**Why there are so few trophic levels: selection against instability explains the pattern**

**Letter to Ecology Letters**

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**Abstract**

Food chains are short, rarely more than five trophic levels long. The cause of this pattern remains unresolved, and no current hypothesis fully explains this phenomenon. We offer an explanation based on the stability of food chains that have been shifted away from linearity to be more web-like. The shift from linear chains to webs was accomplished by making each trophic level consume all levels below its own. The probability of stability for such “universal omnivory” chains declined strongly with chain length, and was as low as 1% with six level chains but highest for two and three level chains. The simple view that longer, reticulated chains are less stable seems to resolve the long-standing question of why there are so few trophic levels in nature.

**Introduction**

Food chains are typically short, often having as few as three levels (Elton 1927; Pimm & Lawton 1977) and rarely more than five (Yodzis 1981; Pimm 1982). The distribution of trophic position, measured as 1 plus the average trophic position of a species’ prey, for 50 published food webs shows that most species have a trophic position around 2 or 3 (**Figure 1a**). Very few species have a trophic position higher than 5 in these food webs (see Supplemental Information for details on the webs used). Alternatively, the single longest chain in each of 50 published webs is most frequently between 3 and 5 levels (**Figure 1b**). A recent study by Ulanowicz et al. (2013) demonstrated that by accounting for the amount of biomass flowing along the links the number of effective trophic levels is approximately 3 for a set of 16 networks. Ulanowicz et al. (2013) speculated that this pattern may result from the elimination of configurations of interacting species that are less likely to persist that others. We think that our results, outlined below, provide strong support for the general ideas developed in their perspectives paper.

The limitation of food chain length has been addressed in a number of ways from energetics to foraging theory to dynamic constraints (Post 2002). Each theory has both strengths and weaknesses, leading many to believe that the limits of food chain length must be a complex blend of multiple causes (Post 2002). Thus, despite the wealth of literature that has been produced in search of an explanation for what limits the length of food chains, a simple theory predicting no more than five trophic levels has not emerged. In the words of MacArthur (1972; 253): “Scientists are perennially aware that it is best not to trust theory until it is confirmed by evidence. It is equally true, as Eddington pointed out, that it is best not to put too much faith in facts until they have been confirmed by theory.” We suggest a theory based on selection against unstable food web structures to explain the observed data (**Figure 1**).

The earliest explanation for food chain shortness is that the efficiency of energy transfer between trophic levels is low. Available energy at trophic level should therefore decrease rapidly going up the chain (Elton 1927; Lindeman 1942; Hutchinson 1959). Areas with higher energy availability (often measured as productivity) should then support longer chains, a prediction not supported by empirical observations. Up to 5 trophic levels are observed in both the highly productive tropics and the low productivity polar regions (Pimm 1982). An alternative explanation is that larger ecosystems allow for longer food chains, although the mechanism for this is unclear (Post 2002). Empirical support for this hypothesis is conflicting, with supporting evidence in lakes and some islands (Post 2002; Takimoto *et al.* 2008) but not on other islands (Young *et al.* 2013). The combination of productivity and ecosystem size, the productive-space hypothesis, has also been proposed to explain variation in food chain length (Schoener 1989; Spencer & Warren 1996; Vander Zanden *et al.* 1999; Post *et al.* 2000). Evidence for the productive-space hypothesis, however, is contradictory with an equal number of studies finding support as those failing to find support (Post 2002, 2007; Young *et al.* 2013).

Morphological or biological constraints (e.g., organism size, gape width, etc.) have been thought to limit food chain length, but this hypothesis is not well supported in the literature, and is generally rejected (Pimm 1982). Alternatively, optimal foraging theory suggests that because there is more available energy, it is evolutionarily more optimal to feed at low trophic levels, (Cohen *et al.* 1986). The question then becomes, why are food chains so long? Short food chains should result from the balance between feeding at low levels with more energy, and feeding at high levels to fulfill dietary/nutritional restrictions (Hastings & Conrad 1979; Cohen *et al.* 1986). Such a balance is very much in the spirit of our “universal omnivory” hypothesis (see below).

