



Why there are so few trophic levels: Selection against instability explains the pattern [☆]



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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. We start with a simple example of food webs of two to six species arranged so that species consume all those with a trophic level less than their 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. We further explored the influence of chain length on food web stability by testing food webs with varying levels of connectance that were constructed either randomly or with the niche model. By additionally altering the relative impacts of predators on prey, and vice-versa, we test the role of our assumptions on the relationship between chain length and stability. Food webs characterized by low to moderate degrees of connectance, asymmetrical interactions, and relatively weak density dependence showed a pattern of reduced stability with longer trophic chains. The simple view that food webs characterized by long trophic chains are less stable seems to resolve the long-standing question of why there are so few trophic levels in nature.

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1. Introduction

Food chains are typically short, often having as few as two steps (Elton, 1927; Pimm and Lawton, 1977) and rarely more than four (Pimm, 1982; Yodzis, 1981). Food chain length is directly related to the number of trophic levels in a food web. A food chain with two steps has three trophic levels: a producer, intermediate consumer, and a top predator. By defining trophic level this way, however, it becomes difficult to determine the trophic levels of species embedded in complex food webs. To better define the trophic level of a given species in a food web, we will use two related, but distinct, definitions: trophic position and longest chain.

The distribution of trophic position, measured as one plus the average trophic position of a species' prey, for 50 published food webs shows that 98.8% of consumer nodes have a trophic position less than or equal to four (Fig. 1a). Very few species have a trophic position higher than five in these food webs (see Appendix A for details on the webs used). Alternatively, the maximum number of steps between a given

consumer and a basal species, the longest chain, in 39 of the 50 published webs (78%) is less than or equal to five levels (Fig. 1b).

A recent study by Ulanowicz et al. (2013) demonstrated that by accounting for the amount of biomass flowing along the links (links with more biomass flow are weighted more heavily) the number of effective trophic levels is approximately three 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 than others.

The most commonly tested hypotheses for variation in food chain length are associated with relatively conflicting support. The earliest explanation for food chain shortness is that the efficiency of energy transfer between trophic levels is low. Available energy at a trophic level should therefore decrease rapidly going up the chain (Elton, 1927; Hutchinson, 1959; Lindeman, 1942). Areas with higher energy availability (often measured as productivity) should then support longer chains, a prediction not supported by empirical observations. Up to five 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 (Post et al., 2000). Ecosystem size has been found to be related to food chain length 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 (Post et al., 2000; Schoener, 1989; Spencer and Warren, 1996; Vander Zanden et al.,

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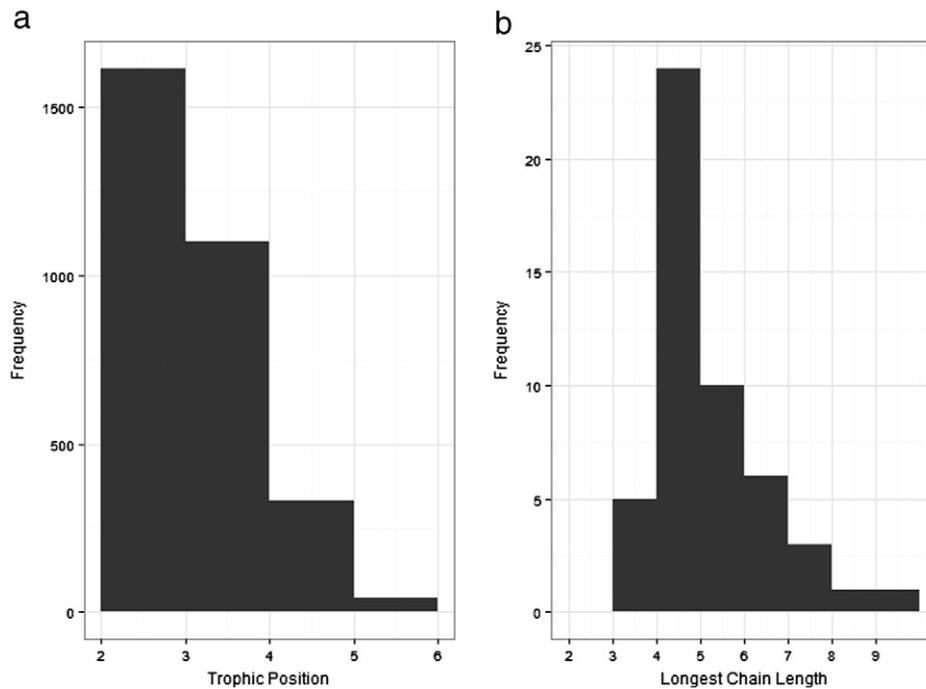


