

Emergence of stable motifs in consumer-resource communities

Priyanga Amarasekare^{1, 7}, Ulrich Brose^{2, 3},
Jonathan Chase^{2, 4}, Tiffany Knight^{2, 5}, and Adam Clark^{2, 6},

¹Department of Ecology and Evolutionary Biology,
University of California Los Angeles, U.S.A

² German Centre for Integrative Biodiversity Research (iDiv) Leipzig, Germany

³Friedrich Schiller University Jena, Germany

⁴ Department of Computer Sciences, Martin Luther University, Halle, Germany

⁵ Helmholtz Centre for Environmental Research (UFZ) and Martin Luther University,
Halle-Wittenberg, Germany

⁶ Institute of Biology, University of Graz, Austria

⁷ Corresponding author: E-mail: amarasek@ucla.edu

ABSTRACT. Understanding how and why complex communities can be stable has preoccupied
2 ecologists for over a century. Data show that real communities tend to exhibit characteristic
motifs and topologies. Despite a large body of theory investigating both ecological (niche par-
4 titioning) and evolutionary (speciation and extinction) mechanisms, a general explanation for
why particular motifs are more common than others remains elusive. Here we develop a mech-
6 anistic framework that investigates the set of possible motifs that can emerge under minimal
conditions of a nutrient-limited system with no external inputs, and no spatial heterogeneity.
8 Focusing on consumer-resource communities structured by competition and predation, we find
that the emergent motifs under these minimal conditions are vertical trophic chains that maxi-
10 mize energy transfer and biomass production. Not only are such motifs stable to perturbations
of species' abundances, but they are also robust to species additions and removals. Our findings
12 provide a mechanistic explanation for why tri-trophic chains are overrepresented in real food
webs. They suggest that, because they maximize energy transfer, and can emerge and persist
14 under minimal conditions, vertical trophic chains may constitute the fundamental architecture
of consumer-resource communities.

16 **Introduction**

Elucidating the mechanisms that stabilize complex ecological communities is a central issue
18 in community ecology. Recent years have seen network theory, the study of interactions and con-
nectivity between the elements of a given system (Alon, 2003), playing a key role in this endeavor.
20 Two network properties have been particularly important in studying complex communities. The
first is modularity, the organization of entities (e.g., genes, cells, individuals, species) into subsets
22 that interact more strongly amongst themselves than with other such groups (Milo et al., 2002;
Kashtan and Alon, 2005). The second is the existence of motifs, small sets of recurring elements

24 that appear at a higher frequency than expected by chance (Milo et al., 2002; Alon, 2007).

The preponderance of modularity in transcription, neuronal and signal transduction networks
26 is attributed to three advantages. First, organization into discrete, individual units confers
robustness (maintenance of structural and functional integrity Wagner (2005)) by containing
28 the impact of perturbations within localized areas of the network. Second, such modules can
be easily reconfigured to adjust to changing environments, thus increasing robustness (Lipson
30 et al., 2002; Alon, 2003). Third, the modular organization can increase the efficiency of network
activity (Kashtan and Alon, 2005).

32 Biological networks also exhibit characteristic motifs. Transcription networks in unicellular
organisms (e.g., yeast and *E. coli*; Milo et al. (2002); Alon (2007)) are characterized by three
34 network motifs: negative autoregulation (NAR), feed-forward loops (FFLs), and single input
modules (SIMs). Signal transduction networks involved in protein modification (e.g., phospho-
36 rylation) exhibit bi-parallel (diamond) motifs, while neural networks exhibit FFLs, bi-parallels,
and bi-fans (two source nodes directly cross-regulating two target nodes; Milo et al. (2002)).

38 Some of these same motifs are also observed in ecological communities (Fig. 1). Negative au-
toregulation is akin to intra-specific competition due to resource limitation. Feed-forward loops
40 can resemble tri-trophic food chains or a closed loop with omnivory, with energy being trans-
ferred from lower to higher trophic levels. Single input modules (SIM) are akin to exploitative
42 and apparent competition motifs in ecological networks, while the bi-parallel (diamond) motif
represents the combination of exploitative and apparent competition. Indeed, previous stud-
44 ies have found that consumer-resource webs (e.g., predator-prey, plant-herbivore, host-parasite)
exhibit four motifs: tri-trophic chain, omnivory, exploitative and apparent competition. Most
46 studies find the tri-trophic chain to be more frequent than expected by chance (Milo et al., 2002;
Camacho et al., 2007). Evidence for omnivory is more equivocal, with some studies finding it to

48 be overrepresented (e.g., Kondoh (2008) and others finding it not (e.g., Milo et al. (2002); Bas-
compte and Melian (2005); Johnson et al. (2014)). Many studies find exploitative and apparent
50 competition to be less frequent than expected by chance (Milo et al., 2002; Camacho et al., 2007).
Only one study that we are aware of found the bi-parallel (diamond) motif to be overrepresented
52 (Milo et al., 2002).

A substantial body of theory has been developed to investigate community stability and
54 complexity (e.g., McCann (2000); Williams and Martinez (2000); Rossberg et al. (2005, 2006*b,a*);
Williams and Martinez (2008); Rossberg et al. (2005, 2006*b,a*); McCann (2011); Stouffer and
56 Bascompte (2011)). Nearly all of these involve developing mathematical models to describe the
structure and properties of food webs. The resulting predictions are compared with statistical
58 measures of equivalent properties of empirical food webs. One approach generates predator and
prey distributions using evolutionary processes of speciation, extinction and migration, which are
60 then compared with equivalent distributions of real food webs (Rossberg et al., 2005, 2006*b,a*).
A second approach uses structural models that do not explicitly model species interactions but
62 use mechanistic rules to reproduce food web properties (Williams and Martinez, 2000, 2008;
Cattin et al., 2004; Stouffer et al., 2005; Allesina and Pascual, 2008). In these models species are
64 randomly assigned to a niche axis such that the niche values form an ordered set, with each species
having a certain probability of feeding on those with lower niche values. This framework includes
66 the niche model (Williams and Martinez, 2000, 2008), the nested hierarchy model (Cattin et al.,
2004), the generalized cascade model (Stouffer et al., 2005), and the minimum potential niche
68 model (Allesina and Pascual, 2008). A third approach utilizes random matrix theory to derive
stability properties of simple food webs under the assumptions of stable point equilibria and self-
70 limitation in all interacting species (e.g., Allesina and Tang (2015); Monteiro and Faria (2016)).
A fourth approach uses explicit dynamical models of species interactions, typically employing the

72 generalized Lotka-Volterra model (e.g., Thébault and Fontaine (2010)) and bioenergetic versions
thereof (e.g., McCann (2011); Stouffer and Bascompte (2011)).

74 As might be expected, given the diversity of approaches, these studies report conflicting
findings. Rule-based structural models suggest that omnivory is unlikely to be a stable motif
76 (e.g., Johnson et al. (2014)), while dynamical models suggest it to be strongly stabilizing (e.g.,
McCann (1997); McCann et al. (1998)). Some structural models find apparent competition to be
78 overrepresented (e.g., Bascompte and Melian (2005)), while others find it to be underrepresented
(e.g., Camacho et al. (2007)). Random matrix approaches that assume stable point equilibria
80 generated by self-limitation in all species find consumer-resource communities to be more stable
than mutualistic communities (e.g., Allesina and Tang (2015)). In contrast, dynamical models
82 that explicitly consider the oscillatory nature of consumer-resource interactions find consumer-
resource interactions to be highly unstable (extinction-prone) and that weak horizontal links (e.g.,
84 competitive interactions) are required to reduce the oscillatory tendency and increase persistence
(e.g., McCann (1997); McCann et al. (1998); McCann (2011)). Even statistical analyses of real
86 communities are divided on the topologies of consumer-resource and mutualistic communities.
Most studies find mutualistic communities to have a nested structure (e.g., Bascompte et al.
88 (2003); Bastolla et al. (2009); Suweis et al. (2013) but some do not (e.g., Thébault and Fontaine
(2010); Payrató-Borrás et al. (2019)). Some studies find consumer-resource communities to be
90 compartmentalized (e.g., Stouffer and Bascompte (2011)), but others find them to be nested
(e.g., Kondoh et al. (2010)), or exhibiting a combination of the two topologies (e.g., Kondoh
92 et al. (2010); Thébault and Fontaine (2010)). The diversity of approaches and outcomes has
been greatly beneficial in enhancing our understanding of how complex communities can be
94 stable. Further progress, however, requires reconciling these differences to find common ground.

Here we attempt a small first step towards addressing this challenge. We develop a mech-

96 anistic framework that combines the topological features of networks with biologically realistic
dynamics of consumer-resource interactions. On the topological side we consider trophic interac-
98 tions as feed-forward loops in which energy is transferred from primary producers to secondary
consumers and top predators. On the dynamical side we consider these interactions as feedback
100 loops in which producers have positive effects on consumers, while consumers have negative ef-
fects on producers. We use this framework to predict the types of network motifs that emerge
102 under minimal conditions of a constant nutrient input, a single niche axis, no external inputs
of nutrients or species, no self-limitation other than that induced by nutrient limitation, and no
104 spatial heterogeneity. Starting from the very basal level — nutrient uptake by primary produc-
ers — we investigate which, if any, motifs emerge from the interplay between competition and
106 predation, and whether they are robust to perturbations.

Conceptual framework

108 We use theory and data on transcription and signal transduction networks to generate hy-
potheses about feasible network motifs in ecological communities. As noted above, transcription
110 networks in unicellular organisms (e.g., yeast and *E. coli*; (Alon, 2007)) exhibit feed-forward
loops (FFLs) that resemble tri-trophic food chains or a closed loop with omnivory (Fig. 1(a)
112 and (b)). For instance, when the biomass of a primary producer exceeds the level at which a
secondary consumer (e.g., herbivore) can persist on it, it opens up the possibility of a primary
114 producer-secondary consumer interaction. Similarly, when primary productivity is sufficiently
high to generate a secondary consumer biomass exceeding the level at which a tertiary consumer
116 (e.g., predator) can persist, a primary producer-secondary consumer-tertiary consumer interac-
tion can form, with the primary producer “controlling” the secondary consumer directly, and the
118 tertiary consumer indirectly, through the provision of energy. The persistence of such loops are

enhanced when there is negative autoregulation (self-limitation) at one or more trophic levels.
120 When the tertiary consumer can derive energy directly from the primary producer, the latter
directly “controls” both consumer trophic levels (Fig. 1). Unicellular transcription networks also
122 exhibit single input modules (SIM), which are akin to exploitative and apparent competition
motifs in ecological communities (Fig. 1(c)). When species engage in both exploitative and ap-
124 parent competition, we get the bi-parallel (diamond) motif found in signal transduction networks
(Fig. 1(d)). When two primary producers each support two secondary consumers, we get the
126 bi-fan motif found in neural networks.