Longer food chains are expected to be dynamically fragile. Pimm and Lawton (1977) explored the role of dynamic constraints in limiting the length of food chains. Using analyses of community matrices of four species food chains, they found that as the number of trophic levels increased, so too did the time it took to return to equilibrium following a small perturbation. A decrease in stability with increasing chain length is also supported by evidence from protest microcosm studies (Morin & Lawler 1996; Holyoak & Sachdev 1998). Sterner *et al.* (1997), however, found that the theoretical result of Pimm and Lawton (1977) was primarily a methodological artifact resulting from differences in the number of negative (density-dependence) terms along the diagonal of the community matrix. Following the results of Sterner *et al.* (1997) studies exploring limits to food chain length have generally not explored the role of dynamic constraints. Most argue that dynamic constraints are less important to regulating the number of trophic levels compared to other mechanisms such as ecosystem size (Post 2002). We argue that a simple theory based on systemic selection against dynamically unstable structures that provides a solid basis for determining why the number of trophic levels is typically low.

Systemic selection occurs when unstable food web structures (here referring to patterns of interactions) lead to the loss of some or all of the species in a web, thus altering web topology by eliminating nodes (species) and links (interactions). Food webs that are stable are more likely to persist over time. Food chain and web stability is typically determined by calculating the eigenvalues of the Jacobian matrix, whose elements *aij* represent the impact of the population of species *j* on the *ith* species’ population(May 1972; Pimm & Lawton 1977; Sterner *et al.* 1997). In order to determine eigenvalues the matrix must first be evaluated based on data that most often are not available (e.g., interaction strengths, population sizes), a significant drawback.

Stability may also be determined based on the particular pattern of signs of the elements of the Jacobian matrix. Purely linear food chains (where A only eats B, B only eats C, etc.), for example, are stable based solely on the signs of the elements of the matrix rather than their magnitude. Such structures are termed qualitatively stable or sign-stable (May 1973). Thus, regardless of the number of levels it contains a purely linear food chain will be stable. Hypothetically one could have a stable ecosystem with one hundred trophic levels, with species that consumed each other sequentially down the food chain.

A sign-stable system must fulfill a set of specific conditions (May 1973), however, that are not met by most natural systems. For example, a sign-stable web cannot contain trophic loops, a feature that is often found in food webs (Neutel *et al.* 2002). Nonetheless, following the very productive idea of Allesina and Pascual (2008), we are able to determine the degree to which a given food chain is sign-stable, termed quasi sign-stability (QSS). QSS is a measure of how often a matrix with a given sign structure is stable given elements (*aij*) whose magnitudes are randomized. We can determine this by the proportion of iterations that a sign structured matrix filled with randomly sampled values is stable.

This proportion is the probability that a matrix with a given sign structure is stable. Because qualitatively stable food chains are stable regardless of changes in the magnitude of the elements of the matrix, chains exhibiting a higher degree of stability (greater QSS) should be able to remain stable given small changes in the values of the *aij.* Webs of interactions that have greater QSS will therefore provide a bufferagainst changes in the magnitudes of the *aij* resulting from stochastic environments, demography, and evolutionary change. We expect that food chains that have greater QSS will therefore be more persistent over time because the region of potentially stable parameter space will be larger, leading to a higher probability that the true values may remain within it. We hypothesize that webs with more trophic levels have lower QSS compared to webs with fewer trophic levels.

**Universal Omnivory**

Omnivory, feeding on more than one trophic level, was found by Pimm and Lawton (1977, 1978) to reduce the number of randomly parameterized matrices that were stable. This result, however, was given less weight compared to return time to equilibrium. They suggested that omnivory should be uncommon because chains that included omnivory were frequently unstable. Thompson et al. (2007), however, found that omnivory is common among species that occupy a trophic position higher than that of herbivores, with relatively few species occupying an integer trophic position (but see Thompson & Hemberg 2009). Likewise, other studies have found that anywhere between 46% (Williams & Martinez 2004) and 87% (Arim & Marquet 2004) of taxa in a given community feed on more than one trophic level.

Our suggestion of “universal omnivory” recognizes that omnivorous interactions are prevalent in nature, and that food chains are less linear and more reticulate. Here we focus on cases of universal omnivory, where each species consumes species from all trophic levels below it. We analyzed food webs with two to six nodes, each occupying a unique trophic level (measured as the longest trophic chain; **Figure 2**). Each species consumes from all levels below its own, rather than only the level directly below itself leading to more reticulate and less linear food chains. While this does represent the extreme case of the prevalence of omnivory we propose that it presents a realistic counterpoint to the traditional view of simple linear chains.

