

# 1 A highly resolved multiplex network reveals the structural role of insects 2 and plants in terrestrial food webs

3  
4 Kayla R. S. Hale<sup>1,2\*</sup>, John David Curlis<sup>1</sup>, Giorgia G. Auteri<sup>3</sup>, Sasha Bishop<sup>1</sup>, Rowan L. K.  
5 French<sup>4</sup>, Lance E. Jones<sup>5</sup>, Kirby L. Mills<sup>1,6</sup>, Brian G. Scholtens<sup>7</sup>, Meagan Simons<sup>1</sup>, Cody  
6 Thompson<sup>8</sup>, Jordon Tourville<sup>9,10</sup>, Fernanda S. Valdovinos<sup>11</sup>  
7

8 1 Department of Ecology & Evolutionary Biology, University of Michigan, Ann Arbor, MI,  
9 USA

10 2 Department of Integrative Biology, University of Guelph, Guelph, ON, CA

11 3 Department of Biology, Missouri State University, Springfield, MO, USA

12 4 Department of Ecology & Evolutionary Biology, University of Toronto, Toronto, ON, CA

13 5 Department of Plant Biology, University of Illinois at Urbana-Champaign, Urbana, IL, USA

14 6 School for Environment & Sustainability, University of Michigan, Ann Arbor, MI, USA

15 7 Department of Biology, College of Charleston, Charleston, SC, USA

16 8 Museum of Zoology, University of Michigan, Ann Arbor, MI, USA

17 9 Department of Environmental Biology, SUNY College of Environmental Science and Forestry,  
18 Syracuse, NY, USA

19 10 Research Department, Appalachian Mountain Club, Boston, MA, USA

20 11 Department of Environmental Science and Policy, University of California, Davis, CA, USA

21

22 \* Corresponding author; e-mail: [kaylasal@umich.edu](mailto:kaylasal@umich.edu)

23

## 24 **ORCID**s

25

26 Hale, <https://orcid.org/0000-0002-2627-9623>; Curlis, <https://orcid.org/0000-0002-2974-7330>;

27 Auteri, <https://orcid.org/0000-0002-5579-8078>; Bishop, <https://orcid.org/0000-0002-0877-3951>;

28 Jones, <https://orcid.org/0000-0001-6368-9720>; Mills, <https://orcid.org/0000-0001-7693-9629>;

29 Thompson, <https://orcid.org/0000-0002-6686-6056>; Tourville, <https://orcid.org/0000-0003-4005-5914>;  
30 Valdovinos, <https://orcid.org/0000-0002-5270-5286>  
31

31

## 32 **Keywords**

33

34 Ecological network, aboveground terrestrial ecosystems, temperate forest, trophic structure,  
35 plant-insect interactions, taxonomic resolution  
36  
37  
38  
39

## 40 **Abstract**

41  
42 Terrestrial ecosystems support rich communities of species feeding on each other in different  
43 ways. Insects and plants comprise much of this species richness, but the structure of their feeding  
44 interactions in aboveground terrestrial food webs is not well known. Historically, food web  
45 research has coarsely or unevenly grouped insects and plants, excluded “mutualistic” feeding  
46 interactions (e.g., pollinators eating nectar), and focused only on subsets of species or feeding  
47 interactions, especially “antagonistic” interactions involving tetrapods. Here, we combine public  
48 data and records from a biological research station into a cumulative food web of ~580,000  
49 interactions among ~3,800 species in a temperate hardwood forest ecosystem. We include all  
50 feeding interactions, subdivided by whether animal tissues or plant leaves, flowers, fruits, or  
51 wood are being eaten. We represent these different types of feeding interactions in a multiplex  
52 food web and study the effect of taxonomic resolution on our understanding of food web  
53 structure. Our results indicate that insect herbivores engage in highly species- and tissue-specific  
54 feeding that is inaccurately represented by coarse taxonomic groups. The food web presented  
55 here is the richest and most evenly-resolved representation of feeding interactions yet reported  
56 and provides a tool for future management and research on terrestrial ecosystems.

57

## 58 **1) Introduction**

59 Empirical food webs are resources both for advancing ecological research and informing  
60 management practices. Food webs represent the potential biomass flows through an ecosystem  
61 by documenting the feeding interactions (links) between taxa (nodes). Studying these  
62 representations has allowed researchers to identify fundamental patterns in the structure of  
63 ecological systems. For example, aquatic and belowground food webs have been shown to be

64 hierarchical, with modular bioenergetic pathways of larger consumers eating smaller resources  
65 (Williams & Martinez 2000, Brose et al. 2006, Petchey et al. 2008, Stouffer et al. 2011, Brose et  
66 al. 2019, Potapov et al. 2019). Increasingly, researchers are using food webs to study how  
67 species might adapt their trophic behavior under novel conditions and to anticipate the  
68 bioenergetic dynamics of both natural and managed ecosystems like fisheries (Pearse &  
69 Altermatt 2013, Boit et al. 2012, Brose et al. 2019, Gauzens et al. 2020, Eloranta et al. 2022,  
70 Ávila-Thieme et al. 2021).

71         Nevertheless, a lack of systematically collected data has limited even a basic account of  
72 the structure of aboveground terrestrial food webs (ATFWs). Most of the few published ATFWs  
73 (Brose et al. 2019) have focused on resolving only a subset of taxa (e.g., tetrapods), interactions  
74 (e.g., carnivory), energy pathways (e.g., a partial food web on a single resource), or potential  
75 habitats (e.g., under a log) in a system. Structural patterns in some subnetworks have been  
76 identified: larger predators eat smaller prey (Brose et al. 2006), while some types of insect  
77 herbivores form nested, specialized associations with plants (Thébault & Fontaine 2010). Yet it  
78 is still unknown how these subnetworks interconnect into ATFWs, or if these patterns are  
79 relevant in the context of a single system (Hale et al. 2023a). Here, we present and study the  
80 structure of a food web that evenly resolves feeding interactions among all plants, insects, and  
81 tetrapods across aboveground terrestrial habitats at a long-term biological research site.

82         In building our empirical food web, we identified three problems that are especially  
83 prominent in aboveground terrestrial ecosystems. The first problem is uneven and coarse  
84 taxonomic resolution. In many cases, tetrapods are recorded to species-level, while insects are  
85 recorded to order or even coarser taxonomic levels, even though they represent a taxonomically  
86 richer part of the system (Harris & Paur 1972, Dunne 2006, O'Connor et al. 2020, Pringle &

87 Hutchinson 2020). As a result, potentially thousands of plant-insect interactions are reduced to a  
88 single trophic link of equal weight in analyses to a species-specific predator-prey interaction  
89 between tetrapods. The coarseness of this approach may undermine the usefulness of food webs  
90 for management, e.g., by missing critical interactions that affect the abundance of emerging  
91 insect pests. In other cases, species with the same or similar sets of consumers and resources are  
92 grouped into a single node and labeled a “trophic species” (Williams & Martinez 2000, Delmas  
93 et al. 2019). This more tractable representation includes only the unique biomass flows in the  
94 food web and is especially appropriate when all species within a taxonomic group have the same  
95 trophic interactions, rendering the resolution of interactions to species level unnecessary.  
96 Nevertheless, even within such a group, species often vary in their resource usage (e.g., by  
97 consuming vegetation versus seeds), with different nutritional and demographic consequences  
98 (Pringle & Hutchinson 2020). A food web that evenly resolves both resource- and species-  
99 specific interactions could be a powerful tool to study the correspondence between taxonomic  
100 groups and trophic species.

101         The second problem in building an ATFW is the sensitivity of food webs to sampling  
102 effort. A single set of observations provides only a “snapshot” of an ecosystem (Dunne et al.  
103 2006, de Aguiar et al. 2019), biased by the specific spatial (vertical versus horizontal transects,  
104 microhabitats) and temporal (seasonal, diurnal, duration) scales of sampling, as well as the  
105 taxonomic expertise of the investigators (including ability to catch and identify organisms).  
106 Species also exhibit adaptive foraging and defensive behaviors, effectively “rewiring” trophic  
107 interactions in response to changing biotic and abiotic conditions (Bartley et al. 2019, Ceron et  
108 al. 2022, Valdovinos et al. 2023). As such, limited surveys miss rare or cryptic species and  
109 interactions, even though such species and interactions likely provide critical contributions to

110 ecosystem dynamics and function (Dee et al. 2019, Simpson et al. 2022). One solution to this  
111 sampling problem is the concept of a cumulative food web or “metaweb” (Dunne 2006), in  
112 which all species and interactions recorded over years and/or across similar habitats are pooled  
113 into one network of all possible interactions between local species. Such an approach risks  
114 missing system-specific interactions or swamping out the common species and links that  
115 comprise the bulk of the bioenergetic flows in the system. However, as human actions change  
116 species’ distributions and habitats, “rare” and novel interactions are increasing in frequency  
117 (Bartley et al. 2019), making cumulative webs all the more important.