Of note, ecological networks are distinct from other biological networks in two ways. First,
128 it is energy, rather than information, that is transferred through the network. Second, species
interactions constitute both feed-forward loops and feedback loops. Energy is transferred unidi-
130 rectionally from primary producers to consumers, with species at lower trophic levels having a
positive effect on those at higher trophic levels. At the same time, by extracting energy through
132 direct feeding or other means, species at higher trophic levels have a negative effect on those
at lower trophic levels. Similarly, species at the same trophic level compete to acquire energy
134 from the lower trophic level, thus leading to mutually negative effects on one another. It is these
feedback loops that define the dynamical nature of consumer-resource communities, with species’
136 abundances changing as a result of interactions within and between trophic levels.

The next step is to make the connection between motifs and modularity. Networks that
138 are locally cohesive, i.e., the fraction of the feasible edges (links) that occur around a given
node (molecules, species), exhibit a high degree of clustering (Watts and Strogatz, 1998). High
140 clustering is a signature of modularity, a group of linked nodes whose collective action achieves a
particular function (Milo et al., 2002). In transcription networks, a module is a set of co-regulated
142 genes that share a common function; in signaling pathways, a module is a chain of interacting

proteins propagating a signal within a cell (Alon, 2003, 2007). In ecological communities, a
144 module is a group of interacting species whose collective action (energy acquisition) leads to
production of biomass.

146 One could hypothesize that motifs such as FFLs, SIMs and bifans are common in unicellular
organisms because they represent the set of minimal modular configurations that can both emerge
148 in a closed system and are robust to perturbations. If this is the case, the preponderance of tri-
trophic chains, and to some extent omnivory, in ecological communities could be because these
150 motifs constitute the feasible configurations that can both emerge in closed communities and are
robust to species invasions. Below we develop this hypothesis in more detail.

152 Consider a community with a constant nutrient input, in which the total nutrient availability
sets the upper limit to the total biomass, and hence the number of species the community can
154 contain. The ways in which species apportion the available biomass determines the number of
species and the types of interactions that the community contains. The basal unit is a nutrient-
156 primary producer interaction. In what follows we refer to the primary producer as a plant, but
the ideas we develop are general and can apply equally well to other primary producers such
158 as phytoplankton. The plant species' growth and reproduction depends on an essential nutrient
(e.g., Nitrogen, Phosphorous), which it converts into biomass, and for which the individuals in
160 the population compete. The plant will compete with other plant species for a common nutrient
pool, and be subject to attack by herbivores. These herbivores in turn are consumed by predators
162 that can also be omnivorous (Fig. 1).

A motif that emerges out of such an interaction has to satisfy two criteria. The first is its
164 feasibility. The possible set of species interactions have to follow the order of nutrient and energy
flow, and trophic status. To give an obvious example, we cannot have a consumer without a
166 basal resource, just as we cannot have a top predator without an intermediate consumer. The

second criterion is robustness. A stable motif is one that is both (i) stable to perturbations
168 of its constituents' abundances, and (ii) cannot be replaced by another configuration, i.e., it is
robust to species additions or removals. Of note, perturbations may lead to substitutions of
170 species occupying a particular position of the motif, but they will not alter its configuration. For
instance, if a tri-trophic food chain is a stable motif, a second herbivore can either invade and
172 exclude the resident herbivore or be excluded by the latter; it cannot invade and coexist with the
resident herbivore species. We quantify stability in terms of permanence (long-term persistence
174 of all interacting species), which also encompasses the notion of mathematical stability (return
to a non-trivial steady state following a perturbation of species' abundances).

176 We make two predictions. First, in a closed community with a constant energy input in
which the primary producer's growth depends on a single limiting nutrient, the emergent motifs
178 are vertical chains (nutrient-plant-herbivore, nutrient-plant-herbivore-predator) with the single
exception of a closed loop in the case of omnivory. We expect the frequency of vertical chains
180 to exceed that of omnivory because more 'coherent' webs in which species feed on only one
trophic level are more stable to perturbations than less coherent ones (Johnson et al., 2014).
182 Second, because vertical chains exhibit high cohesiveness (i.e., the ratio of realized to allowable
links approaches 1), they also constitute modules that achieve the common function of biomass
184 production. Modules also tend to localize perturbation impacts, thus increasing the community's
robustness to perturbations. Below we explain the rationale underlying these expectations.

186 We know from competition theory that, in the absence of local niche partitioning via multiple
limiting factors (Tilman, 1982; Chesson, 2000), environmental heterogeneity that allows for spa-
188 tial or temporal niche partitioning (Chesson, 2000; Amarasekare, 2003), allochthonous nutrient
inputs, or dispersal that allows for species recolonizations or source-sink dynamics (Chase and
190 Leibold, 2003; Leibold et al., 2004; Amarasekare, 2003), the species that reduces its resource to

the lowest level will exclude all other species (R^* ; Tilman (1982)). This is a mechanistic interpretation of the competitive exclusion principle that applies to producers and consumers alike. In the absence of ameliorating factors, there can be only as many species at any given trophic level as there are resources at the level below.

The R^* rule means that, in a closed community with a single limiting factor, a second plant species cannot invade and coexist with the resident. Even in the case that the plant species are active at different times and partition the nutrient supply in time, a herbivore entering the community, save in the unlikely event of identical preferences for both plant species, will cause the exclusion of the plant species more susceptible to herbivory (P^* ; (Holt, 1977)). Hence, diversity can increase only through the addition of a vertical link to the initial nutrient-plant interaction. This link can be either mutualistic (e.g., pollinator, seed disperser) or antagonistic (e.g., herbivore). Here we focus our attention to antagonistic interactions.

The nutrient-plant community can be invaded by a herbivore if standing plant biomass exceeds that required for the herbivore to maintain itself. The R^* rule ensures that only a single species can occupy the secondary consumer trophic level: the herbivore that reduces the plant biomass to a lower level will exclude all other invaders. Temporal partitioning may allow two herbivores to coexist on the plant, but the arrival of a top predator will exclude the herbivore more susceptible to the predator (P^* rule). A second vertical link is therefore the most likely configuration in a closed community. Omnivory (i.e., a species feeding on both plant and herbivore trophic levels) can convert the tri-trophic chain into a closed loop (Fig. 1). Below we formalize these predictions mathematically.

212 Mathematical model

The dynamics of a consumer-resource community are given by:

$$\begin{aligned}
 \frac{dN}{dt} &= b \left(S - N - \sum_{i=1}^n \frac{P_i}{e_{P_i}} - \sum_{j=1}^m \left(\frac{H_j}{e_{H_j}} \right) - \sum_{k=1}^l \left(\frac{q_k C_k}{e_{C_{H_j k}}} \right) - \sum_{k=1}^l \left(\frac{(1 - q_k) C_k}{e_{C_{P_i k}}} \right) \right) - \sum_{i=1}^n a_{P_i}(N) N P_i \\
 \frac{dP_i}{dt} &= e_{P_i} a_{P_i}(N) N P_i - d_{P_i} P_i - \sum_{j=1}^m a_{H_j}(P_i) P_i H_j - \sum_{k=1}^l a_{C_{P_i}}(P_i) P_i C_k \\
 \frac{dH_j}{dt} &= e_{H_j} \sum_{i=1}^n a_{H_j}(P_i) \frac{P_i}{e_{P_i}} H_j - d_{H_j} H_j - \sum_{k=1}^l a_{C_{H_j}}(H_j) H_j C_k \\
 \frac{dC_k}{dt} &= \sum_{i=1}^n e_{C_{P_i}} a_{C_{P_i}}(P_i) \frac{P_i}{e_{P_i}} C_k + \sum_{j=1}^m e_{C_{H_j}} a_{C_{H_j}}(H_j) \frac{H_j}{e_{H_j}} C_k - d_{C_k} C_k
 \end{aligned}
 \tag{1}$$

214 where S is the total nutrient content in the system, b is the nutrient turnover rate, N is the
 nutrient availability at any given time, and P_i , H_j and C_k are, respectively, the biomasses of the
 216 i^{th} plant species, j^{th} herbivore and k^{th} predator/omnivore. Since the system is closed, the total
 nutrient content S remains constant over time, imposing a mass balance constraint (Loreau,
 218 1994, 1995) on the system such that

$$S = \sum_{i=1}^n \frac{P_i}{e_{P_i}} + \sum_{j=1}^m \left(\frac{H_j}{e_{H_j}} \right) + \sum_{k=1}^l \left(\frac{q_k C_k}{e_{C_{H_j k}}} \right) + \sum_{k=1}^l \left(\frac{(1 - q_k) C_k}{e_{C_{P_i k}}} \right).
 \tag{2}$$

The function $a_X(X)$ $X = P_i, H_j, C_k$ is the per capita uptake rate, which can be linear
 220 ($a_X(X) = a_X$) or saturating ($a_X(X) = \frac{a_X}{1 + a_X h_X \frac{X}{e_X}}$ where h_X is the handling time). Importantly,
 $a_X(X)$ represents matter and energy flow through the system (Loreau, 1994, 1995). Although
 222 the model does not explicitly consider energy, the flow of matter to producers and consumers
 is dependent on the flow of energy from photosynthesis (Loreau, 1995); the amount of energy
 224 available to producers and consumers is, therefore, encapsulated in $a_X(X)$. The parameters

$d_X(X = P, H, C)$ and e_X depict respectively, the per capita mortality rate and the unit (e.g.,
226 gram) of biomass generated per unit of nutrient. The fraction $\frac{X}{e_X}$ is, then, the total nutrient
amount contained in species X . Note that q is the proportion of the predator's biomass from
228 feeding on the herbivore, and $1 - q$, the proportion from feeding on the plant. The magnitude
of q determines the strength of omnivory.

230 Equation (1) provides a mechanistic representation of exploitative competition based on the
 R^* rule (Tilman, 1982). Species at each level (plant, herbivore, predator) compete for a resource
232 whose dynamics are explicitly modelled. For instance, plants compete for nutrients, herbivores
compete for plants, predators compete for herbivores, etc. Competition is experienced through
234 the effects that other species have on the abundance of the common "resource". For brevity, we
will refer to the primary producer as plant, and to herbivores and predators as antagonists.

236 Our approach is three-fold. First, we investigate the emergence of stable motifs via community
assembly from the ground up, starting with a plant species that colonizes an empty habitat
238 whose establishment facilitates subsequent invasions by competitors and antagonists. We define
a stable motif as one whose configuration, once attained, is robust to species additions and
240 removals. We use mathematical invasion analysis (i.e., the ability of an incoming species to
increase from initially small numbers when the resident community is at equilibrium) to quantify
242 robustness. Invasion analyses have the drawback that they focus on the stability of a resident
community to a single invader. The mathematical methods involved do not easily lend themselves
244 to investigating the outcomes when more than one species can simultaneously enter a community.