**Model Selection**

A sign matrix with (+) indicating the effect of the prey on the predator, (-) indicating the effect of the predator on the prey, and (0) indicating no interaction was generated for each web. We assumed a predator dependent functional response (Abrams & Ginzburg 2000) where there is mutual interference among consumers. On the spectrum of interference between prey-dependence (no interference) and ratio-dependence (complete interference) our assumed predator-dependent functional response is not as extreme as, but is closer to, ratio-dependence (Arditi & Ginzburg 2012: p 141).

Given “hungry” predators pure ratio-dependent theory predicts that the functional response is approximately linear and the dynamics of the system are donor-controlled (Arditi & Ginzburg 2012: p 92-93). In a donor-controlled system the functional response is independent of predator abundance, and is simply a function of prey abundance in this idealized example. Predator abundance will therefore have no impact on prey abundance. The linear approximation of the ratio-dependent system away from saturation as a donor-controlled model can be considered similar to the way in which Lotka-Volterra equations represent a linear approximation of Hollings’ nonlinear model.

The sign matrix of a donor-controlled system is triangular, with positive values on one side of the diagonal and 0s on the other side. As May (1974) noted, a triangular matrix would imply qualitative stability, thus in this ideal scenario any number of trophic levels will create a stable structure, the same as in a purely linear food chain. With the assumption of a predator-dependent functional response that lies close to, but not at the ratio-dependent end of the spectrum in our numerical simulations we relaxed the conditions of a perfect donor-control model. Instead of 0s for the impact of predators on their prey we substituted small values relative to the impact of prey on predators.

**Simulation Methods**

Using numerical simulations in R version 2.15.2 (R Core Team 2012), we examined the QSS of food chains shifted from linearity by universal omnivory. See the Supporting Information for details on the code used for this simulation, as well as all other code used in our analysis and figures. For all five sign matrices, each (+) was replaced with a random value drawn from a uniform distribution between 0 and 10 (*U(0, 10)*) for the impact of the prey population on the predator population. Each (-) was replaced with a random value sampled from a uniform distribution between -1 and 0 (*U(-1, 0)*) for the impact of the predator on the prey. The mean impact of the predator on the prey was thus assumed to be 10 times weaker than in the other direction and not 0 as in pure donor-controlled approximations. In order to counter the influence of varying the number of density-dependence terms on the diagonal (Sterner *et al.* 1997), all species were assigned -1 along the diagonal, representing the effect of density-dependence. By including density-dependence for all trophic levels we have taken a conservative point of view by allowing the highest probability that the system will be stable.

For each sign matrix, 10,000 random matrices were sampled from the distributions described above. For each sampled matrix we calculated whether or not it was stable by analyzing the eigenvalues of the matrix. The system was considered stable if all real parts of the eigenvalues of the matrix were negative. We then calculated the probability of stability, QSS, for each sign matrix as the percentage of iterations that yielded a stable matrix.

*Sensitivity Analysis*

To determine whether the observed reduction in stability was an artifact of our choice of the distributions from which we sampled, we conducted a sensitivity analysis. We kept the impact of the prey on the predator constant, sampled from a random uniform distribution between 0 and 10 (as above). The range for the impact of the predator on the prey was varied such that on average it was two and three orders of magnitude smaller than the impact of the prey on the predator (drawn from *U(-0.1,0)* and *U(-0.01,0)* respectively). In the opposite direction we altered the impact of the predator on the prey to be drawn uniformly random between -5 and 0 (*U(-5, 0)*). Density-dependence (values along the diagonal) was maintained at -1 for all species and simulations.

**Results**

As the number of trophic levels in the chain increased, the probability of the chain being stable (QSS) decreased (**Figure 3)**. The two-species case is a qualitatively stable food chain given our assumptions; it is a pure chain that is always stable. The largest decrease in QSS occurred between three (85.4%) and four levels (41.7%), dropping by 44%. Adding an additional level, to five species dropped the probability of a chain being stable by 32%, to less than 10%. The chance that a chain of six species would be stable was only approximately 1%.