118         The third problem affecting the construction of empirical food webs is the conceptual  
119 inconsistency in the criteria for including different types of feeding interactions. Ideally, a food  
120 web maps all bioenergetic flows between organisms in an ecosystem. Historical ATFWs have  
121 typically only included feeding interactions with ostensibly antagonistic (+/-) effects, such as  
122 predation, herbivory, and sometimes parasitism/parasitoidy. Other feeding interactions with  
123 ostensibly mutualistic (+/+) effects, such as nectarivory (pollination) and frugivory (seed  
124 dispersal), are excluded. However, mutualistic feeding interactions constitute dynamically  
125 important bioenergetic flows in aboveground terrestrial ecosystems (Baude et al. 2016, Hale et  
126 al. 2020), and ignoring them is more an historical artifact of disciplinary subdivisions than a  
127 useful approach to studying biotic interactions or ecosystem functions (Hale & Valdovinos  
128 2021). Moreover, categorizing interactions by effect is problematic because effects can change  
129 over time, space, and according to biotic and abiotic conditions (Chamberlain et al. 2014). For  
130 example, mutualistic interactions can be antagonistic when nectarivory is not coupled with  
131 sufficiently effective pollination behavior (Bronstein 2001). Similarly, antagonistic interactions  
132 can be mutualistic, such as when herbivory stimulates greater plant production in a phenomenon

133 called overcompensation (Ramula et al. 2019). Therefore, there is growing consensus (Abrams  
134 1987, McCall & Irwin 2006, Holland & DeAngelis 2009, Valdovinos et al. 2023) that feeding  
135 interactions should be differentiated by their mediating traits (phenology, ontogeny,  
136 morphology), tissues (nectar, fruit, leaves), and bioenergetic or demographic consequences  
137 (yields and production costs), rather than their presumptive net effects.

138 We began to address these problems by building a food web for a temperate hardwood  
139 forest based upon ~100 years of study by diverse specialists at a biological research station. In  
140 constructing the food web, we emphasized the even resolution of plant, insect, and tetrapod taxa,  
141 resulting in ~580,000 feeding interactions among ~3,800 species. Interactions were collected  
142 from public records and online databases, supplemented by experts and vetted for local  
143 plausibility given species' spatial and temporal co-occurrences, traits, and behaviors. We  
144 included all types of trophic interactions in a “multiplex” food web subdivided by resource type  
145 (i.e., animal and plant tissue types) rather than presumptive effect (i.e., antagonistic versus  
146 mutualistic). Using this food web, we discuss the effects of taxonomic resolution on our  
147 understanding of food web structure.

## 148 **2) Methods**

### 149 **a) Conceptual framework**

150 To determine criteria for including interactions in our food web, we applied a recently-  
151 proposed framework for studying aboveground terrestrial food webs (ATFWs, Valdovinos et al.  
152 2023). This framework asserts that the complexity of plant tissues fundamentally distinguishes  
153 aboveground terrestrial ecosystems from their aquatic and belowground counterparts, shaping  
154 the structure and dynamics of ATFWs through distinctive patterns of growth and turnover.  
155 Different plant tissue types are often only expressed at certain times phenologically and

156 ontogenetically and often require consumers to possess specific morphological and/or  
157 physiological traits to access them. The availability and nutritional yield to the consumer, as well  
158 as the costs of production, maintenance, and loss to the resource, vary substantially between  
159 tissue types. Such differences are highly consequential; tissue-specific feeding may underlie  
160 bioenergetic flows, such as primary production and consumption, in aboveground terrestrial  
161 ecosystems and explain how species coexist even when their partners (consumers or resources)  
162 are otherwise similar. Accounting for this tissue-specific complexity therefore provides more  
163 information than traditional static food web structures and may be key for moving food webs  
164 from simple graphical representations to useful tools for research and management.

165         With this in mind, we chose to include all direct interactions among species in our system  
166 with a bioenergetic flow (i.e., one species consuming another, regardless of their potential  
167 ecological effects), differentiated by their focal resource. We broadly categorized the resources  
168 as (1) animal tissues (live and scavenged) and plant tissues, grouped into (2) leaves and stems ,  
169 (3) flowers, nectar, pollen, etc., (4) seeds, fruits, etc., and (5) wood and bark. Hereafter, we refer  
170 to these resource types simply as “animals,” “leaves,” “flowers,” “seeds,” and “wood.” Due to  
171 our focus on aboveground terrestrial plants and insects, we excluded fungi and detritus resources.  
172 The tissues in each resource category do not have uniform nutritional content, but our framework  
173 provides a start towards representing the different types of resource use and associated foraging  
174 behaviors in food webs.

## 175         **b) Site description**

176         The University of Michigan Biological Station (UMBS) includes ~10,000 acres of land  
177 that is used for teaching and research in northern lower Michigan, USA (45°35.5' N, 84°43' W).  
178 The property is composed predominantly of dry-mesic, northern hardwood forests with patches

179 of wooded wetlands (hardwood conifer swamp) flanked by two lakes (Barnett et al. 2022). This  
180 is a strongly seasonal, temperate system with historically cold, snowy winters (average minimum  
181 temperature of  $-12.1^{\circ}\text{C}$  in January) and hot, humid summers (average maximum temperature of  
182  $26.2^{\circ}\text{C}$  in July; Wang & Ibanez 2022). Soil composition varies across microhabitat patches from  
183 sandy outwash plain to moraine. Prior to acquisition by the University of Michigan in 1909, the  
184 landscape was almost completely logged and burned, with only a few old-growth forest tracts  
185 remaining. Therefore, the vegetative landscape is relatively uniform in age, with variation in  
186 stand structure and composition attributable to glacial landforms and differences in soil  
187 composition (Nave et al. 2017, Ricart et al. 2020).

188 UMBS is contiguous to other forested habitats, allowing free movement in and out for  
189 mobile species, including those that seasonally migrate. Such transient organisms, coupled with  
190 those that are only active or present aboveground during certain times of year, lead to strong  
191 effects of seasonality on species composition. Though their impacts may only be temporary, we  
192 included these species in our analyses because they may represent critical consumers or  
193 resources for local species at certain times of year. In particular, most species of ectotherms at  
194 UMBS are inactive during winter months, and many migratory bird species are present only  
195 during the spring and summer. By pooling observations into a cumulative web, we avoid  
196 sensitivity of food web structure to this spatial and temporal transience.

### 197 **c) Species list**

198 To construct the food web, we began from taxonomic lists of mammals, amphibians,  
199 reptiles, vascular plants, birds, insects, and non-insect arthropods. These lists represent an  
200 accumulation of decades of records at UMBS, from resident biologists' personal observations,  
201 student papers and research projects, regional lists, museum specimens, online databases (such as

202 eBird and iNaturalist), and semi-regular BioBlitz events, in which teams of biologists roamed the  
203 site and identified as many organisms as possible.

204         Where possible, we updated records to the most recently accepted species names  
205 according to the Integrated Taxonomic Information System (ITIS) using the “taxize” package in  
206 R (Chamberlain et al. 2013). We excluded taxa that could not be resolved to at least genus-level  
207 (e.g., parasitoid wasp family Diapriidae). For taxa that could only be resolved to genus, we  
208 excluded those that are highly speciose in the Nearctic (> 20 species, e.g., the bloodworm genus  
209 *Chironomus*) and those that had congeners already included in the food web (e.g., six species  
210 of masked bee *Hylaeus* were included, but another unidentified species was excluded). Finally,  
211 we treated variants and subspecies (e.g., deer mouse *Peromyscus maniculatus gracilis*) as their  
212 binomial species name. Hereafter, we refer to all taxa occurring at UMBS as “species,” though a  
213 small fraction (4.5%) are genera.

214         The species lists were vetted and approved by experts (generally, the authors) that have  
215 extensive knowledge of the communities and natural histories of the organisms that occur in the  
216 region. In determining which species to include or exclude, we excluded any species that do not  
217 occur at UMBS or do not have a significant lifestage or feeding behavior in aboveground  
218 terrestrial habitats (O’Connor et al. 2020). We defined “aboveground terrestrial habitats” as land  
219 above the soil layer (including leaf litter and above), on terrestrial plants (growing potentially  
220 over but not exclusively in water), or in air (above other terrestrial habitats). Thus, we excluded  
221 species that live and feed primarily on the surface of aquatic habitats, such as waterlilies  
222 (Nymphaeaceae) and water bugs (Belostomatidae). Additionally, given our primary focus on even  
223 resolution among plants, arthropods, and tetrapods, we chose to exclude some major groups,  
224 such as bryophytes, fungi, lichens, and molluscs.

225 **d) Feeding interactions**

226 To assemble a list of potential feeding interactions between species, we referenced  
227 region-specific field guides, online databases (e.g., Animal Diversity Web, Birds of the World),  
228 and central repositories that automatically scrape data from museum records and the web (e.g.,  
229 Global Biotic Interactions). Trained undergraduate researchers searched sources by species name  
230 and recorded predators, diet, and other potential feeding interactions with as much resolution as  
231 possible. Each focal taxon was resolved to species-level, but their interaction partners could be  
232 recorded at any taxonomic level (e.g., species  $x$  eats Family  $y$ ). If we could not find information  
233 on a given focal species, we did not extrapolate from closely related species. Our records were  
234 supplemented, revised, and annotated by the same experts who vetted the species lists. Where  
235 possible, records were assigned to experts for both the focal species and its partner's group (that  
236 is, two separate experts). We provide the final list of annotated interactions and their experts  
237 online (Hale et al. 2023b).