Fig. 1. The trophic position of each species in 50 published food webs (a) and the length of the single longest chain in each web (b). The data sources and code for generating this figure can be found in Appendix A.

1999). 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).

Longer food chains are also expected to be dynamically fragile. Pimm and Lawton (1977) explored the role of dynamic constraints in limiting the length of food chains. Dynamic constraints would occur if the number of trophic levels in a community was limited by population dynamics of the constituent species. Using analyses of community matrices of four species food webs, 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 protist microcosm studies (Holyoak and Sachdev, 1998; Morin and Lawler, 1996).

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). Dynamic constraints due to colonization and extinction in a spatial context, however, have also been suggested as an alternative (Holt, 2002) that seems to fit in with ecosystem size based hypotheses.

Nonetheless through systemic selection against dynamically unstable structures as suggested by Ulanowicz et al. (2013), dynamic constraints can provide a foundation 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 unstable are less likely to persist over time and more likely to undergo a change in species composition (e.g., through extinction) or interactions (such as by prey-switching). If systemic selection against unstable food web configurations leads to shorter food chains, then food webs made of longer chains (meaning more trophic levels) should be less stable.

Webs of interactions that have a higher degree of stability, measured as quasi sign-stability (QSS; Allesina and Pascual, 2008), should provide a buffer against changes in the magnitudes of interaction strengths resulting from stochastic environments, demography, and evolutionary change. Food webs that have greater QSS should 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.

Omnivory, feeding on a range of trophic positions, was found by Pimm and Lawton (1977, 1978) to reduce the probability that a food web would be 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 and Hemberg, 2009). Likewise, other studies have found that anywhere between 46% (Williams and Martinez, 2004) and 87% (Arim and Marquet, 2004) of taxa in a given community feed on more than one trophic level. Furthermore, omnivory does not become less common when only looking at the strongest interactions in the web (Fig. A1).

Below we examine how increasing food chain length (more trophic levels) impacts the degree to which the web is stable. We use food webs constructed at three levels of ecological realism; oversimplified chains with omnivory, random webs, and niche model food webs. The simplest example of chains with omnivory is used to demonstrate the expected relationship, while the random and niche model constructed webs allow us to further explore the impact of our assumptions, and determine under what conditions there is a relationship between food chain length and stability.

2. Methods

The stability of food chains and food webs is typically determined by calculating the eigenvalues of the Jacobian matrix, whose elements a_{ij} represent the impact of the population of species j on the i th species'

population (May, 1972; Pimm and 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 regardless of their magnitude. This can be useful for studies of food webs, because while the interaction strengths and population sizes of the constituent species are rarely known, it is relatively simple to convert an adjacency matrix (a species by species matrix where a one denotes an interaction and a zero is no interaction) to a sign matrix. Food webs that consist of predator–prey interactions would assign each pair (a_{ij}/a_{ji}) a plus/minus. 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 chains or webs 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 food web must fulfill a set of specific conditions (May, 1973) that are not met by most webs in nature. For example, a sign-stable web cannot contain trophic loops (A eats B, B eats C, C eats A), 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 (a_{ij}) whose magnitudes are randomized. While a sign-stable web will be stable regardless of the magnitudes of the elements of the Jacobian matrix (how large an impact each species has on those it interacts with), quasi sign-stable webs will only be stable for some range of magnitudes.