In our second approach we use numerical analyses to determine which species combinations
246 persist in the long term when two or more species simultaneously invade a community. If a given
motif were truly robust to perturbations, we would expect it to be stable to invasions by single and
248 multiple species. Our third approach to quantifying robustness is species sorting and community

disassembly. In the case of sorting, we initiate each community with the full complement of
250 species, allow interactions to proceed, and determine which configurations are persistent. In
the case of disassembly, we start with the full complement of species and sequentially remove
252 competitors, antagonists, and primary producers. We determine which motifs remain stable to
species removals.

254 **Model analysis**

We use a combination of analytical methods and numerical simulations to investigate commu-
256 nity assembly, species sorting, and community disassembly. In the simpler cases of community
assembly (e.g., two and three-species interactions), we use mathematical invasion analyses to
258 derive the conditions under which an incoming species can maintain a positive per capita growth
rate when the resident species are at equilibrium. Details of these analyses are given in the online
260 Appendix A. We investigate the more complex cases of community assembly and all cases of sort-
ing and disassembly using extensive numerical simulations of the biologically feasible parameter
262 space. In the case of species invasions, we initiate the community at the boundary equilibrium
in the absence of the invader(s), and introduce the invader(s) once the resident community has
264 reached its steady state. In all cases the initial invader abundance was set to one individual.
In the case of sorting, we initiate each community with the full complement of species (e.g.,
266 two plant species, two herbivore species, one predator/omnivore), allow interactions to proceed
for 25,000 time units, and determine which configurations are persistent. In the case of dis-
268 assembly we allow the full community to interact for 25,000 time units and, after determining
that the community has achieved a steady state, sequentially remove competitors, antagonists,
270 and primary producers. We determine which motifs remain stable to species removals. In all
cases, we consider a given interaction to be stable to species additions or removals if its topology

272 (e.g., vertical chain, triangle, diamond) remains intact (i.e., resident species are either resistant
to invasion or invading species replace the residents without altering the topology). Parameter
274 definitions and values are given in Table 1.

Results

276 **Community assembly: invasion by one species at a time**

1. Invasion by a plant species

278 One would expect initial colonizers of empty habitats (e.g., early successional plant species)
to exhibit strategies for reproduction and seed dispersal that do not depend on mutualistic
280 partners. Examples involve obligately selfing plant species with wind-dispersed seeds, and
facultatively outcrossing species that can revert to selfing in the absence of animal pol-
282 linators. In either case, a plant species can increase when rare and reach a steady state
with the nutrient as long as the nutrient input exceeds the level to which the plant species
284 suppresses the nutrient at equilibrium, i.e., $S > \frac{d_{P_i}}{e_{P_i} a_{P_i}}$ (Appendix A).

2. Nutrient-plant (NP) community: invasion by a herbivore

286 A herbivore can successfully invade a nutrient-plant community provided the plant biomass
at the steady state with the nutrient exceeds the level to which the herbivore would suppress
288 it, i.e., $\frac{b(S - \frac{d_{P_i}}{e_{P_i} a_{P_i}})}{a_{P_i}(b + d_{P_i})} > e_{P_i} \frac{d_H}{e_H a_H}$ (Fig. 2(a), Appendix A, Fig. S1).

3. Nutrient-plant-herbivore (NPH) community: invasion by a top predator

290 A predator can invade a plant-herbivore community provided the herbivore biomass at the
nutrient-plant-herbivore steady state exceeds the level to which the predator would depress
292 it (Fig. 2(b), Appendix A, Fig. S1).

4. Nutrient-plant-herbivore (NPH) community: invasion by an omnivore

294 An omnivore can invade a plant-herbivore community provided the plant and herbivore
biomass at the nutrient-plant-herbivore steady state exceeds the level that the omnivore
296 requires to maintain itself (Fig. 2(c), Appendix A, Fig. S1). However, invasion leads to
the exclusion of the herbivore. Coexistence via omnivory is much less frequent (Fig. 2(c)).
298 This is because the omnivore has the advantage of feeding on two trophic levels, while the
herbivore has the constraint of feeding only on the level below while being fed on by the
300 level above. Exclusion of the herbivore occurs even when relative non-linearity (Armstrong
and McGehee, 1980), mediated via Type II functional responses in the plant, herbivore and
302 omnivore, allows an additional coexistence opportunity (Fig. S2).

5. Addition of horizontal links

304 Consistent with expectations, when plant growth is limited by a single essential nutrient,
the operation of R^* and P^* rules prevent the formation of horizontal links even when plant
306 and herbivore species exhibit trade-offs in resource acquisition ability or susceptibility to
herbivory. This is because such trade-offs can only increase fitness differences between
308 species (i.e., differences in per capita growth rates in the absence of density-dependent
feedbacks; Chesson (2000)); they cannot in themselves generate the stabilizing negative
310 feedbacks that allow species to limit themselves more than they do others (Chesson, 2000).
Generating such feedbacks requires more than one niche dimension. In a closed system
312 with a single limiting nutrient and no spatial heterogeneity, the only possible dimension is
time. As noted above, temporal partitioning of the basal nutrient by two plant species may
314 generate a horizontal link, but this link is susceptible to invasion by a herbivore, which
would set the P^* rule in motion.

316 To see this consider the two possible mechanisms of temporal partitioning. First, if the

two plant species respond differentially to temporal variation such that one species has
318 a high nutrient uptake rate during periods of the year when the other species exhibits
little or no activity (e.g., spring and summer annuals), they may coexist via temporal
320 niche partitioning (Fig. 3, Appendix B, Fig. S2). Second, if the plant species differ in the
non-linearity of their resource uptake functions such that the species with the more non-
322 linear response generates oscillations in nutrient-plant abundance, a second plant species
with a less non-linear response can invade and coexist through the mechanism of relative
324 non-linearity (Armstrong and McGehee, 1980). Coexistence via relative non-linearity can
occur when the species with the less non-linear response is better at utilizing the nutrient
326 when it is rare, and the species with the more non-linear response is better at utilizing the
nutrient when it is abundant (Fig. 3, Appendix B, Fig. S2). However, neither coexistence
328 mechanism is stable to invasion by a herbivore. Such invasion leads to the exclusion of the
plant species more susceptible to herbivore attack (Fig. 3, Fig. S2).

330 As expected, R^* and P^* rules prevent the formation of horizontal links when the nutrient-
plant-herbivore (NPH) interaction is invaded by additional plant or herbivore species. The
332 same goes for the tri-trophic chain ($NPHC$) and omnivory ($NPHO$). Below we provide
details of each case.

334 (i) When the NPH interaction is invaded by a second plant or herbivore species, two
outcomes are possible: the original NPH interaction is stable to invasion, or the
336 invading plant or herbivore species replaces the resident species (Fig. 4). There are
no species additions at plant or herbivore trophic levels. These results are robust to
338 plant and herbivore species having linear functional responses or saturating ones that
allow for relative non-linearity (Figs. 4 and S3).

340 (ii) The same two outcomes occur when the tri-trophic food chain ($NPHC$) is invaded by
a second plant or herbivore species. However, invasion failure is more frequent than
342 replacement of the resident plant and herbivore species by the invaders (Fig. 5).

(iii) In contrast to the linear chains ($NP, NPH, NPHC$), omnivory is not stable to in-
344 vasions by additional plant or herbivore species (Fig. 5). This is because omnivory
itself is rare in closed systems with a limited nutrient supply (see above). Invasion
346 by a second plant species does not alter the omnivore's advantage of being able to
feed on two trophic levels. The herbivore is excluded, and the plant species that is
348 less susceptible to omnivore attack will exclude the other. The overall outcome is
a nutrient-plant-omnivore interaction with the omnivore relying solely on herbivory.
350 Similarly, invasion by a second herbivore species results in the exclusion of the inferior
competitor for the common plant resource (Fig. 5).

352 6. Community assembly via invasion by single species: summary of results

When community assembly occurs in the absence of niche partitioning mechanisms that
354 allow the addition of horizontal links, increase in diversity can occur only through the
addition of a vertical link. If the plant species' per capita growth rate does not depend
356 on a mutualist (e.g., because it is obligately selfing or has wind-dispersed seeds), the first
vertical link is most likely be a herbivore, which opens up the possibility of invasion by
358 a top predator or an omnivore. Vertical chains ($NP, NPH, NPHC$) are more robust to
species invasions than omnivory. This is because omnivory involves resource partitioning,
360 the opportunity for which is constrained in a closed system with a limiting nutrient supply
that sets the upper limit to community biomass.

362 **Community assembly: simultaneous invasion by multiple species**

As noted previously, mathematical invasion analysis focuses on the conditions under which a
364 single species can increase from initially small numbers when the rest of the community is at a
steady state. In reality, more than one species can enter a community at any given time. Nu-
366 merical simulations spanning a large parameter space show that vertical chains (NPH , $NPHC$)
are robust to the simultaneous invasion of competitors and antagonists, but omnivory ($NPHO$)
368 is not (Fig. 5). Below we explain these results in detail.

1. **Nutrient-plant-herbivore (NPH) community: invasion by plant and herbivore 370 species**

When plant and herbivore species simultaneously invade the NPH community, the outcome
372 is invasion failure or the replacement of resident species by invaders (Fig. 5). This is a direct
result of the combined operation of R^* and P^* rules. The plant species that can, overall,
374 extract more of the nutrient supply while evading or resisting herbivory will exclude the
other. In the case of the herbivore, the species that reduces plant biomass to the lowest
376 level will exclude the other. While it is possible for one plant species to be the superior
nutrient competitor and be more susceptible to herbivory, such trade-offs generate only
378 fitness differences and not the the stabilizing niche partitioning mechanisms required for
coexistence (Chesson, 2000).

380 2. **Nutrient-plant-herbivore-predator ($NPHC$) community: invasion by plant and herbivore species**

The outcome is the same as that for the NPH community. The plant species that extracts
382 more of the nutrient in the face of herbivory will exclude the other, and the herbivore that
can consume as much plant biomass as possibly while evading predation will exclude the
384

other (Fig. 5). Invasion by a second top predator in combination with a plant or herbivore species leads to the same outcome.

3. **Nutrient-plant-herbivore-omnivore (*NPHO*) community: invasion by plant and herbivore species**

In contrast to the vertical chains, omnivory proves to be unstable to simultaneous invasion by multiple species. Regardless of which combination of species invades (plant and herbivore, plant and omnivore, herbivore and omnivore), the outcome is the exclusion of the herbivore and the emergence of a vertical chain with the omnivore acting as a top predator (Fig. 5). This is because, as shown above in the single invasion case, the omnivore has the advantage of feeding on multiple trophic levels while the herbivore has the dual disadvantage of competing with the omnivore for the plant resource while also being fed on by omnivore. In a closed system with a limiting nutrient supply and no external inputs, the herbivore being a superior competitor for the plant species does not generate sufficient niche partitioning opportunities to allow for herbivore-omnivore coexistence.