238 Experts were asked to assess the plausibility of the recorded interactions occurring at  
239 UMBS. Interactions between species  $x$  and  $y$  were considered plausible if the two species co-  
240 occur (with respect to phenology, activity patterns, microhabitat usage) and have no trait  
241 incompatibilities (it would not be possible for  $x$  to acquire, ingest, or assimilate  $y$ ). Interactions  
242 were considered plausible even if they could be considered inefficient ( $x$  can consume  $y$ , but this  
243 is rare or unlikely, especially if more rewarding and easily acquired foods than  $y$  are available).  
244 Interactions that are non-consumptive (e.g., nesting or hunting locations) or occur outside of  
245 aboveground terrestrial habitats were excluded even if they occur between local species (e.g.,  
246 least sandpiper *Calidris minutilla* preys upon toad *Anaxyrus americanus* tadpoles, but this occurs  
247 exclusively in aquatic habitats).

248 Experts were also asked to assess the plausibility of the taxonomic level at which  
249 interactions were recorded. For example, when Wilson’s warbler (*Cardellina pusilla*) is recorded  
250 to eat beetles (order Coleoptera), it is unclear if: (case 1) *C. pusilla* eats every species of  
251 Coleoptera, potentially or opportunistically, including all local Coleopterans, or (case 2) *C.*  
252 *pusilla* eats (at least) one species of Coleoptera that was not identified in the original record and  
253 which may or may not be local. Either case may be possible, depending on the biology of the  
254 species. At one extreme (case 1), the lack of taxonomic resolution in the record could reflect an  
255 ecologically relevant lack of discrimination by the focal species (e.g., opportunism due to  
256 sensory capabilities in distinguishing between predators or resources), with the probability of  
257 interactions occurring between any given partner species determined more by interaction  
258 efficiency or abundance than by taxonomy. At the other extreme (case 2), the lack of taxonomic  
259 resolution could simply reflect a lack of knowledge, representing a summary of potentially  
260 highly specific interactions. In the first case, experts accepted the interaction, while in the  
261 second, experts rejected the interaction unless it could be plausibly revised for local taxa.

262 In the original sources, interactions were often recorded following traditional disciplinary  
263 categorizations. In the absence of other information, we assumed that animals recorded as  
264 “eating,” “feeding on,” “consuming,” “parasitizing,” or “hosted by” plants were consuming plant  
265 leaves. We assumed that animals recorded as “pollinator of,” “visiting flowers of,” “visiting,” or  
266 “mutualist of” plants were consuming flowers. Other mutualisms involving potential feeding  
267 such as seed dispersal (through frugivory, scatterhoarding, etc.) and ant protection (of  
268 hemipterans or plants) were noticeably underrepresented in our records. We assumed animals  
269 recorded as “disperser of” plants were consuming seeds. We assumed that interactions between  
270 animals recorded as “kills,” “predates upon,” “scavenges,” “host of,” “parasite of,” or “parasitoid

271 of” involved consumption of animal tissue. When necessary, these default assumptions were  
272 revised by experts to reflect true feeding on another tissue or a lack of feeding altogether.

### 273 e) **Network representation and analysis**

274 To translate our list of interactions into a food web, we used a “multiplex” network  
275 approach in which feeding on different types of tissues is represented by different types of links  
276 between the same set of nodes (species). This allows us to distinguish between the niches of  
277 animals feeding on different tissues of the same plant, while also representing that these tissues  
278 are coupled to each other in the same organism. Specifically, we defined a node for each focal  
279 species  $i$  in our list. Then, we defined a directed link of type  $k$  between nodes  $i, j$  if  $i$  consumes  
280 tissue type  $k$  of  $j$  or tissue type  $k$  of a broader taxonomic group including  $j$ . Links are binary,  
281 indicating the presence or absence of potential feeding, not its frequency, probability, rate, or  
282 strength. We retained only unique links, but tracked the most resolved taxonomic level from  
283 which each link was sourced.

284 To assess the extent to which taxonomic groupings represent the unique trophic functions  
285 in food webs, we calculated trophic similarities across taxonomic resolutions. We used the  
286 Jaccard index, which ranges from 1, when a pair of species have all consumers and resources  
287 (both species and tissue types) in common, to 0, when species have completely unique sets of  
288 consumers and resources. For each genus, family, and order containing  $> 1$  species, we  
289 calculated the average of the minimum trophic similarities between each species  $i$  with all other  
290 species  $j$  in its taxonomic group. We also calculated trophic similarity between each pair of  
291 species ( $i, j$ ) in our food web and created a “trophic species web” by grouping species with  
292 trophic similarities of 1 into single nodes. This grouping removes functionally redundant nodes

293 and links. All data cleaning and network analyses were performed in MATLAB R2021b  
294 (Mathworks).

### 295 **3) Results**

#### 296 **a) Species composition and database**

297 Our final species list includes 3,802 local species, representing 2,073 genera in 451  
298 families of 86 orders (Fig. 1). Insects (2,669 species) and vascular plants (781 species)  
299 numerically dominate the food web, accounting for ~90% of the taxa, compared to tetrapods  
300 (313 species) and non-insect arthropods (39 species). The richest orders in our list are insects,  
301 especially Lepidoptera (butterflies and moths, 1,168 species), Coleoptera (beetles, 512 species),  
302 Diptera (flies, 390 species), Hymenoptera (bees, wasps, and ants, 265 species), and Hemiptera  
303 (true bugs, 211 species). Worldwide, there are more than twice as many named species of  
304 Coleoptera as Lepidoptera; therefore, Lepidopterans are likely substantially overrepresented in  
305 our list. The vascular plants are our most taxonomically diverse group, with 38 orders  
306 represented primarily by two groups of flowering plants, Poales (grasses, sedges, and rushes, 149  
307 species) and Asterales (composite flowers, 96 species). Our tetrapod species are birds (226  
308 species, including 127 passeriform birds), mammals (52 species, including 7 bats), amphibians  
309 (18 species), and reptiles (17 species). Finally, our non-insect arthropods primarily include  
310 spiders and mites, but overall, this group is significantly underrepresented in our list, both in  
311 terms of richness and taxonomic diversity.

312 Our database of feeding interactions between local species amounted to 26,747 approved  
313 records. In sum, our final food web totals 2,541 species of consumers (including 4 carnivorous or  
314 parasitic plants) and 3,782 species of resources. We have no records for 19 plants (~0.5% of  
315 local species), including most of the Lycopodiales (clubmosses, 5 of 6 species) and the

316 Polypodiales (ferns, 11 of 19 species), two of the major groups of non-seed plants in our system.  
317 Additionally, our records include no diet information for 485 species of insects (~16.3% of local  
318 animals), primarily from the richest orders (183 Lepidopterans, 145 Dipterans, 109  
319 Coleopterans), but also including all Blattodea (cockroaches, 2 species), Plecoptera (stoneflies, 2  
320 species), Mecoptera (scorpionflies, 4 species), and Zygentoma (silverfish, 1 species). Some of  
321 these do not feed in aboveground terrestrial habits (or at all) during a certain lifestage or feed  
322 entirely upon resources we excluded (fungi, detritus, lichens, etc.), limiting their potential diet in  
323 our food web. However, these gaps in our dataset may also indicate broader gaps in our natural  
324 history knowledge for these species.

#### 325 **b) Feeding interactions**

326 Our final food web totals 586,601 unique feeding interactions between local species.  
327 These interactions consist primarily of feeding on animals (89.7%), especially insects, with the  
328 remaining interactions consisting of feeding on plant leaves (6.8%), flowers (2.2%), seeds  
329 (1.2%), or wood (0.17%). Though numerous, these interactions are only a small fraction of the  
330 possible links. Separating feeding on each type of resource, we calculate that only 5.8% of the  
331 carnivory interactions are realized among the 3,023 participating species, with similarly low  
332 connectance for the different types of herbivory (leaves: 3.1% among 2,480 species, flowers:  
333 2.2% among 1,537 species, seeds: 5.0% among 804 species, wood: 9.8% among 200 species).  
334 Comparisons to similarly rich networks are not available in the literature. However, our  
335 carnivory subnetwork is both more connected given its richness than expected from a scaling law  
336 fit to previous food webs (1.5%, Cohen & Briand 1984, Montoya & Solé 2003, Ings et al. 2009)  
337 and more connected than a recently published metaweb of only tetrapods (3.9% with 1,136  
338 species, O'Connor et al. 2020).

339 Carnivory is the numerically dominant interaction in our food web, but only  
340 approximately one-third (35.9%) of consumers feed on animal tissues. These consumers exhibit  
341 a heavily skewed diet breadth distribution, where most feed on a small number of animal species  
342 but a few (primarily the bats and birds) are hypergeneralists (Fig. 2A). In fact, the 127  
343 passeriform bird species (5.0% of consumers) contribute over half (51.4%) of the unique  
344 carnivory links in our network, sourced from only 711 (2.7%) records of focal bird species  
345 thought to feed opportunistically upon entire insect orders (especially Coleoptera and  
346 Lepidoptera). Records of feeding on insect orders by any taxon contribute 87.1% of unique  
347 carnivory links overall, meaning that they are not otherwise included by records at lower  
348 taxonomic levels (Supplementary Fig. 1A). In comparison, feeding between tetrapods accounts  
349 for only 1.3% of carnivory links.