2.1. General model

The Jacobian matrix is found by taking the partial derivative of species growth equations. One of the benefits of using quasi sign-stability to determine the stability of food webs is that we do not need to explicitly define a model structure for the predator–prey equations. Rather, the elements of the Jacobian matrix can be sampled from an underlying distribution that can be based on the predictions from a general model.

We assumed a general predator dependent functional response (Abrams and Ginzburg, 2000) where there is mutual interference among consumers. This means that the functional response is dependent on both the prey and predator densities, rather than only on prey density (as in prey-dependent). On the spectrum of interference between prey-dependence (no interference) and ratio-dependence (complete interference where the functional response is dependent on the number of prey per predator) our assumed predator-dependent functional response is not as extreme as, but is closer to, ratio-dependence (Arditi and Ginzburg, 2012).

Assuming “hungry” predators a ratio-dependent functional response is approximately linear and the dynamics of the system are donor-controlled (Arditi and Ginzburg, 2012). In a donor-controlled system the mortality imposed by predation is independent of predator abundance (when abundance is high) 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 zeros on the other side. As May (1973) 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. Rather than assuming that predators have no impact on their prey we substituted small values relative to the impact of prey on predators. Thus the elements of the Jacobian matrix may be drawn from distributions that are asymmetrical, meaning that the distribution of the impact of the prey on the predator will have a mean that is larger (in absolute magnitude) than the distribution of the impact of the predator on the prey. For the random and niche model webs, we altered this assumption to test for a wider range of potential distributions varying in asymmetry.

2.2. Web construction

2.2.1. Simple webs

To illuminate our hypothesis we start with a simple example of webs with two to six species arranged in a chain. These webs are characterized by universal omnivory, where each species consumes from all levels below its own, making the chain more web-like (Fig. 2). For example, the fourth species eats species one, two, and three. Each web was then converted into a signed matrix, with (+/–) assigned to each predator prey link, a (+) indicating the positive effect of prey consumption on the predator's population growth and a (–) indicating the negative effect of the predator's consumption on the prey's population growth. A (–) assigned to the diagonal, indicating negative density dependence, to avoid the problems illustrated by Sterner et al. (1997) Due to our use of universal omnivory, the sign matrices consist

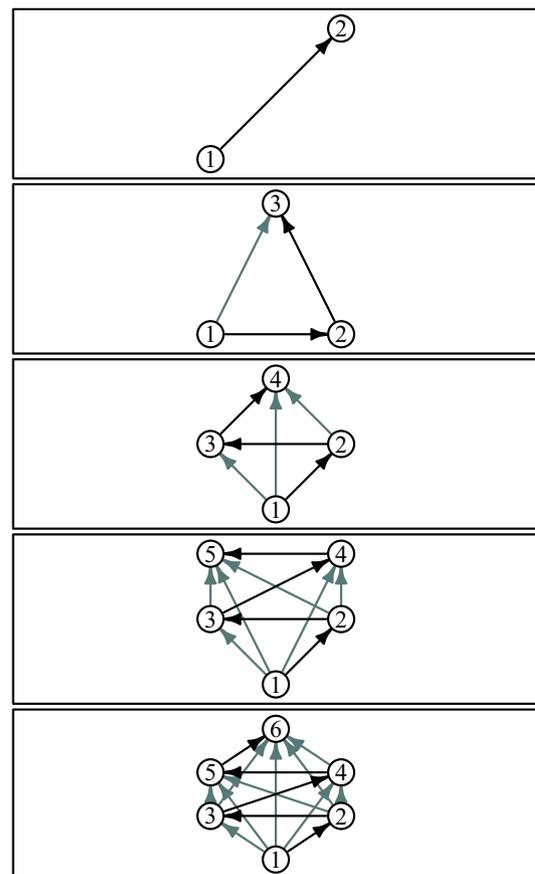


Fig. 2. The five simple food webs with two to six trophic levels. The measured longest chain is highlighted in bold. Code for making these webs and generating this figure can be found in Appendix A.

of positives on the upper triangle of the matrix, and negatives on the lower triangle.