Species sorting

In this step we start with the full assemblage of species for each of the three communities (*NPH*, *NPHC* and *NPHO*) and allow the dynamics to proceed naturally. We find that species sorting occurs via the operation of R^* and P^* rules, with the result that the stable motifs to emerge are, again, the vertical chains (*NPH*, *NPHC* and *NPO*).

1. **Nutrient-two plant-two herbivore community ($NP_1P_2H_1H_2$)**

Starting from the full community, species sorting leads to the emergence of the *NPH* chain (Fig. 5). Which plant species persists depends on the cumulative effect of resource

acquisition ability and susceptibility to herbivory. Which herbivore species persists depends
408 on the level to which each herbivore can depress plant biomass.

2. **Tri-trophic chain** ($NP_1P_2H_1H_2C$)

410 Starting from the full community, species sorting leads to the emergence of the $NPHC$
chain as the dominant motif (Fig. 5). Other motifs that occur in low frequency (e.g.,
412 $NP_1P_2, NP_iH_1H_2, i = 1, 2$) are the result of transient coexistence of species, driven by
strong trade-offs, at plant and herbivore trophic levels.

3. **Omnivory** ($NP_1P_2H_1H_2O$)

414 As with assembly, species sorting leads to the exclusion of the herbivore by the omnivore,
416 with the vertical chain (NPO) being the emergent outcome (Fig. 5).

Community disassembly

418 Here we start with the full complement of species for each community, and sequentially remove
species starting with the highest trophic level. We find that, across all community types, the
420 motifs that are robust to disassembly are the vertical chains ($NPH, NPHC$ and NPO). When
fitness differences between species are strong, transient coexistence of plant or herbivore species
422 can occur, but this outcome is restricted to the nutrient-plant-herbivore community (NPH); it
is not observed in $NPHC$ or $NPHO$ interactions.

1. **Nutrient-two plant-two herbivore community** ($NP_1P_2H_1H_2$)

424 When one herbivore species is removed, the community simplifies to two nutrient-plant-
426 herbivore chains ($NP_iH, i = 1, 2$) (Fig. 6(a) and (b)). Removal of one plant species also
leads to the formation of nutrient-plant-herbivore chains ($NPH_i, i = 1, 2$; Fig. 6(c) and (d)).

428 Simultaneous removal of one plant and one herbivore species leads to the same outcome
(Fig. 6(e) and (f).)

430 2. **Tri-trophic chain** ($NP_1P_2H_1H_2C$)

When one herbivore species is removed, the community simplifies to two nutrient-plant-
432 herbivore chains (NP_iH , $i = 1, 2$) (Fig. 6(a) and (b)). Removal of one plant species also
leads to the formation of nutrient-plant-herbivore chains (NPH_i $i = 1, 2$; Fig. 6(c) and (d)).
434 Simultaneous removal of one plant and one herbivore species leads to the same outcome
(Fig. 6(e) and (f)).

436 3. **Omnivory** ($NP_1P_2H_1H_2O$)

When one herbivore species is removed, the community simplifies to two nutrient-plant-
438 omnivore chains (NP_iO $i = 1, 2$) with the omnivore excluding the remaining herbivore
(Fig. 7(a) and (b)). When one plant species is removed, we get a single nutrient-plant-
440 omnivore chain (NPO ; Fig. 7(c) and (d)). Simultaneous removal of one plant and one
herbivore species leads to the same outcome (Fig. 7(e) and (f)). When the omnivore
442 itself is removed, the community simplifies to one of four nutrient-plant-herbivore chains
(NP_iH_j $i, j = 1, 2$).

444 **Summary of results**

Taken together, the outcomes of community assembly, species sorting, and community dis-
446 assembly show that in a closed system with a constant supply of a limiting nutrient, no spatial
heterogeneity, and no external nutrient inputs or immigration, the only motifs that can emerge
448 are vertical chains of nutrient-plant-herbivore or nutrient-plant-herbivore-predator. This is true
even in the presence of temporal niche partitioning at the plant level and relative non-linearity
450 at plant and herbivore trophic levels.

Discussion

452 There is strong empirical evidence that ecological communities exhibit recurrent elements
(motifs) that characterize other types of biological networks (e.g., transcription, neural signal
454 transduction; Milo et al. (2002); Alon (2003); Bascompte and Melian (2005); Kashtan and Alon
(2005); Alon (2007)). Analyses of network properties in a wide variety of food webs have identified
456 four dominant motifs: exploitative competition, apparent competition, omnivory and tri-trophic
chain (Milo et al., 2002; Bascompte and Melian, 2005; Camacho et al., 2007). Nearly all studies
458 identify tri-trophic chains as a dominant motif, but there is some disagreement as to whether
omnivory is one (Bascompte and Melian, 2005; Camacho et al., 2007; Johnson et al., 2014). A
460 few studies find exploitative and apparent competition to be dominant (Bascompte and Melian,
2005), but the consensus appears to be that they are less prevalent across different types of food
462 webs than tri-trophic chains or omnivory. At least one study (Milo et al., 2002) has found the
diamond motif that arises from a combination of exploitative and apparent competition.

464 In unicellular organisms such as yeast and *E. coli*, transcription, neural and transduction
networks exhibit dominant motifs that resemble those seen in ecological communities. For in-
466 stance, feed-forward loops (FFLs) in transcription networks include motifs resembling tri-trophic
chains and omnivory, and single input modules (SIM) that resemble exploitative and apparent
468 competition. Signal transduction networks exhibit a bi-parallel (diamond) motif, akin to the
diamond food web arising from the combination of exploitative and apparent competition. The-
470 ory suggests that these motifs are dominant because they constitute the optimal configurations
for information transfer that are also robust to perturbations (Milo et al., 2002; Kashtan and
472 Alon, 2005; Alon, 2007). Extending this idea to ecological communities in which the transfer
is of energy rather than information, we can hypothesize that the dominant motifs observed in
474 ecological communities are those that represent configurations that are both feasible and sta-

ble: they can emerge under minimal conditions in closed communities, and they are robust to
476 invasions by other species.

Here we test this hypothesis using a mechanistic framework that combines the topological
478 features of networks with biologically realistic dynamics of consumer-resource interactions. On
the topological side we consider trophic interactions as feed-forward loops in which energy is
480 transferred from primary producers to secondary consumers and top predators. On the dynamical
side we consider these interactions as feedback loops in which producers have positive effects on
482 consumers, while consumers have negative effects on producers. We use three approaches —
community assembly, species sorting, community disassembly — to investigate the robustness
484 of the five motifs (exploitative competition, apparent competition, omnivory, tri-trophic chain
and diamond) found to be prevalent in real food webs (Milo et al., 2002; Bascompte and Melian,
486 2005; Camacho et al., 2007; Johnson et al., 2014; Monteiro and Faria, 2016).

Our work differs from previous studies in several ways. First, instead of assembling communi-
488 ties by randomly assigning species to a niche axis under prescribed rules, we explicitly investigate
community assembly from the ground up, starting with a single primary producer (plant) that
490 colonizes an empty habitat. Second, we investigate how, in a nutrient-limited system subject to
a mass balance constraint, sequential colonizations by primary and secondary consumers (herbi-
492 vores and predators) lead to community assembly in the absence of any self-limitation mechanism
save that arising from the constant nutrient input. Third, we do not restrict our investigations
494 to situations in which only stable point equilibria are possible. By incorporating non-linear (sat-
urating) functional responses at all trophic levels, we explicitly allow for the oscillatory dynamics
496 that characterize consumer resource interactions. To our knowledge, this is the first time that
these biological realities have been incorporated into investigations of food web assembly.

498 We find that, in a closed community in which the total nutrient availability sets the upper

limit to the total biomass, the only motifs that can emerge are vertical chains of nutrient-
500 plant, nutrient-plant-herbivore, and nutrient-plant-herbivore-predator interactions. Although
temporal variation, either through relative non-linearity in functional responses or temporal
502 nutrient partitioning can allow the coexistence of plant species, such coexistence is not robust
to invasion by a herbivore. The plant species whose susceptibility to herbivory, when averaged
504 over the year (in temporal niche partitioning) or nutrient cycle (in relative non-linearity) is lower
will exclude the other plant species. The same process happens at the herbivore level. In the
506 absence of a top predator, the herbivore species that depresses plant biomass to the lowest level
will exclude all other species; in the presence of a top predator, the herbivore, that can extract
508 more energy from the plant while withstanding predation will exclude all other species.

On the face of it, this result may seem trivial. After all, what we are seeing is the operation
510 of the R^* and P^* rules. However, looking beneath the surface reveals several important insights.
First, just as feed-forward loops maximize information transfer in transcription networks, vertical
512 chains maximize energy transfer in ecological communities. Since the total amount of energy is
constant in a closed community, coexistence at any trophic level means the apportionment of
514 the same amount of energy amongst species (since the amount of energy at that level cannot
exceed the amount procured by the species best at resource acquisition) with extra losses during
516 conversion of energy to biomass (determined by the conversion efficiency parameter) and mor-
tality. In a vertical chain, more energy is transferred from one level to another because having a
518 single species at each level minimizes energy loss due to biomass conversion and mortality. Thus,
a vertical chain also leads to greater overall biomass and hence productivity of the community.
520 The key point is that the ecological constraint imposed by the R^* and P^* rules not only serves
to make the linear chains more robust to perturbations, but they also maximize energy transfer.
522 The second insight is that the operation of the R^* and P^* rules increases the trophic coherence

of the community. Coherence is determined by the number of trophic levels that a given consumer occupies (Johnson et al., 2014); a top predator feeds only on the trophic level below it (herbivore) but an omnivore feeds on two trophic levels below it (herbivore and plant). The fewer trophic levels a given consumer extracts energy from, the more coherent a network is, and the less self-regulation required to stabilize it (Johnson et al., 2014). This is why we observe the vertical chains to be not only persistent but also stable to perturbations of species' abundances. Vertical trophic chains not only maximize energy transfer and biomass production, but they are also stable both in the ecological sense (long-term persistence) and the mathematical sense (recovery from perturbations to species' abundances). What is notable is that stability is achieved through the minimum possible level of self-regulation: a single negative feedback loop at the primary producer level.

Importantly, the vertical trophic chains that emerge as stable motifs also confer modularity. Vertical chains exhibit high clustering coefficients (i.e., the ratio of realized to allowable links approaches 1; Watts and Strogatz (1998)). Clustering is a signature of modularity, a group of a linked nodes with strong interactions (Alon, 2003). Vertical trophic chains satisfy these criteria. They are highly cohesive (i.e., all allowable links are realized), and they achieve the common function of converting energy into biomass. This conversion is what ultimately constitutes community productivity, be they phytoplankton or forests. Because they can convert energy into biomass in the absence of other interactions, and because perturbations occurring at one or more nodes (species) are contained within the chain and not transmitted horizontally, vertical chains constitute the minimal modular structure that can arise even under the restrictive conditions of a limited energy supply that places an upper limit on biomass production.