350 Herbivory interactions are less numerous than carnivory, but most consumers (86.0%) in  
351 our food web feed on plants, with nearly half (46.0%) feeding on a single plant tissue. These are  
352 primarily insects, dominated by Lepidopterans eating leaves (as caterpillars), but also including  
353 Hymenopterans and Dipterans eating flowers (nectar). Like carnivores, herbivores across  
354 resource types have skewed diet breadth distributions (Fig. 2B-E). Considering specialization in  
355 terms of number of taxonomic resource families rather than resource species richness, we also  
356 see a skewed distribution, with many insect families feeding on a single plant family and a long  
357 tail of a few taxonomically generalized insect families (Fig. 2F). Perhaps reflecting this  
358 taxonomic specialization, over half of our herbivory interactions (66.4%) stem from records of  
359 feeding between insects and plants at the genus- and species-level, with only 4.1% of unique  
360 herbivory interactions contributed by order-level records across all taxonomic groups  
361 (Supplementary Fig. 1B). Therefore, in contrast to carnivory, our herbivory records at coarser

362 taxonomic levels do not include or are redundant to interactions from more taxonomically-  
363 resolved records.

364 Over one-third of consumers (40.1%) feed upon more than one type of resource. Around  
365 half of these consumers feed on leaves and flowers (19.1% of consumers, primarily  
366 Lepidopterans and Coleopterans). A smaller fraction (11.3%) feed on > 2 types of resources, but  
367 these are a more diverse set of insects, mammals, and birds feeding on animals, leaves, and  
368 flowers or seeds, or, less frequently, leaves, flowers, and wood. Among these consumers, we  
369 observed significant positive correlations between diet breadths when feeding on animals and  
370 plant leaves (Pearson correlation:  $r = 0.28$ ,  $p = 2.0 \times 10^{-7}$ ,  $N = 340$ ), animals and plant seeds ( $r =$   
371  $0.15$ ,  $p = 0.044$ ,  $N = 202$ ), plant leaves and seeds ( $r = 0.42$ ,  $p = 7.2 \times 10^{-9}$ ,  $N = 178$ ), and plant  
372 leaves and wood ( $r = 0.23$ ,  $p = 0.017$ ,  $N = 98$ ; also see Supplementary Fig. 2). In other words,  
373 among animals that access multiple types of resources, generalists on one resource type also tend  
374 to be generalists on others. Interestingly, though many consumers access multiple types of  
375 resources, only a very small fraction of interactions (0.65%) are between the same pair of  
376 consumer and resource species, indicating feeding on multiple plant tissues by the same  
377 consumer.

378 In contrast to the tissue specialization by most animals, most plants (91.3% of 781  
379 species) support consumers on more than one of their tissues, with a small set of diverse plants  
380 (85 species in 13 orders) sustaining feeding on all four recorded tissue types. We observed  
381 significant positive correlations between the richnesses of consumers feeding on plants' leaves  
382 and flowers (Pearson correlation:  $r = 0.16$ ,  $p = 3.4 \times 10^{-5}$ ,  $N = 653$ ), leaves and seeds ( $r = 0.35$ ,  $p$   
383  $= 8.1 \times 10^{-17}$ ,  $N = 548$ ), and leaves and wood ( $r = 0.61$ ,  $p = 1.7 \times 10^{-11}$ ,  $N = 98$ ; also see  
384 Supplementary Fig. 3). In other words, the plants most consumed by leaf-herbivores are also

385 most likely to host rich communities of consumers eating their other tissues. However, the  
386 richnesses of animals eating plants' flowers and seeds was negatively correlated ( $r = -0.11$ ,  $p =$   
387  $0.013$ ,  $N = 514$ ). This may suggest a trade-off in plants' ability to support flower and seed eaters  
388 (potential pollinator and seed dispersal mutualists, respectively) or a deterrence effect between  
389 seed- and flower-eaters in our system (primarily birds and insects, respectively).

### 390 **c) Trophic similarity**

391 Two thirds of our taxonomic species (2,396 of 3,802, 63.0%) are unique trophic species  
392 (Fig. 3A), meaning that they have unique sets of consumers and resources. Of these, 29 species  
393 are distinguished only by feeding on different plant tissue types. In total, all tetrapods, nearly all  
394 non-insect arthropods (97.4%), over three-quarters of plants (77.1%), and almost two-thirds of  
395 insects (62.7%) are trophically unique species. The remaining 30.9% of taxonomic species are  
396 pooled into 231 trophic species groups, each composed of species from a single taxonomic order.  
397 This may be because entire orders of insects share the same opportunistic/generalist predators  
398 and are therefore only distinguished by their diets. Indeed, over half of these species (54.1%,  
399 760) are represented in only 27 trophic species groups; these comprise most (82.9%) of the 485  
400 animal species without diet information (that is, the species most likely lacking resolution in our  
401 food web). The remaining trophic species groups include closely related taxonomic species, but  
402 do not perfectly correspond to lower taxonomic levels. For example, the 10 species of *Zale*  
403 moths in our food web are present in 8 different trophic species groups with other Lepidopterans  
404 across 8 families.

405 Even if they are technically unique, closely related taxonomic species tend to be  
406 trophically similar. Most genera and families have an average minimum trophic similarity close  
407 to one (median among genera: 0.884, families: 0.745, Fig. 3B-C), indicating that species share

408 most (but not strictly all) trophic interactions with their congenics and confamilars. On the  
409 other hand, taxonomic orders have a very low trophic similarity ( $< 0.05$ , Fig. 3D), indicating the  
410 presence of species that share very few or no trophic links with other species in their order. This  
411 result is primarily driven by plants, which generally show low trophic similarity even within  
412 families (median among plant orders: 0.023, families: 0.148, genera: 0.688).

413 Relative to the original food web, our trophic species web includes more richness  
414 (81.5%) and more unique links (75.1%) among herbivory interactions than among carnivory  
415 interactions (67.1% and 62.5% of the original richness and links). In other words, the herbivory  
416 interactions are more frequently functionally distinct than carnivory interactions in our food web  
417 and therefore provide the key source of niche differentiation (decreased trophic similarity)  
418 between species.

#### 419 **4) Discussion**

420 Aboveground terrestrial ecosystems contain immense taxonomic diversity, especially  
421 among insect and plant species. Studying these interactions in aboveground terrestrial food webs  
422 (ATFWs) has been limited by three problems: taxonomic resolution of species, sensitivity to  
423 sampling effort, and conceptual inconsistency in the definition of feeding interactions. To  
424 overcome the problem of taxonomic resolution, we built our food web with taxa evenly resolved  
425 to species level and investigated the effect of resolution on unique trophic functions. To  
426 overcome the problem of sampling, we pooled public records and decades of biological research  
427 at a single site into an expert-approved, cumulative food web. This reduces the likelihood that we  
428 missed cryptic or rare species in our system and provides a more comprehensive accounting of  
429 the potential feeding interactions. Finally, to overcome the problem of conceptual  
430 inconsistencies, we extended a framework for studying ATFWs in which we included all types

431 of feeding interactions represented in a multiplex network as different types of feeding links by  
432 the type of resource (animals or plant tissues) being consumed.

433 Our ATFW is the largest food web yet published and begins to shine light on the  
434 remarkable richness of feeding interactions between plants and animals in temperate forests. Our  
435 approach allowed us to evenly resolve the diets of both tetrapod and insect feeding guilds,  
436 revealing a clear division between herbivory and carnivory interactions in our food web.  
437 Carnivory interactions were numerous and non-specific, primarily sourced from interaction  
438 records resolved to the order-level. Herbivory interactions were less numerous but more specific,  
439 both taxonomically and in terms of different resource types. Most unique herbivory interactions  
440 were sourced from records resolved to the genus- or species-level, and this specificity  
441 corresponded to decreased trophic similarity (i.e., increased niche differentiation) among species  
442 in our food web. The lack of taxonomic resolution in our carnivory records may simply reflect  
443 limited knowledge about dietary preferences. However, our results are consistent with previous  
444 food web research (primarily in aquatic systems) showing that larger species tend to have higher  
445 trophic levels and more generalized diets in terms of number of resources (Brose et al. 2006).

446 Species in our food web shared many of their consumers and resources with other species  
447 in their genus or family (i.e., were trophically similar). This is not surprising – close taxa share  
448 most of their evolutionary histories and therefore many of the traits (e.g., body size, shape of  
449 mouthparts, bio/phytochemistry) that govern their interactions (Ibanez et al. 2016). Insect  
450 herbivores are particularly specialized to sense and tolerate the chemical and physical cues and  
451 defenses of plant hosts with which they have coevolved (Loxdale & Harvey 2016). Indeed, insect  
452 families in our food web not only share the same bird predators but also most frequently are  
453 specialists on a single plant family, limiting their potential diet differences. A global study of diet

454 breadth among insect herbivores (Forister et al. 2015) showed even more frequent taxonomic  
455 specialization than we observed, but we also expect that our temperate site, inclusion of non-  
456 angiosperm host plants, and likely under-sampling of leaf-gallers leads to less specialization in  
457 our system than globally. Given this and the immense richness of insects, it is surprising that we  
458 resolved most insects in our food web as unique trophic species. We expect that further study  
459 would reveal nearly all taxonomic species to be trophically unique (Hutchinson & Pringle 2020).  
460 Niche theory suggests that distinct species (even closely related ones) should vary in their  
461 resource usage, though potentially in dimensions we did not record, including spatially,  
462 temporally, within our resource groupings, on resources we excluded, or outside of our system  
463 boundaries (i.e., in aquatic or belowground habitats). Regardless, the higher resolution herbivory  
464 records in our system differentiated insects by the species or tissue types of their plant resources.  
465 if we had focused primarily on tetrapod interactions as in previous work, coarse insect groupings  
466 would appear to be justified. Instead, our findings suggest that coarse taxonomic groupings  
467 (order- and family-level) are not an appropriate proxy for trophic species groupings in ATFWs.