2.2.2. Random webs

Random ten-species webs were generated with five different levels of connectance (0.12, 0.16, 0.20, 0.24, and 0.28). Connectance is the proportion of all possible links between species that are realized (the number of links divided by the number of species squared). To ensure that we were sampling webs with all possible chain lengths the construction of each random web was started with a chain of two to ten species (one to nine links). Then, depending on the connectance, any remaining links were randomly assigned among species. For example, a ten species food web with a connectance (links per species squared) of 0.12 has 12 links. Thus a random web initiated with a ten species chain would have three more links randomly distributed, while a random web initiated with a five species chain would have eight more links distributed among the species. For these random webs, omnivory is included and increases with increasing connectance but is not universal as was assumed in the simple webs.

Each link was given a (+/−) to generate the sign matrix, with zeros indicating no interaction. Negatives were assigned to the diagonal. All random webs were constrained so that each species either consumed another species directly, or was consumed itself (i.e. no unconnected nodes). For each level of connectance 225 webs were generated.

We chose to use a random model to construct these food webs for a thorough exploration of the parameter space of potential food web configurations. Food webs built using the cascade or niche model have similar structural properties to those that are observed in nature. Both the cascade and niche models arrange species along some hypothetical niche axis and use simple rules that determine what each species consumes to construct food webs. Using the random model we can include webs that we would not expect to find in nature, which is why it is useful to test our hypotheses. Additionally, many of the commonly found food web motifs are also found in these webs, such as tritrophic chains, apparent competition, direct competition, and intraguild predation. However, due to the way we built these webs there are no trophic loops.

2.2.3. Niche model webs

The niche model (Williams and Martinez, 2000) uses two parameters, the number of species and connectance, to construct food webs. Species are assigned a randomly drawn niche value and feeding range. The center of the feeding range is randomly placed at a point lower than the species' own niche value. Each species then feeds on all species whose niche values lie within the feeding range. Trophic loops are allowed in this model, because only the center of the feeding range must be below the given species' niche value up to half the feeding range can be on species with a greater niche value. It has been shown that the niche model accurately reproduces many structural properties of food webs (Camacho et al., 2007; Stouffer et al., 2005, 2007). As with the random model omnivory is included in these webs, but is not universal.

For each of five levels of connectance (0.12, 0.16, 0.20, 0.24, and 0.28) 105 ten-species niche model webs were generated. Each web was then converted into the corresponding sign matrix, and negatives were assigned along the diagonal for all species.

2.3. Simulations

All simulations were completed in R version 3.1.1 (R Core Team, 2014). Once webs were constructed, the signs of the interactions were replaced by random draws from predefined uniform distributions. For each randomly drawn matrix the eigenvalue with the largest real part was calculated. This process was repeated multiple times for each web (see below for details). Quasi sign-stability could then be

computed as the proportion of randomly drawn matrices with eigenvalues (largest real part) that were all negative.

2.3.1. Simple webs

For the simplified webs we sampled the impact of the predator on the prey from a random uniform distribution between -1 and 0 . The impact of the prey on the predator was drawn from a uniform distribution between 0 and 10 . These distributions fulfill our expectations based on the predictions of the general predator-dependent function response outlined above (asymmetrical impacts) but are otherwise not based on empirical data. For the diagonal of the Jacobian matrix, negative ones were assigned to all species. Thus density dependence was as large as the maximum possible impact of a predator on its prey for all species.

For each of the five sign matrices we constructed we sampled 10,000 Jacobian matrices and computed the eigenvalue with the largest real part for each. The proportion of these eigenvalues' real parts that were negative was then recorded as the web's quasi sign-stability.