These results beg the following question: real communities constitute complex webs of interacting species. While they do contain vertical chains, they also contain a multitude of horizontal

links. If it is the vertical chains that maximize energy transfer and are robust to perturbations,
548 how do complex communities with numerous horizontal links persist in the face of abiotic (i.e.,
nutrient influxes, toxins and pollutants) and biotic (invasions of competitors and antagonists)
550 perturbations? We propose the following explanation: vertical trophic chains constitute the
dominant motif because they comprise the backbone of all consumer-resource communities. The
552 reason for this is simple. Vertical chains constitute the set of minimal configurations that can
assemble under the most restrictive of conditions: a single limiting nutrient, no external energy
554 inputs, no immigration, no spatial heterogeneity, and minimal self-limitation. Vertical chains are
what is left when everything is taken away. They are the foundation on which complex structures
556 are built.

It is noteworthy that our theoretical finding is consistent with the empirical finding that
558 tri-trophic chains are the dominant motif in a wide variety of food webs (e.g., Milo et al. (2002);
Camacho et al. (2007)). Previous theory has demonstrated that the dynamical behavior of tri-
560 trophic chains can be greatly altered when embedded in complex webs (Otto et al., 2007; Kondoh,
2008; Cohen et al., 2010), raising the issue of whether it is possible to identify tri-trophic chains
562 that can persist in the absence of other interactions. Our theoretical finding that vertical trophic
chains can persist independently even under the most restrictive conditions lends credence to
564 previous empirical findings that tri-trophic chains are the dominant motif in real food webs.

It is also noteworthy that our findings contradict the empirical findings that omnivory, ex-
566 ploitative and apparent competition, and the diamond web can be common in natural commu-
nities. These discrepancies serve to illustrate important biological realities. Consider first, the
568 omnivory motif. There is disagreement in the empirical literature as to whether omnivory con-
stitutes a dominant motif in food webs. Some studies find it to be prevalent while other do not
570 (Schneider et al., 2012; Brose et al., 2019). There is a considerable body of theory showing that

a trade-off between resource acquisition ability and susceptibility to omnivory is insufficient to
572 guarantee herbivore-omnivore coexistence (S. and Feissel, 2000; Amarasekare, 2007, 2008). Our
findings serve to demonstrate this result in a closed system that is nutrient-limited and subject
574 to a mass-balance constraint. (Interestingly, when omnivory is prevalent, as in size-structured
communities (Schneider et al., 2012; Brose et al., 2019), it is because the link between the basal
576 resource and the omnivore is weak.) The inadequacy of fitness differences to provide stabilizing
negative feedbacks is also why we do not observe exploitative and apparent competition. The
578 minimalist scenario we explore provides no opportunities for the niche partitioning mechanisms
required to sustain such interactions. This is particularly interesting because we do not observe
580 coexistence above the primary producer (plant) level even in the presence of temporal coexis-
tence mechanisms such as relative non-linearity and temporal niche partitioning. When multiple
582 species occupy multiple trophic levels, we need more than two niche dimensions; resource/natural
enemy and time are no longer sufficient. We need to invoke space, external resource inputs, and
584 immigration.

The need to move beyond the minimal conditions of limited energy takes us to considerations
586 of the conditions required for the assembly and persistence of complex ecological communities.
We propose that, just in the way that macromolecules (e.g., DNA, protein) are formed by the
588 intertwining of molecular chains that subsequently fold into complicated structures held together
by relative fragile bonds, complex communities are formed by the coming together of vertical
590 chains that are then held together by relatively fragile horizontal links that can break when
the energy inputs that make them possible are removed, or when perturbations to the existing
592 structure occur in terms of species additions or removals. Let us consider a simple example,
the coming together of two trophic chains, each supported at the base by a different nutrient
594 or a different supply of the same nutrient separated in space (e.g., soil space occupied by the

root systems of individual plants). Since each chain has an independent base (energy input),
596 the R^* and P^* rules no longer hold, resulting in coexistence at primary producer and secondary
consumer levels. A top predator that attacks secondary consumers of both chains, or an omnivore
598 that feeds on a plant species from one chain and a herbivore from the other, will be able to do
so without species losses at lower trophic levels, leading to a compartment that now contains
600 multiple motifs: tri-trophic chain, omnivory, exploitative and apparent competition, and the
diamond web. Extending our framework to incorporate multiple vertical chains into models with
602 energy limitation and mass balance constraints is an important next step.

Acknowledgements

604 This research was supported by the National Science Foundation grant DEB-1949796 to P.A.

References

- 606 Allesina, S., and M. Pascual. 2008. Network structure, predator-prey modules, and stability in
large food webs. *Theoretical Ecology* 1:55–64.
- 608 Allesina, S., and S. Tang. 2015. The stability–complexity relationship at age 40: a random matrix
perspective. *Population Ecology* 57:63–75.
- 610 Alon, U. 2003. Biological networks: The tinkerer as an engineer. *Science* 301:1866–1867.
- . 2007. Network motifs: theory and experimental approaches. *Nature Genetics* 8:450–461.
- 612 Amarasekare, P. 2003. Diversity-stability relationships in multi-trophic systems: an empirical
exploration. *Journal of Animal Ecology* 72:713–724.
- 614 ———. 2007. Trade-offs, temporal variation and species coexistence in communities with in-
traguild predation. *Ecology* 88:2720–2728.

- 616 ———. 2008. The coexistence of intraguild predators and prey in resource-rich environments.
Ecology 89:2786–2797.
- 618 Armstrong, R., and R. McGehee. 1980. Competitive exclusion. *American Naturalist* 115:151–170.
- Bascompte, J., P. Jordano, C. Melian, and J. Olesen. 2003. The nested assembly of plant–
620 animal mutualistic networks. *Proceedings of the National Academy of Sciences of the USA*
100:9383–9387.
- 622 Bascompte, J., and C. J. Melian. 2005. Simple trophic modules for complex food webs. *Ecology*
86:2868–2873.
- 624 Bastolla, U., M. Fortuna, A. Pascual-Garcia, A. Ferrera, B. Luque, and J. Bascompte. 2009. The
architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature*
626 458:1018–1021.
- Brose, U., P. Archambault, B. A.D., L. Bersier, T. Boy, J. Canning-Clode, E. Conti, M. Dias,
628 and C. Digel. 2019. Predator traits determine food-web architecture across ecosystems. *Nature*
Ecology and Evolution 3:919–927.
- 630 Camacho, J., D. Stouffer, and L. Amaral. 2007. Quantitative analysis of the local structure of
food webs. *Journal of Theoretical Biology* 246:260–268.
- 632 Cattin, M., L. Bersier, C. Banasek-Richter, R. Baltensperger, and J. Gabriel. 2004. Phylogenetic
constraints and adaptation explain food-web structure. *Nature* 427:835–839.
- 634 Chase, J., and M. A. Leibold. 2003. *Ecological niches: linking classical and contemporary*
approaches. University of Chicago Press.

- 636 Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31:343–366.
- 638 Cohen, J., D. Schittler, D. Raffaelli, and D. Reuman. 2010. Food webs are more than the
sum of their tritrophic parts. *Proceedings of the National Academy of Sciences of the USA*
640 106:22335–22340.
- Holt, R. 1977. Predation, apparent competition, and the structure of prey communities. *Theo-*
642 *retical Population Biology* 12:197–229.
- Johnson, S., V. Domínguez-García, D. L., and M. Muñoz. 2014. Trophic coherence determines
644 food-web stability. *Proceedings of the National Academy of Sciences of the USA* 111:17923–
17928.
- 646 Kashtan, N., and U. Alon. 2005. Spontaneous evolution of modularity and network motifs.
Proceedings of the National Academy of Sciences of the USA 102:13773–13778.
- 648 Kondoh, M. 2008. Building trophic modules into a persistent food web. *PNAS* 105:16631–16635.
- Kondoh, M., S. Kato, and Y. Sakato. 2010. Food webs are built up with nested subwebs. *Ecology*
650 91:3123–3130.
- Leibold, M. A., M. Hoyoak, N. Mouquet, P. Amarasekare, J. Chase, M. Hoopes, R. Holt,
652 J. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity
concept: a framework for multi-scale community ecology. *Ecology Letters* 7:601–613.
- 654 Lipson, H., J. Pollack, and P. Suh. 2002. On the origin of modular variation. *Evolution* 56:1549–
1556.

- 656 Loreau, M. 1994. Mass and energy flow in closed ecosystems: do ecological or mathematical constraints prevail? *Journal of Theoretical Biology* 168:237–243.
- 658 ———. 1995. Consumers as maximizers of matter and energy flow in ecosystems. *American Naturalist* 145:22–42.
- 660 McCann, K. 2000. The diversity stability debate. *Nature* 405:228–233.
- 662 McCann, K., A. Hastings, and G. R. Huxel. 1998. Weak trophic interactions and the balance of nature. *Nature* 395:794–798.
- 664 McCann, K. S. 1997. Re-evaluating the omnivory–stability relationship in food webs. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 264:1249–1254.
- . 2011. *Food Webs*. Princeton University Press.
- 666 Milo, R., S. Shen-Orr, S. Itzkovitz, N. Kashtan, D. Chklovskii, and U. Alon. 2002. Network motifs: Simple building blocks of complex networks. *Science* 298:824–827.
- 668 Monteiro, A., and L. Faria. 2016. The interplay between population stability and food-web topology predicts the occurrence of motifs in complex food-webs. *Journal of Theoretical Biology* 409:165–171.
- 670 ———. 2016. The interplay between population stability and food-web topology predicts the occurrence of motifs in complex food-webs. *Journal of Theoretical Biology* 409:165–171.
- 672 Otto, S., B. Rall, and U. Brose. 2007. Allometric degree distributions facilitate food-web stability. *Nature* 450:1226–1230.
- 674 Payrató-Borrás, C., L. Hernández, and Y. Moreno. 2019. Breaking the spell of nestedness: The entropic origin of nestedness in mutualistic systems. *Physical Review X* 9:2160–3308.
- 676 Rossberg, A., H. Matsuda, T. Amemiya, and K. Itoh. 2005. An explanatory model for foodweb structure and evolution. *Ecological Complexity* 2.