#### 468 **a) Limitations**

469 Though we sought to document all species and feeding interactions at UMBS, our approach  
470 still had methodological limits. As in all food webs, our system boundaries were largely  
471 arbitrary. Many of our species live or feed in aquatic or belowground habitats during a certain  
472 lifestage, and interactions coupling these different habitats can significantly affect ecosystem-  
473 level processes (e.g., through plant growth). Our lists excluded fungi, non-vascular plants, most  
474 non-insect invertebrates, and detritus, though these likely account for a substantial fraction of the  
475 species richness and feeding interactions in our system. Furthermore, regional lists suggest that  
476 there should be many more insect species (especially beetles, wasps, and true bugs) than have

477 been directly recorded at UMBS. We also are aware that many of our species are missing  
478 interactions because we were not able to find or verify species-specific data (due to taxonomic or  
479 other data limitations) or because records were too vague (e.g., “eating seeds” without further  
480 specificity). Together, this meant that 3.0% of our species had interactions only from order-level  
481 records, while 14.1% and 20.6% of our species (primarily insects) had interactions only from  
482 family- or genus-level records, respectively. In contrast, interactions with common, charismatic,  
483 or economically important species are likely more comprehensively documented in our food  
484 web. Lastly, just as we designated different plant tissues (see *Conceptual Framework*), feeding  
485 by or on different animal tissues (e.g., blood) or lifestages (e.g., eggs) likely has different  
486 implications for the relevant consumer and resource species, as well as anticipated biomass flows  
487 in the food web. Future work should investigate the effect of separating these interaction types in  
488 a multiplex network.

#### 489 **b) A path forward**

490 We are in a new era of ecological big data, which provides an opportunity for a new era  
491 of food web ecology. Building databases of potential species interactions at research stations is a  
492 scalable process that could facilitate management decisions and stimulate ecological networks  
493 research. In this way, our approach complements recent advances in DNA barcoding, text-  
494 mining, and remote sensing that could ultimately lead to automated approaches to collecting,  
495 analyzing, and interpreting ecological networks using artificial intelligence and machine  
496 learning.

497 Nevertheless, the construction of our food web demonstrated that the role of ecological  
498 expertise (natural history and taxonomic) remains invaluable for at least three reasons: (1)  
499 identifying taxonomic conflicts, (2) clarifying nomenclature across ecological subdisciplines,

500 and (3) interpreting the scale of interactions. First, because taxonomic names are consistently  
501 updated, experts were critical for clarifying the relevant interaction records and the most up-to-  
502 date species nomenclature. Second, when interaction records listed species as “host,” “parasite,”  
503 “mutualist,” etc., experts could clarify whether feeding occurred and on what type of resource.  
504 Third, and most critically for the network presented here, experts assessed whether an interaction  
505 could feasibly occur in our system given species’ temporal and spatial co-occurrence and  
506 whether the taxonomic level of the record (genus, family, etc.) was representative of true  
507 potential interactions between species given their biologies (sensory capabilities, size, mobility,  
508 etc.). Some of these issues could be resolved with better data management (e.g., clearly defining  
509 the types of identifiers used to report species interactions), but local and organism-specific  
510 knowledge will likely remain an important part of building and using ecological networks (also  
511 see Poisot et al. 2023). Our work therefore highlights both the opportunity and the challenge to  
512 develop large collaborations among specialists, students, and the public as we seek to understand  
513 the complexity of natural ecosystems.

514 Finally, ecological networks have historically been published and analyzed as static  
515 structures, encapsulating the biases and practical limitations of their collection. As such,  
516 publication in online databases and consistent re-use in meta-analyses by network scientists can  
517 perpetuate errors (Hutchinson & Pringle 2020). Our ATFW represents a first attempt at  
518 documenting the immense complexity of aboveground terrestrial ecosystems. We advocate a  
519 shift in mindset when it comes to ecological networks, considering them as living datasets that  
520 can be revised and expanded as collaborations and knowledge grows. To that end, our database  
521 is publicly available (Hale et al. 2023b), and we are soliciting revisions, corrections, and  
522 additions that will allow its continual improvement.

523

## 524 **Acknowledgements**

525 We thank Adam Schubel, Jason Tallant, Aimee Classen, Knute Nadelhoffer, and other current  
526 and former University of Michigan BioStation (UMBS) staff for providing the original species  
527 lists and hosting the living version of the dataset. We are immensely grateful to Teresa Pegan,  
528 Eric Gulson, Simone Oliphant, Nate Sanders, Daniel Swanson, Anton Reznicek, Erika Tucker,  
529 and undergraduate research team Kathrine Northman, Taylor Brubaker, John Kelly, Lynnae  
530 Gilman, Matthew Palumbo, Lex Newman, and Stephan Verral for contributions to data  
531 acquisition and vetting. We acknowledge that the Indian Point Reserve (gifted to UMBS in  
532 1987) includes lands of the Burt Lake Band of Ottawa and Chippewa Native Americans from  
533 which they were brutally and illegally evicted in 1900. The University of Michigan  
534 Undergraduate Research Opportunities Program (UROP) paid the undergraduate researchers for  
535 their time. This work was partially funded by NSF grants DEB-2129757 and DEB-2224915 to  
536 F.S.V.

537

## 538 **Data Availability Statement**

539 Species and interaction data are openly available via the Environmental Data Initiative at  
540 <https://doi.org/10.6073/pasta/840d70788bde4692a7d6d45f8d04376f>. Supplementary figures are  
541 available in the online version of this article.

542

## 543 **References**

544 Abrams P. A. 1987 On classifying interactions between populations. *Oecologia*, 73(2), 272–281.  
545 (doi:10.1007/BF00377518)

546 Ávila-Thieme MI *et al.* 2021 Alteration of coastal productivity and artisanal fisheries interact to  
547 affect a marine food web. *Scientific Reports*, 11(1). (doi:10.1038/s41598-021-81392-4)

548 Bartley TJ, *et al.* 2019 Food web rewiring in a changing world. *Nat Ecol Evol.* 3, 345–354.  
549 (doi:10.1038/s41559-018-0772-3)

550 Baude M, Kunin WE, Boatman ND, Conyers S, Davies N, Gillespie MAK, Morton RD, Smart  
551 SM, Memmott J. 2016 Historical nectar assessment reveals the fall and rise of floral resources in  
552 Britain. *Nature* 530, 85–88. (doi:10.1038/nature16532)

553 Boit A, Martinez, ND, Williams RJ, Gaedke U. 2012 Mechanistic theory and modelling of  
554 complex food-web dynamics in Lake Constance. *Ecology Letters*, 15(6), 594–602.  
555 (doi:10.1111/j.1461-0248.2012.01777.x)

556 Bronstein JL. 2001 The exploitation of mutualisms. *Ecol Lett* 4, 277–287. (doi:10.1046/j.1461-  
557 0248.2001.00218.x)