2.3.2. Random webs

For each of the 225 webs per level of connectance the sign matrix was filled in with randomly drawn values from one of nine different pairs of distributions. All distributions were uniform, but were varied in their maximum/minimum values. The impact of the prey on the predator was set to a minimum of zero and a maximum of either one, five, or ten. The impact of the predator on the prey was set to a maximum of zero and a minimum of negative one, five or ten. This leads to nine possible combinations of the two distributions, along with the five levels of connectance used yields 45 distinct combinations of distributions and connectance. The (described above) values for the Jacobian matrices in the simple model were drawn from the respective distributions and used to compute the eigenvalue with the largest real part. This process was repeated 1000 times for each web and distribution combination. Quasi sign-stability was again recorded as the number of randomly sampled matrices whose largest real eigenvalue was negative.

2.3.3. Niche model webs

The same simulation procedure was completed for the niche model webs as for the random webs. We used the same uniform distributions for the relative impacts as well, from zero to one, five, or ten for the impact of the prey on their predator (and the same, but negative for the predator on the prey). For each pair of distributions we sampled values to fill in the sign matrix of each web 1000 times. Quasi sign-stability was determined as the proportion of those 1000 iterations that were stable, whose eigenvalue with the largest real part was negative.

3. Results

3.1. Simple webs

As the number of trophic levels in the chain increased, the probability of the chain being stable (QSS) decreased (Fig. 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 (85.7%) and four levels (41.4%), dropping by 44%. Adding an additional level, to five species reduced the probability of a chain being stable by 31%, to nearly 10%. The chance that a chain of six species would be stable was only approximately 1%.

3.2. Random webs

Asymmetry in interaction strength, and number of interactions impact the relationship of QSS and food chain length in random webs (Fig. 4). As long as there is some degree of asymmetry in the interactions ($10/-1$, $5/-1$, $1/-5$, $1/-10$), whether it leans toward the impact of

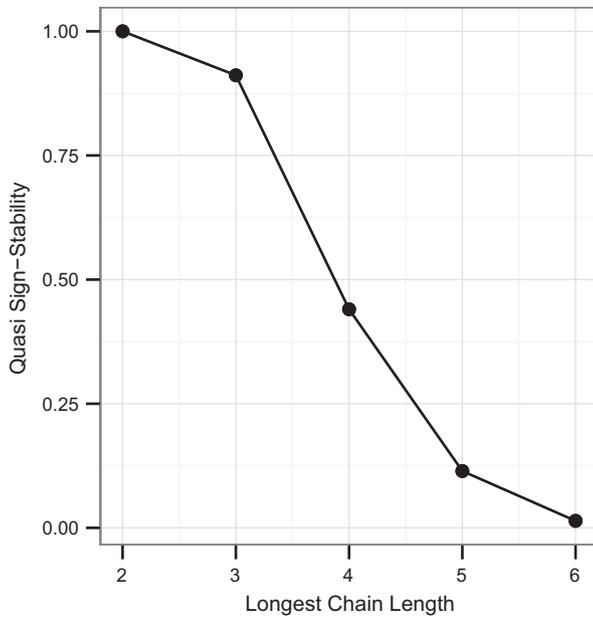


Fig. 3. The quasi sign-stability of the simple webs with two to six trophic levels, pictured in Fig. 2. Quasi sign-stability is the proportion of matrices with randomly sampled elements (a_{ij}) that have an eigenvalue whose largest real part is negative. Code for the simulation and producing this figure can be found in Appendix A.

the prey on the predator or vice versa, webs with longer chains on average are less likely to be stable at equilibrium (lower QSS). When the relative impacts are drawn from symmetrical distributions the negative relationship of QSS and trophic level disappeared. Drawing from a symmetrical distribution ($1/-1$) that is equal in magnitude to the strength of density dependence, however, an increase in the longest trophic chain slightly increases quasi sign stability. Increasing the total number of interactions (connectance) always decreased stability with respect to any given maximum trophic position.