- . 2006*a*. Foodwebsl: experts consuming families of experts. *Journal of Theoretical Biology*
678 241:552–563.
- . 2006*b*. Some properties of the speciation model for foodweb structure - mechanisms for
680 degree distribution and intervality. *Journal of Theoretical Biology* 238:401–415.
- S., D., and M. Feissel. 2000. Effects of enrichment on threellevel food chains with omnivory.
682 *American Naturalist* 155:200–218.
- Schneider, F., S. Scheu, and U. Brose. 2012. Body mass constraints on feeding rates determine
684 the consequences of predator loss. *Ecology Letters* 15:436–443.
- Smith, D. J., and P. Amarasekare. 2018. Toward a mechanistic understanding of thermal niche
686 partitioning. *American Naturalist* 191:E57–E75.
- Stouffer, D., and J. Bascompte. 2011. Compartmentalization increases food-web persistence.
688 *Proceedings of the National Academy of Sciences of the USA* 108:3648–3652.
- Stouffer, D., J. Camacho, R. Guimerà, C. Ng, and L. L. Amaral. 2005. Quantitative patterns in
690 the structure of model and empirical food webs. *Ecology* 86:1301–1311.
- Suweis, S., F. Simini, J. Banavar, and A. Maritan. 2013. Emergence of structural and dynamical
692 properties of ecological mutualistic networks. *Nature* 500:449–452.
- Thébault, E., and C. Fontaine. 2010. Stability of ecological communities and the architecture of
694 mutualistic and trophic networks. *Science* 329:853–856.
- Tilman, D. 1982. *Resource Competition and Community Structure*. Princeton University Press.
- 696 Wagner, A. 2005. Robustness, evolvability, and neutrality. *FEBS Letters* 579:1772–1778.

Watts, D., and S. Strogatz. 1998. Collective dynamics of ‘small-world’ networks. *Nature* 393:440–
698 442.

Williams, R., and N. Martinez. 2000. Simple rules yield complex foodwebs. *Nature* 404:180–183.
700 ———. 2008. Success and its limits among structural models of complex food webs. *Journal of
Animal Ecology* 77:512–519.

Table 1: Parameter definitions and values

Parameter definitions and values		
S	Constant nutrient input	10 – 50
b	nutrient turnover rate	1.0 – 2.0
$a_{X_1}, X = P, H, N$	Per capita attack rate of resident species at trophic level X	1.0 – 2.0
$p = \frac{a_{X_2}}{a_{X_1}}$	Ratio of invader and resident species' attack rates	0.0 – 2.0
$h_{X_1}, X = P, H, N$	Handling of resident species at trophic level X	0.0 – 0.1
$h_X = \frac{h_{X_2}}{h_{X_1}}$	Ratio of invader and resident species' handling times	0.0 – 2.0
$e_{X_1}, X = P, H, N$	Conversion efficiency of resident species at trophic level X	0.1 – 2.0
$e = \frac{e_{X_2}}{e_{X_1}}$	Ratio of invader and resident species' conversion efficiencies	0.0 – 2.0
$d_{X_1}, X = P, H, N$	Per capita mortality of resident species at trophic level X	0.0 – 0.2
$s = \frac{d_{X_2}}{d_{X_1}}$	Ratio of invader and resident species' mortality rates	0.0 – 2.0

Table 2: Parameter values used in simulations

1. Nutrient-plant interaction

$S = 50, b = 2.0, a_{P_1} = 1.0 - 2.0, h_{P_1} = 0.1 - 1.0, e_{P_1} = 1.0 - 2.0, d_{P_1} = 0.1$

2. Nutrient-plant-herbivore interaction

$a_{H_1} = p_1 a_{P_1}, h_{H_2} = h_1 h_{P_1}, e_{H_1} = e_1 e_{P_1}, d_{H_1} = s_1 d_{P_1}, p_1, e_1, h_1, s_1 \in (0.0, 2.0)$

3. Nutrient-plant-herbivore-predator interaction

$a_{H_1} = p_1 a_{P_1}, a_C = p_2 a_{P_1}, h_{H_2} = h_1 h_{P_1}, h_C = h_2 h_{P_1}, e_{H_1} = e_1 e_{P_1}, e_C = e_2 e_{P_1}, d_{H_1} = s_1 d_{P_1}, d_C = s_2 d_{P_1}$
 $p_1, p_2, h_1, h_2, e_1, e_2 \in (0.0, 2.0), d_{P_1} = 0.1, s_1 = s_2 = 1.0$

4. Nutrient-plant-herbivore-omnivore interaction

$a_{H_1} = p_1 a_{P_1}, a_{O_P} = p_2 a_{O_H}, h_{H_2} = h_1 h_{P_1}, h_{O_P} = h_2 h_{O_H}, e_{O_P} = p_2 e_{O_H}, e_{H_1} = e_1 e_{P_1}, e_{O_H} = e_2 h_{O_P}, d_{H_1} = s_1 d_{P_1}, d_O = s_2 d_{P_1}$
 $p_1, p_2, h_1, h_2, e_1, e_2, \in (0.0, 2.0), d_{P_1} = 0.1, s_1 = s_2 = 1.0$

5. Nutrient-plant-interaction invaded by second plant species

5.1 Plant coexistence via relative non-linearity

$a_{P_1} = 1.0, a_{P_2} = p_1 a_{P_1}, h_{P_1} = 0.1, h_{P_2} = h_1 h_{P_1}, e_{P_1} = 1.0, e_{P_2} = e_1 e_{P_1}, d_{P_2} = s_1 d_{P_1}$
 $p_1, p_2, h_1, e_1, \in (0.0, 2.0), d_{P_1} = 0.1, s_1 = s_2 = 1.0$

5.2 Plant coexistence via temporal niche partitioning

$a_{P_1 T_{\text{opt}}} = 1.0, a_{P_2 T_{\text{opt}}} = p_1 a_{P_1 T_{\text{opt}}}, s_{a_{P_1}} = 5.0, s_{a_{P_2}} = v s_{a_{P_1}}, e_{P_1} = 1.0, e_{P_2} = e_1 e_{P_1}, d_{P_2} = s_1 d_{P_1}, T_{\text{opt} a_{P_1}} = 292, x = -2,$
 $p_1, e_1 \in (0.0, 2.0), x \in (-4, 4), d_{P_1} = 0.1, s_1 = s_2 = 1.0$

6. Nutrient-two plant-interaction invaded by herbivore

6.1 Plant coexistence via relative non-linearity

$a_{H_1} = p_2 a_{P_1}, h_{P_1} = 0.1, h_{P_2} = h_1 h_{P_1}, e_{P_1} = 1.0, e_{P_2} = e_1 e_{P_1}, e_{H_1} = e_2 e_{P_1}, d_{P_2} = s_1 d_{P_1}, d_{H_1} = s_2 d_{P_1}, d_{P_1} = 0.1, s_1 = s_2 = 1.0$
 $p_1, p_2, h_1, e_1, e_2 \in (0.0, 2.0),$

6.2 Plant coexistence via temporal niche partitioning

$a_{H_1} = p_1 a_{H_1}, h_{P_1} = 0.1, h_{P_2} = h_1 h_{P_1}, e_{H_1} = e_2 e_{P_1}, d_{P_2} = s_1 d_{P_1}, d_{H_1} = s_2 d_{P_1}, d_{P_1} = 0.1, s_1 = s_2 = 1.0,$
 $p_1, h_1, e_1, e_2 \in (0.0, 2.0), x \in (-4, 4)$

7. Nutrient-plant-herbivore interaction invaded by second plant and/or herbivore species

$a_{P_1} = 1.0, a_{P_2} = p_1 a_{P_1}, a_{H_1} = p_2 a_{P_1}, a_{H_2} = p_3 a_{H_1}, h_{P_1} = 0.1, h_{P_2} = h_1 h_{P_1}, h_{H_2} = h_2 h_{H_1}, e_{P_1} = 1.0, e_{P_2} = e_1 e_{P_1},$
 $e_{H_2} = e_2 e_{H_1}, d_{P_1} = 0.1, d_{P_2} = s_1 d_{P_1}, d_{H_2} = s_2 d_{H_1}, d_{P_1} = d_{H_1} = 0.1, s_1 = s_2 = 1.0$
 $p_1, p_2, p_3, h_1, h_2, e_1, e_2 \in (0.0, 2.0)$

8. Nutrient-plant-herbivore-predator interaction invaded by second plant and/or herbivore species

$a_{P_1} = 1.0, a_{P_2} = p_1 a_{P_1}, a_{H_1 P_2} = p_2 a_{H_1 P_1}, a_{H_2 P_2} = p_3 a_{H_2 P_1}, a_{C H_2} = p_4 a_{C H_1}, e_{P_1} = 1.0, e_{P_2} = e_1 e_{P_1}, e_{H_2} = e_2 e_{H_1},$
 $e_C = e_3 e_{H_1}, d_{P_2} = s_1 d_{P_1}, d_{H_2} = s_2 d_{H_1}, d_C = s_3 d_{P_1}$
 $p_1, p_2, p_3, p_4, e_1, e_2, e_3 \in (0.0, 2.0), d_{P_1} = d_{H_1} = 0.1, s_1 = s_2 = s_3 = 1.0$

9. Nutrient-plant-herbivore-omnivore interaction invaded by second plant and/or herbivore species

$a_{P_1} = 1.0, a_{P_2} = p_1 a_{P_1}, a_{H_1 P_2} = p_2 a_{H_1 P_1}, a_{H_2 P_2} = p_3 a_{H_2 P_1}, a_{O H_2} = c_1 a_{O H_1}, a_{O P_2} = c_2 a_{O P_1}, e_{P_1} = 1.0, e_{P_2} = e_1 e_{P_1},$
 $e_{H_2} = e_2 e_{H_1}, e_O = e_3 e_{H_1}, d_{P_2} = s_1 d_{P_1}, d_{H_2} = s_2 d_{H_1}, d_O = s_3 d_{P_1}$
 $p_1, p_2, p_3, c_1, c_2, e_1, e_2, e_3 \in (0.0, 2.0), q \in (0.0, 1.0), d_{P_1} = d_{H_1} = 0.1, s_1 = s_2 = s_3 = 1.0$