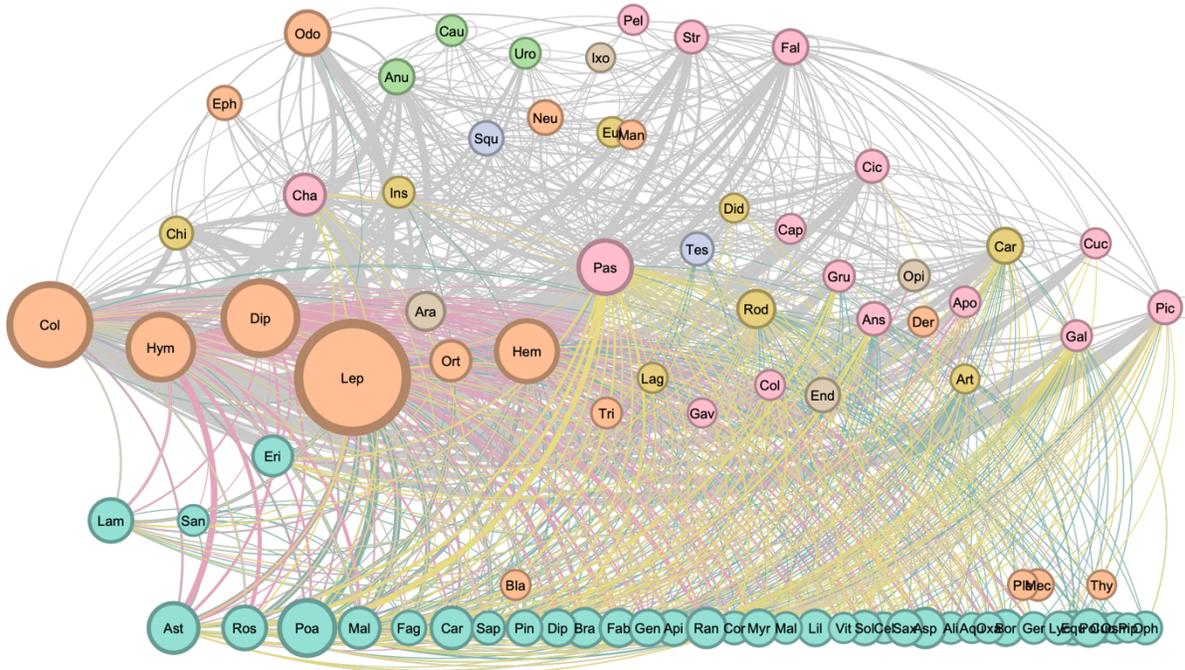
- 558 Brose U *et al.* 2019 Predator traits determine food-web architecture across ecosystems. *Nat Ecol*  
559 *Evol* 3, 919–927. (doi:10.1038/s41559-019-0899-x)
- 560 Brose U, Williams RJ, Martinez ND. 2006 Allometric scaling enhances stability in complex food  
561 webs. *Ecol Lett* 9, 1228–1236. (doi:10.1111/j.1461-0248.2006.00978.x)
- 562 Ceron, K, *et al.* 2022. Differences in Prey Availability across Space and Time Lead to  
563 Interaction Rewiring and Reshape a Predator–Prey Metaweb. *Ecology* 103(8): e3716.  
564 (doi:10.1002/ecy.3716)
- 565 Chamberlain SA, Bronstein JL, Rudgers JA. 2014 How context dependent are species  
566 interactions? *Ecol Lett* 17, 881–890.
- 567 Chamberlain, SA, Szöcs, E 2013 taxize: taxonomic search and retrieval in R. *F1000Research*, 2,  
568 191. (doi:10.12688/f1000research.2-191.v2)
- 569 Cohen JE, Briand F. 1984 Trophic links of community food webs. *Proc. Natl. Acad. Sci.* 81(13),  
570 4105–4109.
- 571 De Aguiar MAM *et al.* 2019 Revealing biases in the sampling of ecological interaction networks.  
572 *PeerJ* 2019. (doi:10.7717/peerj.7566)
- 573 Dee LE *et al.* 2019 When do ecosystem services depend on rare species? *Trends Ecol. Evol.*, 1–  
574 1. (doi:10.1016/j.tree.2019.03.010)
- 575 Delmas E *et al.* 2019 Analysing ecological networks of species interactions. *Biological Reviews*  
576 94, 16–36. (doi:10.1111/brv.12433)
- 577 Dunne JA. 2005 The Network Structure of Food Webs. *Structure*, 27–86.
- 578 Eloranta AP, Perälä T, Kuparinen A. 2023 Effects of temporal abiotic drivers on the dynamics of  
579 an allometric trophic network model. *Ecol Evol.* 13(3):e9928. (doi:10.1002/ece3.9928)
- 580 Forister ML, *et al.* 2015 The global distribution of diet breadth in insect herbivores. *PNAS*,  
581 112(2), 442–447. (doi:10.1073/pnas.1423042112)
- 582 Gauzens B, Rall BC, Mendonça V, Vinagre C, Brose U. 2020 Biodiversity of intertidal food  
583 webs in response to warming across latitudes. *Nature Climate Change*, 10(3), 264–269.  
584 (doi:10.1038/s41558-020-0698-z)
- 585 Hale KRS, Thébault E, Valdovinos FS. 2023a A general trait-based model for multiplex  
586 ecological networks. *BioRxiv*. (doi:10.1101/2023.08.08.552546)

- 587 Hale, KRS, Curlis, J, Auteri, GG, Bishop, S, French, RL, Jones, LE, Mills, KL, Scholtens, BG,  
588 Simons, M, Thompson, C, Tourville, J Valdovinos, FS. 2023b University of Michigan Biological  
589 Station cumulative food web data for terrestrial habitats ver 1. *Environmental Data Initiative*.  
590 (doi: 10.6073/pasta/840d70788bde4692a7d6d45f8d04376f)
- 591 Hale KRS, Valdovinos FS, Martinez ND. 2020 Mutualism increases diversity, stability, and  
592 function of multiplex networks that integrate pollinators into food webs. *Nat Commun* 11.  
593 (doi:10.1038/s41467-020-15688-w)
- 594 Hale KRS, Valdovinos FS. 2021 Ecological theory of mutualism: Robust patterns of stability and  
595 thresholds in two-species population models. *Ecol Evol* 11, 17651–17671.  
596 (doi:10.1002/ece3.8453)
- 597 Harris LD, Paur LF. 1972 A quantitative food web analysis of a shortgrass community.  
598 *Technical report (US International Biological Program Grassland Biome)*, 11–21.
- 599 Holland JN, DeAngelis DL. 2009 Consumer-resource theory predicts dynamic transitions  
600 between outcomes of interspecific interactions. *Ecol Lett* 12, 1357–1366. (doi:10.1111/j.1461-  
601 0248.2009.01390.x)
- 602 Ibanez S, Arène F, Lavergne S. 2016 How phylogeny shapes the taxonomic and functional  
603 structure of plant–insect networks. *Oecologia*, 180(4), 989–1000. (doi:10.1007/s00442-016-  
604 3552-2)
- 605 Ings TC, *et al.* 2009 Ecological networks - Beyond food webs. *Journal of Animal Ecology*, 78(1),  
606 253–269. (doi:10.1111/j.1365-2656.2008.01460.x)
- 607 McCall, AC, Irwin, RE 2006 Florivory: the intersection of pollination and herbivory. *Ecology*  
608 *Letters*, 9, 1351-1365.
- 609 Montoya JM, Solé RV. 2003 Topological properties of food webs: from real data to community  
610 assembly models. *Oikos*, 102(3), 614–622.
- 611 Nave LE, Gough CM, Perry CH, Hofmeister KL, le Moine JM, Domke GM, Swanston CW,  
612 Nadelhoffer, KJ. 2017 Physiographic factors underlie rates of biomass production during  
613 succession in Great Lakes forest landscapes. *Forest Ecology and Management*, 397, 157–173.  
614 (doi:10.1016/j.foreco.2017.04.040)
- 615 O’Connor L, *et al.* 2020 Unveiling the food webs of tetrapods across Europe through the prism  
616 of the Eltonian niche. *J Biogeogr* 47: 181– 192.
- 617 Pearse IS, Altermatt F. 2013 Predicting novel trophic interactions in a non-native world. *Ecology*  
618 *Letters*, 16(8), 1088–1094. (doi:10.1111/ele.12143)

- 619 Petchey OL, Beckerman AP, Riede JO, Warren PH. 2008 Size, foraging, and food web structure.  
620 *Proc Natl Acad Sci U S A* 105, 4191–4196. (doi:10.1073/pnas.0710672105)
- 621 Poisot T, Dalla Riva G, Desjardins-Proulx P, Luccioni AS, Valentino G, Riva D. 2023 The  
622 future of ecological research will not be (fully) automated. *Authorea*  
623 (doi:10.22541/au.169384322.27179185/v1)
- 624 Potapov AM, Brose U, Scheu S, Tiunov A V. 2019 Trophic Position of Consumers and Size  
625 Structure of Food Webs across Aquatic and Terrestrial Ecosystems. *American Naturalist* 194,  
626 823–839. (doi:10.5061/dryad.4dq31c5)
- 627 Pringle RM, Hutchinson MC. 2020 Resolving Food-Web Structure. *Annu Rev Ecol Evol Sys.* 51,  
628 55–80. (doi:10.1146/annurev-ecolsys-110218)
- 629 Ramula S, Paige KN, Lennartsson T, Tuomi J. 2019 Overcompensation: a 30-year perspective.  
630 *Ecology* 100, 1–6. (doi:10.1002/ecy.2667)
- 631 Ricart RD, Pearsall DR, Curtis PS. 2020 Multidecadal shifts in forest plant diversity and  
632 community composition across glacial landforms in northern lower Michigan, USA. *Canadian*  
633 *Journal of Forest Research*, 50(2), 126–135. (doi: 10.1139/cjfr-2019-0138)
- 634 Simpson DT, *et al.* (2022). Many bee species, including rare species, are important for function  
635 of entire plant-pollinator networks. *Proceedings of the Royal Society B: Biological Sciences*,  
636 289(1972). <https://doi.org/10.1098/rspb.2021.2689>
- 637 Stouffer DB, Rezende EL, Amaral LAN. 2011 The role of body mass in diet contiguity and  
638 food-web structure. *Journal of Animal Ecology*, 80: 632-639. (doi:10.1111/j.1365-  
639 2656.2011.01812.x)
- 640 Thébault E, Fontaine C. 2010 Stability of ecological communities and the architecture of  
641 mutualistic and trophic networks. *Science*, 329(5993), 853–856. (doi:10.1126/science.1188321)
- 642 Valdovinos FS *et al.* 2023 A bioenergetic framework for aboveground terrestrial food webs.  
643 *Trends Ecol Evol.* 38, 301–312. (doi:10.1016/j.tree.2022.11.004)
- 644 Williams RJ, Martinez ND. 2000 Simple rules yield complex food webs. *Nature* 404, 180–183.