3.3. Niche model webs

There is a negative relationship between the longest food chain length and quasi sign-stability in for most of our simulated niche model webs (Fig. 5). In webs with asymmetrical distributions there tends to be a negative trend that appears more consistently across different connectance levels when average interaction strength is lower. Asymmetrical webs with comparatively high interaction strength (e.g., $10/-5$, $5/-10$) the negative trend is not consistent across connectance levels. Drawing from symmetrical distributions ($10/-10$, $5/-5$) there was no clear trend between longest chain length and quasi sign-stability. Again, when density dependence was strong relative to the impacts of predation ($1/-1$) webs were consistently stable.

4. Discussion

Our results support the hypothesis that webs with more trophic levels are less likely to be stable. We argue that quasi sign-stability is a good predictor of 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 has 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 number of trophic levels in food chains made more reticulate by omnivory and in webs, reinforcing the results of Pimm and Lawton (1977). We found 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 predictions closely mirror reality, where most non-basal species occupy trophic positions between two and three, and very few occupy a position higher than five (Beaudoin et al., 2001; Vander Zanden et al., 1999). Furthermore, in most scenarios webs whose longest chain length was high were typically much less likely to be stable than webs with shorter chains.

The primary focus of prior work on the impact of omnivory on the stability of food chains (Holyoak and Sachdev, 1998; Long et al., 2011; Morin and Lawler, 1996; Pimm and Lawton, 1978) has been on whether or not omnivory should be observed in nature due to its destabilizing impact on food chain dynamics. Alternatively, we have chosen to assume that omnivory, in the sense of feeding on prey occupying a range of trophic positions, is prevalent, and investigate how that will impact the probability of observing food chain length patterns in food webs. We would not expect that predictions 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). While omnivory may not be as ubiquitous as we have assumed in our simple webs (Thompson and Hemberg, 2009), we propose that chains with universal omnivory are a more useful abstraction than linear chains because in nature food chains are embedded in reticulate webs. The predictions from our simple webs are reflected in the results of our analysis of random and niche model food webs.

Our choice for the distributions from which values for the impact of species on each other were drawn was not based on empirical evidence. By using multiple different distributions for the relative impacts of the predator and prey, however, we 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. When there is asymmetry in interaction strengths, and moderate levels of connectance the pattern is maintained. It is not surprising that simulations with weak asymmetry but relatively strong interaction strength ($10/-5$, $5/-10$) showed a weak trend towards decreasing QSS with more trophic levels, following May's (1972) result.

May (1972) showed that highly connected random webs were less stable than those that were less connected. Similarly when the total number of interactions was high (24 and 28 interactions, connectance of 0.24, 0.28) all webs had a low probability of stability, with the exception of webs with high density dependence. As we have suggested for webs with more trophic levels, webs with high connectance values should be selected against. It is unlikely however, that systemic selection against highly connected communities is resulting in the observed pattern of food chain length. Highly connected webs are typically characterized by shorter food chains on average, and thus fewer trophic levels. We may then consider that the observed limitation of food chain length to three or four is the result of a balancing of dynamic constraints operating on both the number of trophic levels and the overall connectance of the web. Such a balance would need to be struck by shorter food chains, but lower connectance.

Dynamic constraints seem to offer a reasonable explanation for the observed pattern of food chain length in nature. We anticipate that the results of our simulations merely offer qualitative descriptions of the relationship between food chain length and stability rather than precise quantitative estimates. Nonetheless previous studies (Post, 2002; Post et al., 2000; Young et al., 2013) have demonstrated that other possible mechanisms may be at work by finding relationships between chain length and productivity or ecosystem size. However, in these studies food chain length does not exceed 6 as predicted by the dynamic constraint hypothesis and their results often conflict.