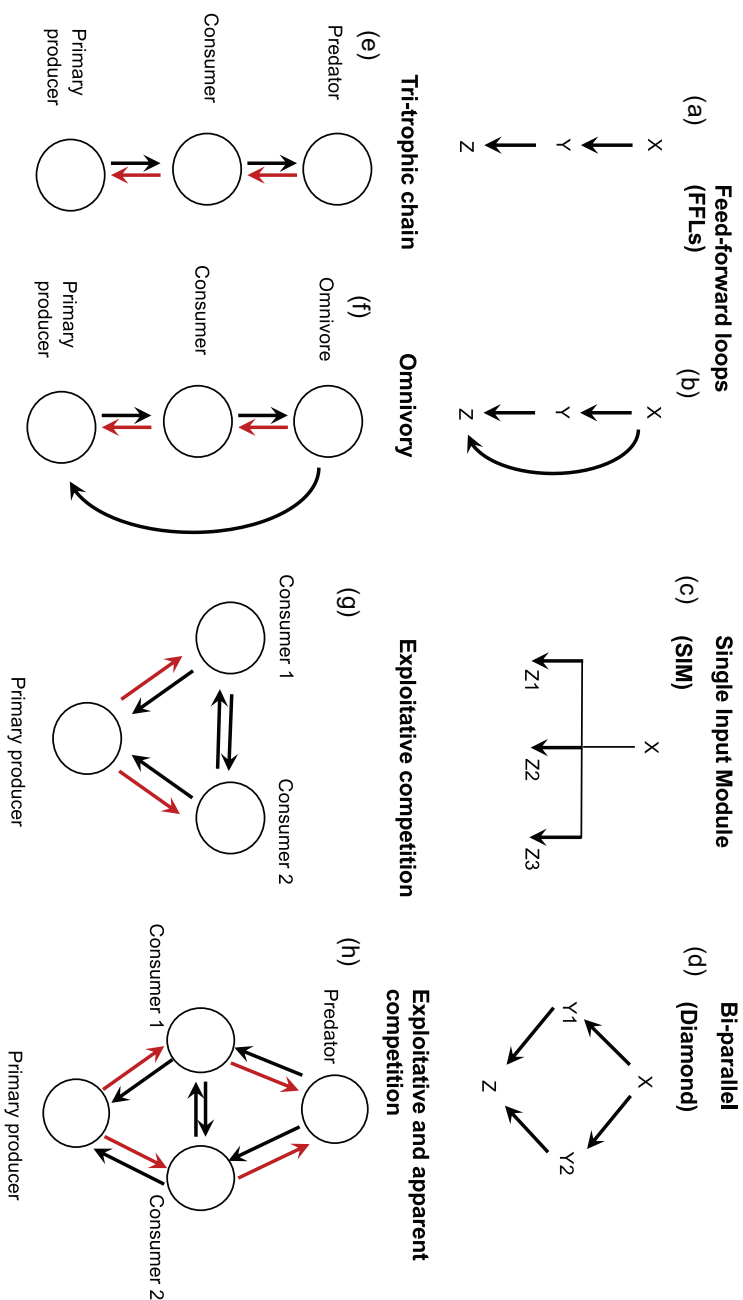


Figure 1: Dominant motifs in biological networks. The top row depicts the Feed-forward loops (FFLs) and Single Input Modules (SIMs) found in transcription networks, and the bi-parallel (diamond) motif found in signal transduction networks. In the FFLs, X and Y are transcriptional activators and Z is a promoter (Alon, 2007); In SIMs, X is a regulator and Z_i $i = 1, \dots, 3$ are a group of target genes. In the bi-parallel motif, X, Y_i ($i = 1, 2$), Z represent signaling proteins and the arrows represent processes such as phosphorylation (Alon, 2007). The bottom row depicts the equivalent food web motifs: try-trophic food chain, omnivory, exploitative competition and the diamond motif arising from the combination of exploitative and apparent competition. Note that the ecological motifs constitute feed-forward loops in terms of energy transfer but feedback loops in terms of interactions among consumers and resources.

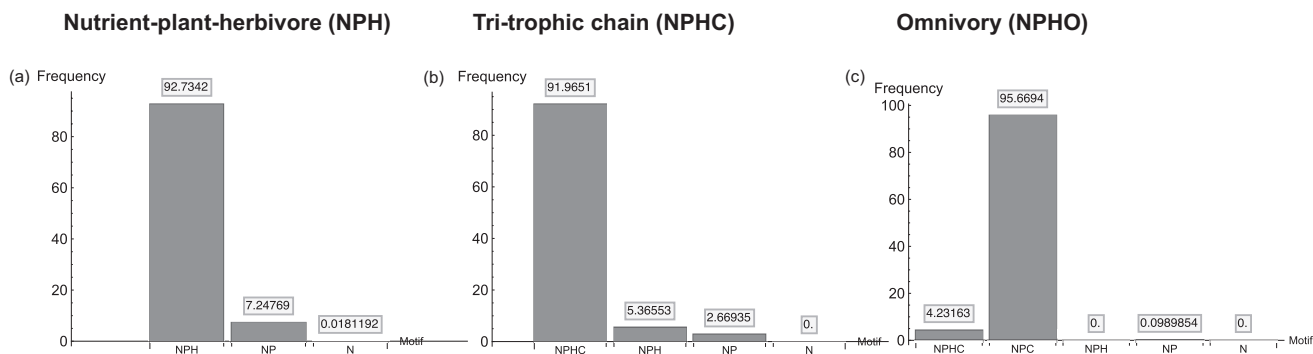


Figure 2: Emergence of vertical chains through sequential species invasions of a nutrient-plant interaction. Panels (a)-(c) depict the frequency distribution of emergent motifs when a nutrient-plant interaction is invaded by a herbivore (panel (a)), a nutrient-plant-herbivore interaction is invaded by a top predator (panel (b)) and nutrient-plant-herbivore interaction is invaded by an omnivore (panels (c)). Parameter definitions and values are given in Tables 1 and 2.

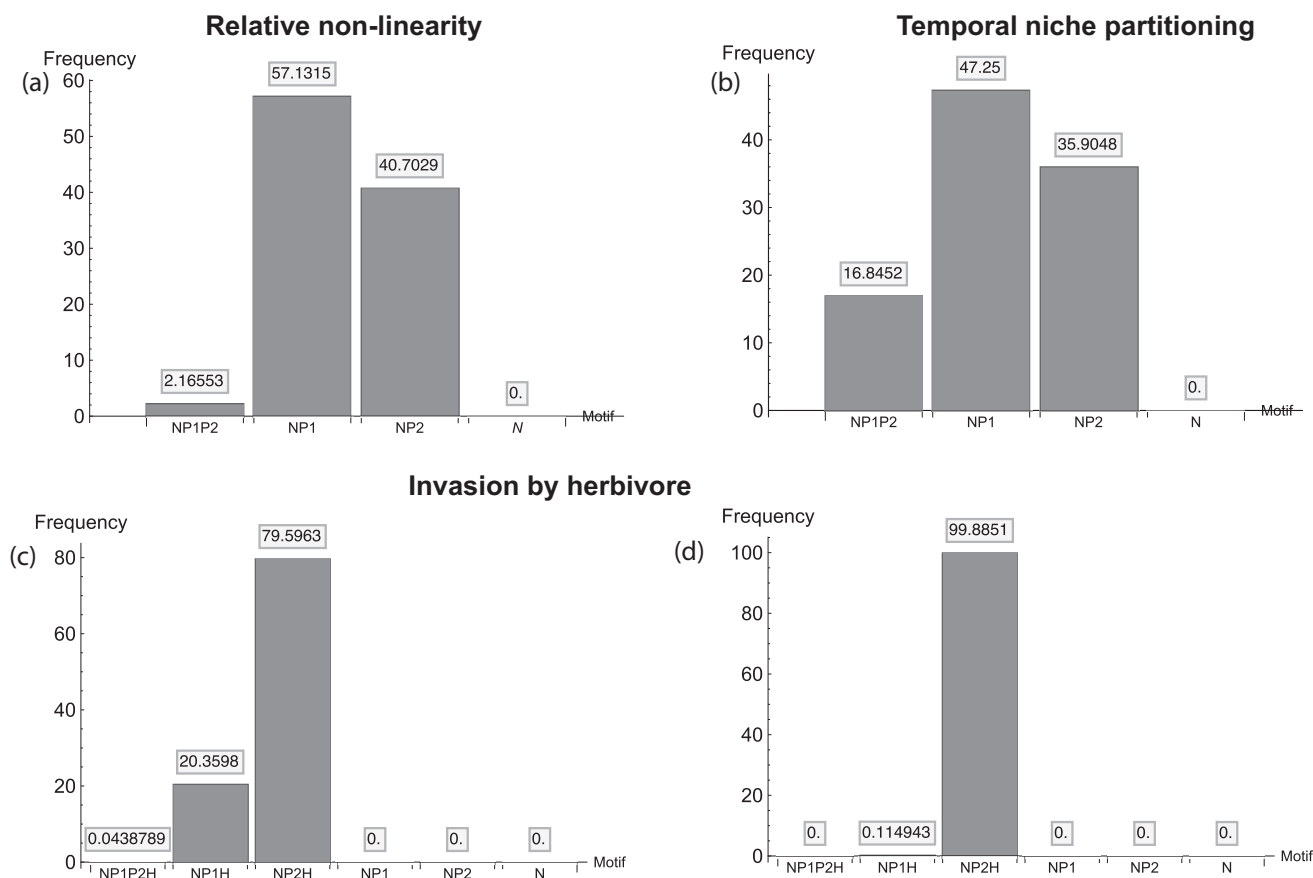


Figure 3: Plant species coexistence via relative non-linearity (RN; panel (a)) and temporal niche partitioning (TNP; panel (b)), and robustness coexistence to invasion by a herbivore (RN: panel (c); TNP: panels (f) and (d)). Parameter definitions and values are given in Tables 1 and 2.