645 **5) Figures**

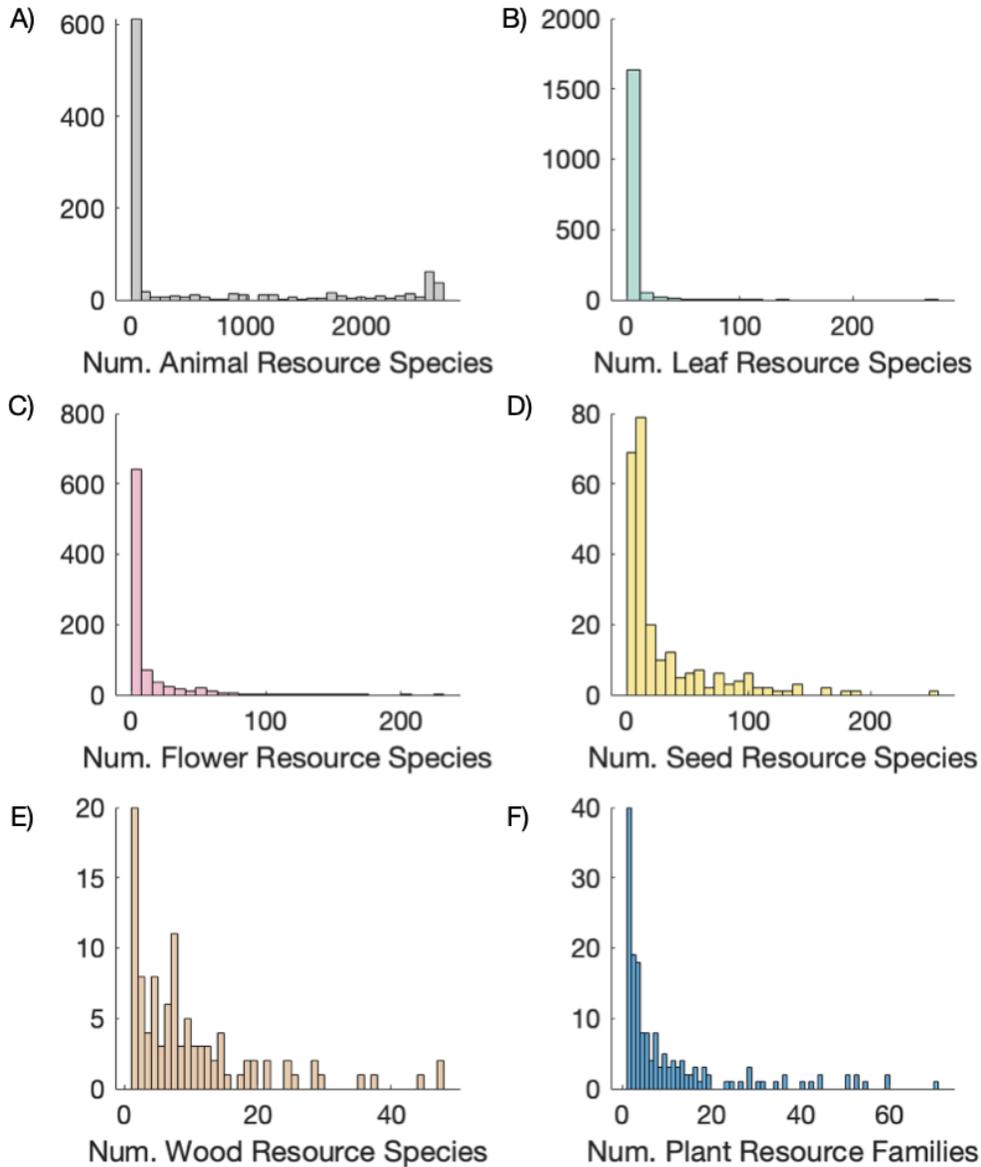
646



647

648 **Figure 1 Visualization of a temperate forest food web in northern Michigan**

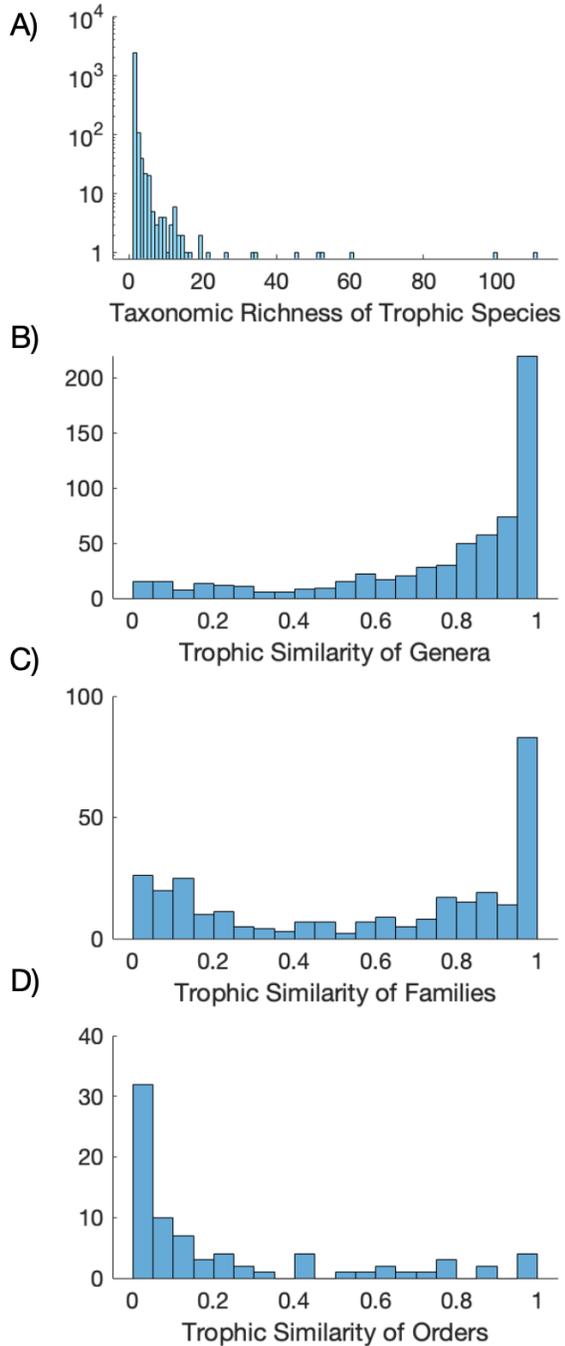
649 Multiplex food web for the aboveground habitats in the University of Michigan Biological  
650 Station, grouped to taxonomic order. Each node is a taxonomic order, sized according to the  
651 number of species in each order and colored according to taxonomic group (plants in dark green,  
652 insects orange, birds in pink, mammals in yellow, amphibians in green, reptiles in blue, non-  
653 insect arthropods in brown). Each link is a feeding interaction between orders, with width scaled  
654 to the total number of feeding interactions by participating species, and colored according to the  
655 type of resource being fed upon (both live and scavenged animals in gray, leaves and stems in  
656 green, floral resources in pink, seeds and fruits in yellow, wood and bark in brown). Self-links  
657 indicate feeding among species within the order, including cannibalism. Nodes are ordered  
658 horizontally by their number of consumers, from most on the left to least on the right, and  
659 vertically by their trophic level (TL), from basal resources on the bottom (TL = 1) to carnivores  
660 at the top. Three carnivorous or parasitic plant orders and four basal animal orders with no  
661 resources (see Main Text) were assigned trophic levels between 1 and 2. The 86 orders here  
662 (labeled by their first three letters) represent 3,082 taxonomic species.



663

664 **Figure 2 Distribution of diet breadths across resource types**

665 (A-E) Histograms showing the frequency of consumers' diet breadths in terms of number of  
666 resource species (in-degree) when feeding on (A) animals, both live and scavenged (N = 913),  
667 (B) leaves and stems (N = 1,738), (C) flowers, including nectar and pollen (N = 866), (D) seeds  
668 and fruit (N = 243), and (E) wood and bark (N = 102). (F) Histogram showing the counts of diet  
669 breadths for insect families in terms of number of plant resource families they use as hosts,  
670 pooled across plant tissue types (N = 264). Histograms include only consumer species (A-E) or  
671 (F) insect families that feed on the focal resource.

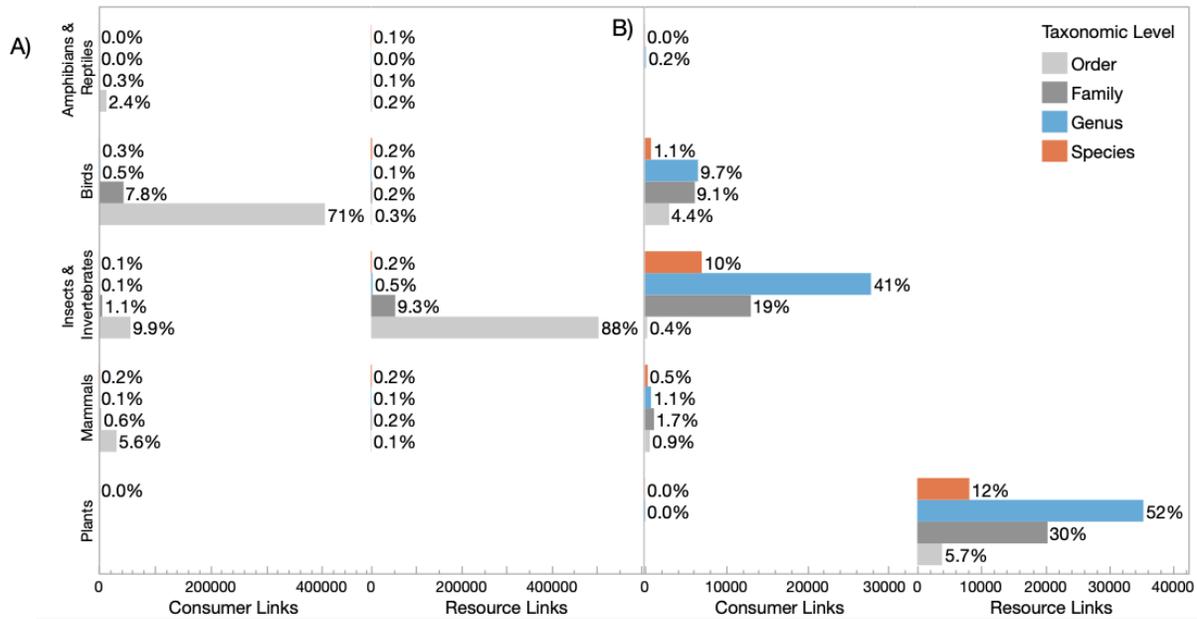


672

673 **Figure 3 Trophic similarity across taxonomic groupings**

674 (A-C) Histograms showing the frequency of the average minimum trophic similarities among  
675 species in each (A) genus (N = 635), (B) family (N = 296), and (C) order (N = 78). Trophic  
676 similarity is the similarity (quantified by the Jaccard index) between a pair of species' consumers  
677 and resources. (D) Histogram showing the frequency of taxonomic species richness in each  
678 trophic species grouping. Trophic species are groups of taxonomic species that have the same  
679 sets of consumers and resources (that is, have a trophic similarity = 1). For visual clarity, the y-  
680 axis is scaled to  $\log_{10}(\text{frequency}) + 1$ .

