i=\frac{R_i}{R_{ref}}¿\left(\frac{M_i}{M_{ref}}\right)^{-0.25} \qquad x_i=\frac{X_i}{R_{ref}}¿\frac{a_x}{a_r}\left(\frac{M_i}{M_{ref}}\right)^{-0.25} \qquad y_j=\frac{Y_j}{X_j}¿\frac{a_y}{a_x}$$
(Eq. 4)

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

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

740 "fast-slow" axis to determine parameters ($R_i¿$, (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

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 (Eq. 3 of Box 1) as:

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

where p_{ji} is the foraging effort consumer j assigns to resource i and v_{ij} is the anti-predator 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), while 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 Eq. 5 is. The higher the anti-predator effort of a resource against a consumer, the lower the capture efficiency of that consumer and the smaller Eq. 5 is. Adaptive foraging and inducible defenses are incorporated into Eq. 5 by allowing p_{ji} and v_{jk}, respectively, to adapt over time:

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

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

33

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 $s'_i < 1$, 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, γ_j, defined as:

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

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

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

818 then $p_{ji}=0$, Eq. 6 is zero, and γ_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
$$\sum_{l \in resources} p_{jl} + \sum_{k \in consumers} v_{jk} = 1$$
(Eq. 9)