*Sensitivity Analysis*

As the number of trophic levels increased, QSS decreased for all webs with greater than four levels regardless of our choice of distributions of values for the impact of the predator on the prey. The more asymmetrical the distributions were on average, the more likely webs with more trophic levels were going to be stable. When the means of the distributions were two orders of magnitude apart, webs with up to three levels were all stable (**Figure 3**). With a difference between means three orders of magnitude, 99% of webs with up to four levels were stable (**Figure 3**). When the means became more symmetrical the decline in QSS was slightly larger at three (66.5%) and four (37.6%) levels, but slightly smaller at five (17.5%) and six levels (6.7%). No more than 7% of webs with six levels were stable regardless of the degree of symmetry (**Figure 3**).

**Discussion**

We found a simple theory that predicts the observed pattern of food chain lengths in nature. Food webs with fewer trophic levels have a larger range of parameter space (magnitudes of the elements of the Jacobian matrix) within which they exhibit stability; they have a greater buffer against perturbation due to environmental and demographic stochasticity. The ability to buffer against change will have long-term consequences for the dynamics and structure of food webs observed in nature. Over time species participating in webs that are unstable will have a higher likelihood of going extinct, changing the structure of the web. In contrast webs that have a higher probability of being stable will likely persist, increasing the chances that they are observed in nature.

Here we have demonstrated that quasi sign-stability declines with increasing numbers of trophic levels in food chains made more reticulate by omnivory. Our theory predicts that two- and three-level webs should be most prevalent, with four- and five-level webs less likely, while webs with chains greater than six levels should be rare. Thus, our theory’s predictions closely mirror reality, where most species occupy trophic positions between two and three, and very few occupy a position higher than five (Vander Zanden *et al.* 1999; Beaudoin *et al.* 2001).

Our choice for the distributions from which values for the impact of species on each other were drawn was not based on empirical evidence. Instead we made assumptions based on the degree of interference along the spectrum between pure ratio-dependence and prey-dependence. The degree of interference among predators was assumed to be closer to the case of ratio-dependence than prey-dependence. Along with our focus on the case of hungry predators we were confident in assuming a relatively small impact of the predator on the prey population. Sensitivity analysis showed that our results are relatively robust to our choice of the magnitudes of the impact of the predator on the prey and vice versa.

The impact of omnivory on the stability of food chains has been previously studied in some depth (Pimm & Lawton 1978; Morin & Lawler 1996; Holyoak & Sachdev 1998; Long *et al.* 2011). The primary focus of these studies has been on whether or not omnivory should be observed in nature due its destabilizing impact on food chain dynamics. Alternatively, we have chosen to assume omnivory is prevalent, and investigate how that will impact the probability of observing food chain length patterns in food webs. While omnivory may not be as ubiquitous as we have assumed (Thompson & Hemberg 2009), we argue that chains with universal omnivory are a better abstraction than linear chains, since, food chains in nature are embedded in reticulate webs. We would not expect that theory pertaining to purely linear food chains should match the observation of short food chains, and for the most part it has not (Sterner *et al.* 1997).

Studies that test the relationship between food chain length and productivity or ecosystem size have found conflicting evidence. Post (2000) found that maximum trophic position increased with ecosystem size (measured as lake volume), but not productivity in lake ecosystems. In contrast, Young et al. (2013) found that food chain length increased with productivity but not ecosystem size (measured as island area) for tropical islands. The variation in trophic chain length in both studies, however, ranged between two and six. In a thorough analysis of food chain length variation in freshwater springs, Glazier (2012) showed that, for a biologically tolerable range of temperatures, food chain length does not change significantly and has a mean around 3.2. Our systemic selection hypothesis eliminates many of these apparent contradictions by proposing a mechanism that predicts the distribution of food chain lengths observed most often in nature (**Figure 1**).

Ecosystem size and productivity influence population dynamics. It is somewhat intuitive that larger areas should support larger populations, on average. Similarly, theory based on predator interference predicts that with increasing basal productivity we should expect proportional increases in equilibrium population sizes for all trophic levels (Ginzburg & Akçakaya 1992). Larger populations are less susceptible to extirpation resulting from stochastically varying demography or environments. Thus, gains in the stability of populations through larger numbers of individuals may buffer against losses in QSS resulting from increased length of chains. Different types of environment (e.g., lakes or islands) may also differ in the relative importance of variables such as ecosystem size and productivity for population size. The contradictory patterns observed by Post (2000) and Young (2013) may therefore be explained by slight modification to the general theory we have outlined above.

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**Figure Legends**

**Figure 1:**