681 **6) Electronic Supplementary Information**



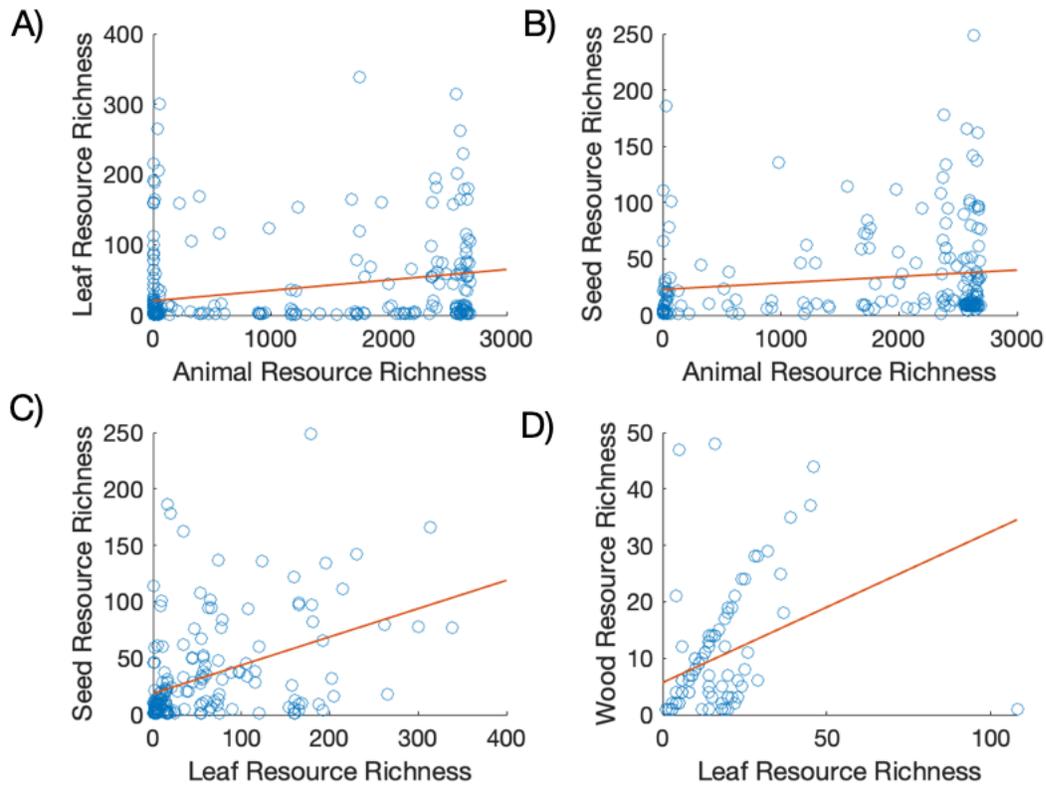
682

683

684 **Supplementary Figure 1 Taxonomic source and level of food web links**

685 The taxonomic resolution of feeding links on **(A)** animals ( $N = 520,851$  links) and **(B)**, including  
 686 leaf, flower, seed, and wood tissues ( $N = 59,898$  links total). Bar graphs represent the fraction of  
 687 unique links between taxonomic groups of consumer (left sub-panel) and resources (right sub-  
 688 panel), colored by the coarsest level of taxonomic resolution in each group of feeding links. For  
 689 example, panel **(A)** shows that among carnivory links, most are birds consuming insects, and  
 690 furthermore that in most of these links one partner is most coarsely resolved to taxonomic order.  
 691 Consumer and resource link percentages both total to 100% because all feeding links are directed  
 692 between a consumer and resource taxa.  $N = 586,601$  total links are represented, including  
 693 526,206 carnivory links and 60,395 herbivory links.

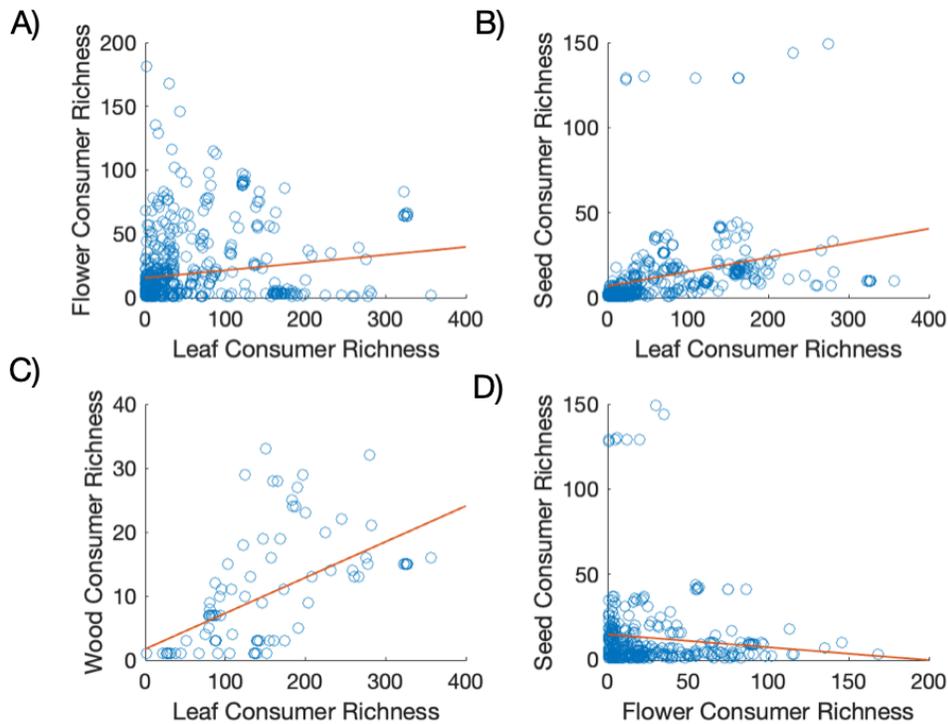
694



695

696 **Supplementary Figure 2 Correlations between consumer diet breadths feeding on different**  
697 **resources**

698 Scatter plots showing the relationship between consumers' diet breadths in terms of number of  
699 resource species when feeding on (A) animals and plant leaves ( $r = 0.28$ ,  $p = 2.0 \times 10^{-7}$ ,  $N =$   
700  $340$ ), (B) animals and plant seeds ( $r = 0.15$ ,  $p = 0.044$ ,  $N = 202$ ), (C) plant leaves and seeds ( $r =$   
701  $0.42$ ,  $p = 7.2 \times 10^{-9}$ ,  $N = 178$ ), and (D) plant leaves and wood ( $r = 0.23$ ,  $p = 0.017$ ,  $N = 98$ ). Each  
702 point is a species that feeds on both focal resources. Lines are least squares fits. Only  
703 relationships with significant Pearson's correlations ( $r$ ) are shown.



704

### 705 **Supplementary Figure 3 Correlations between animal richesses hosted by plants on** 706 **different tissues**

707 Scatter plots showing the relationship between the richness in terms of number of consumers  
708 species when feeding on plant species' (A) leaves and flowers ( $r = 0.16$ ,  $p = 3.4 \times 10^{-5}$ ,  $N = 653$ ),  
709 (B) leaves and seeds ( $r = 0.35$ ,  $p = 8.1 \times 10^{-17}$ ,  $N = 548$ ), (C) leaves and wood ( $r = 0.61$ ,  $p = 1.7 \times$   
710  $10^{-11}$ ,  $N = 98$ ), and (D) flowers and seeds ( $r = -0.11$ ,  $p = 0.013$ ,  $N = 514$ ). Each point is a plant  
711 species with consumers that feed on both focal resources. Lines are least squares fits. Only  
712 relationships with significant Pearson's correlations ( $r$ ) are shown.

713

### 714 **Lay Summary**

715 Terrestrial ecosystems are immensely complex, including diverse species feeding in diverse  
716 ways. Plants and insects engage in highly-specific interactions that have often been excluded  
717 from terrestrial food webs due to limited sampling and expertise. Here, we use records from a  
718 biological research station accumulated over  $\sim 100$  years to construct a food web for a northern  
719 hardwood forest. We report  $\sim 580,000$  interactions among  $\sim 3,800$  species in a living dataset that  
720 is openly available to be supplemented and revised. This is the largest and most detailed food  
721 web yet reported and provides a valuable tool for ecosystem management and research.