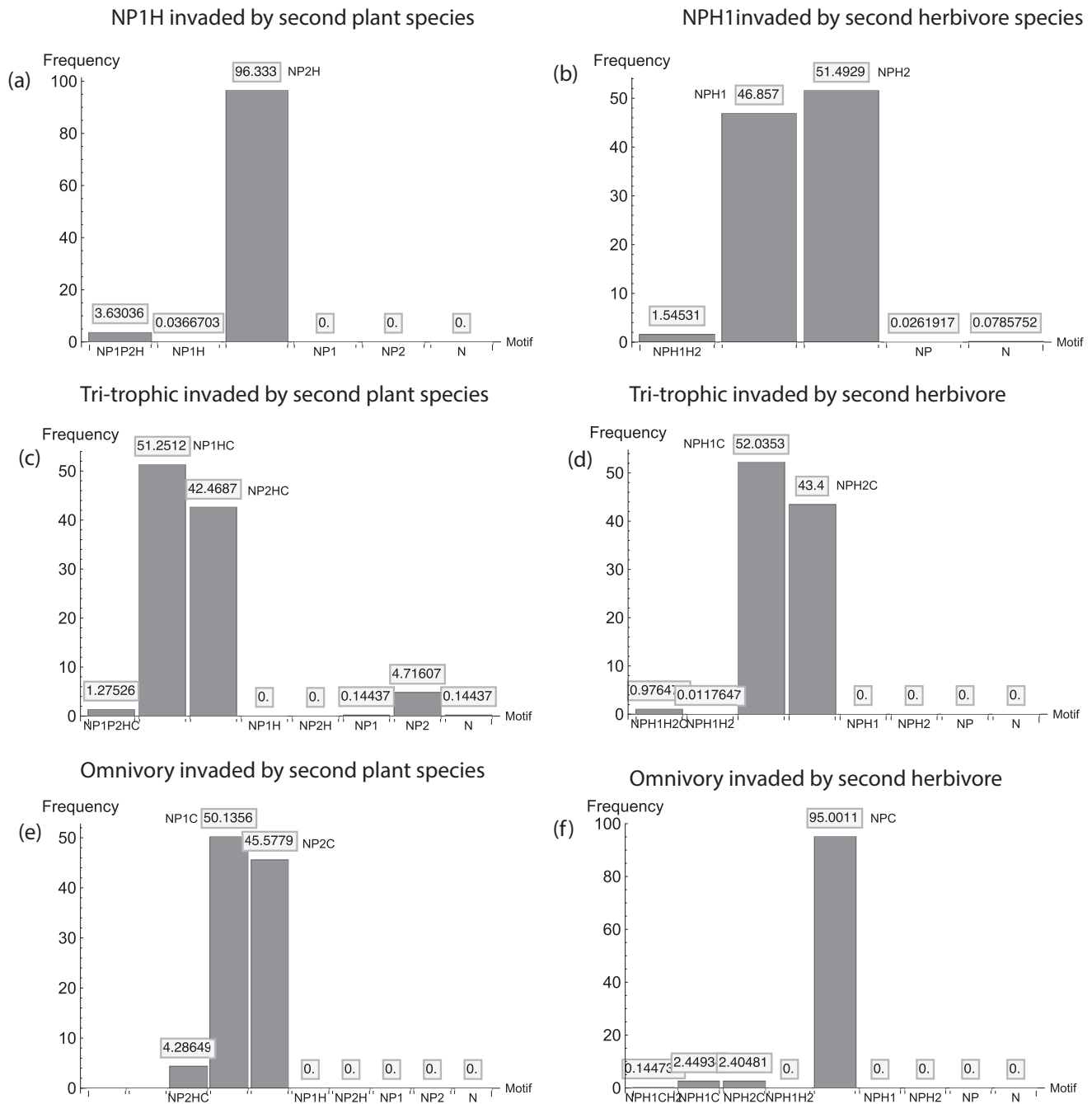


Figure 4: Vertical trophic chains invaded by a second plant or herbivore species. Panels (a) and (b) depict, respectively, the invasion of a NPH interaction by a second plant and second herbivore species. Panels (c) and (d) and (e) and (f) depict the same for the tri-trophic chain and omnivory. Parameter definitions and values are given in Tables 1 and 2.

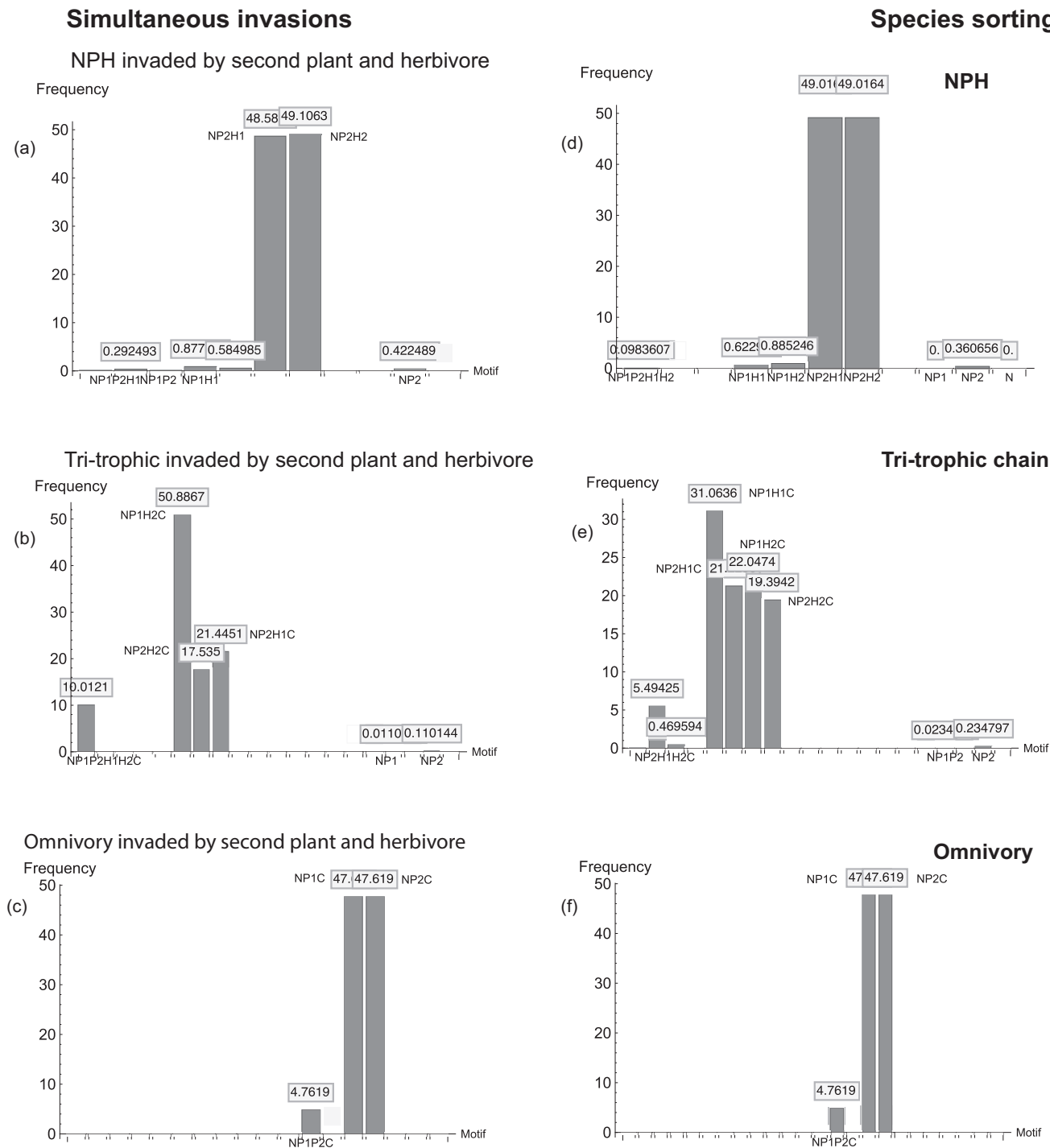


Figure 5: Simultaneous invasion by multiple species and species sorting in vertical trophic chains. Panels in the left column ((a)-(c)) depict simultaneous invasion by a second plant and herbivore species in nutrient-plant-herbivore, tri-trophic, and omnivory interactions. Panels in the right column depict the outcome of species sorting. In the case of sorting, each community is started with the full complement of species ($NP_1P_2H_1H_2$, $NP_1P_2H_1H_2C$, $NP_1P_2H_1H_2O$), and allowed to interact for 50,000 time units. All panels depict the frequency distributions of species in the three communities at the long-term steady state. Parameter definitions and values are given in Tables 1 and 2.

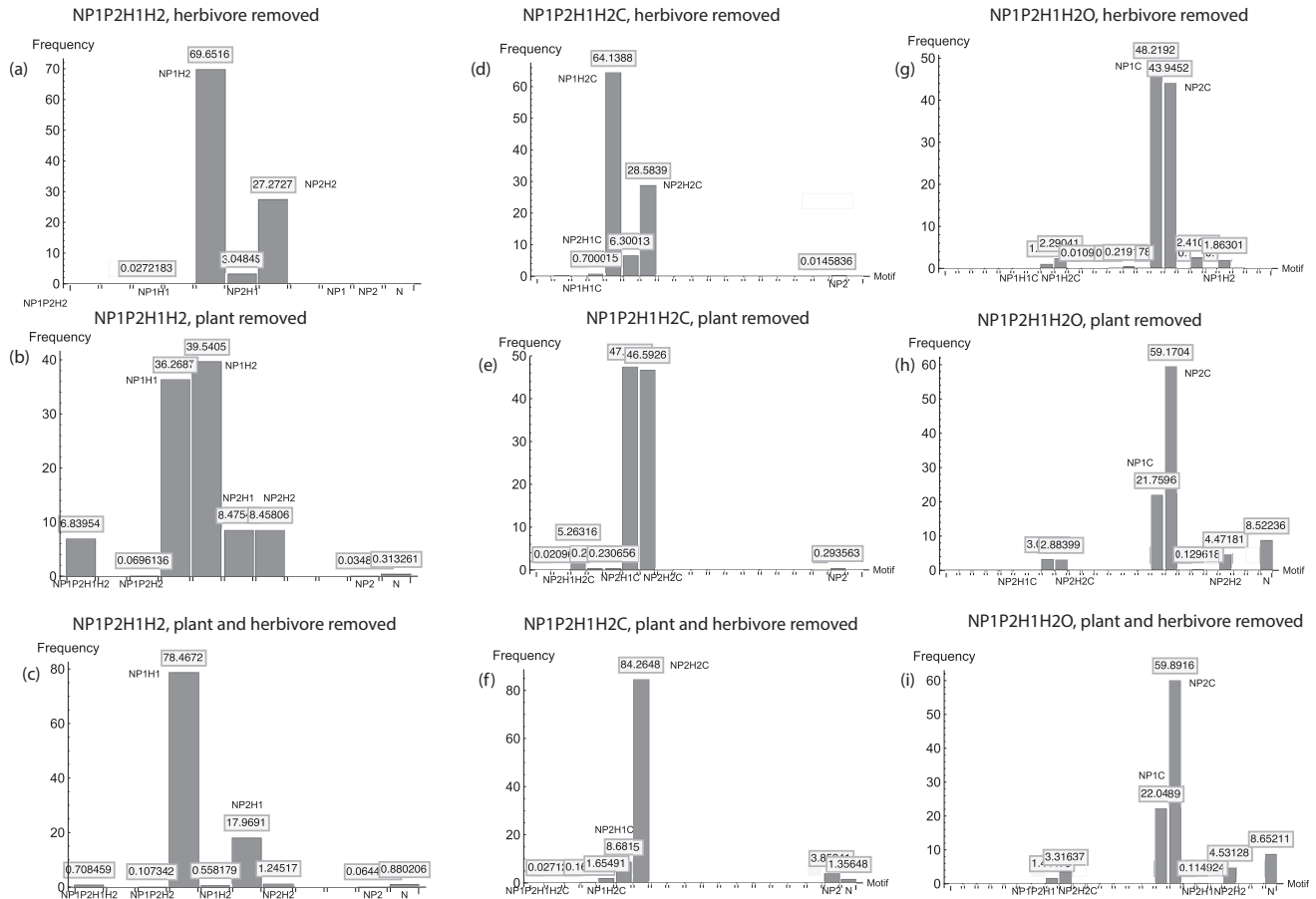


Figure 6: Disassembly of nutrient-plant-herbivore (panels (a)-(c)), tri-trophic (panels (d)-(f)), and omnivory ((g)-(j)) communities. Each community is started with the full complement of species ($NP_1P_2H_1H_2$, $NP_1P_2H_1H_2C$, $NP_1P_2H_1H_2O$), allowed to reach steady state, and subjected to sequential species removals (omnivore, predator, herbivore, plant). Parameter definitions and values are given in Tables 1 and 2.