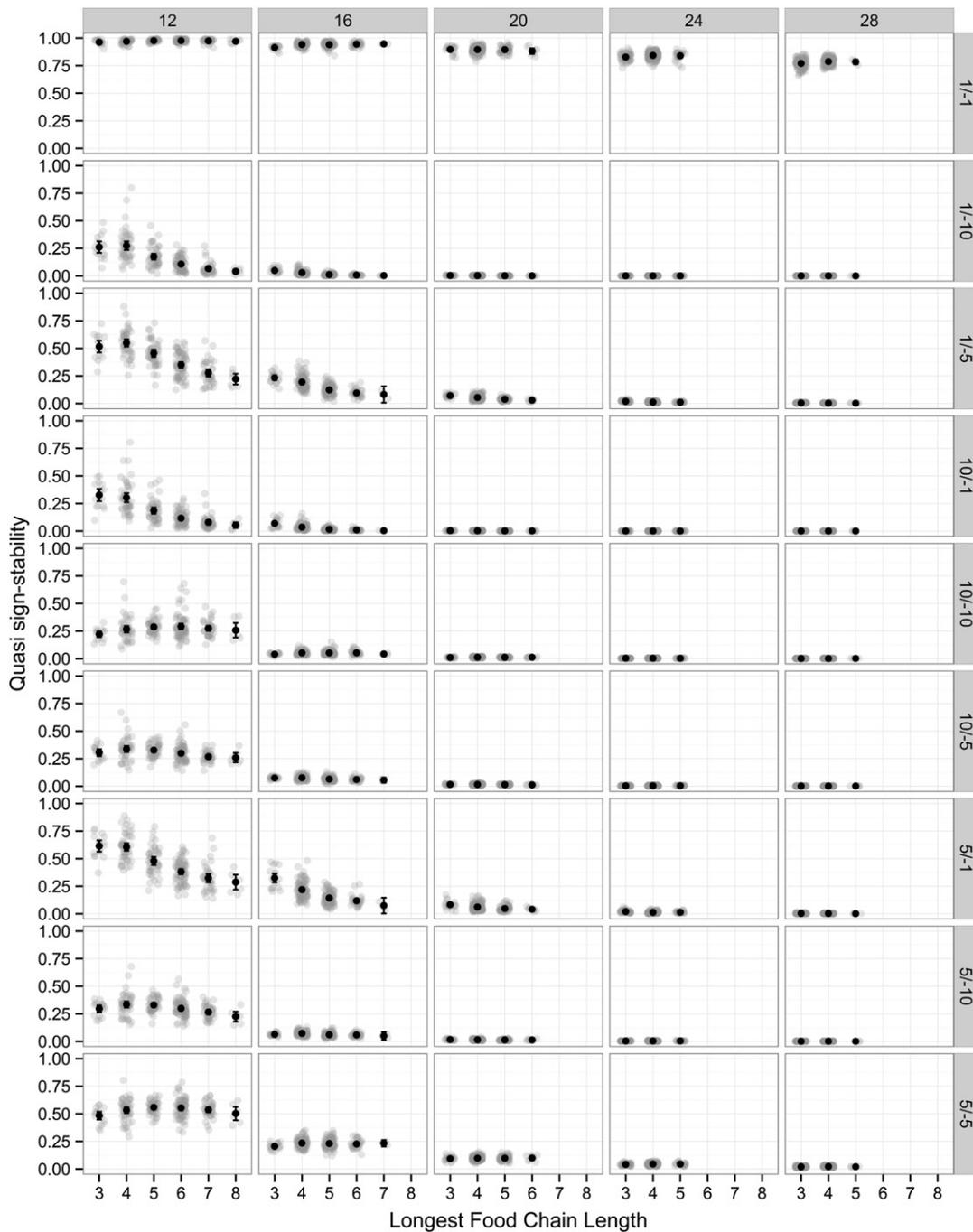


Fig. 4. Plot of quasi sign-stability against longest chain length in random food webs. Gray dots are individual data points (data has been jittered to avoid overlap) while black dots are the mean. Error bars are 95% confidence intervals calculated as the mean plus/minus 1.96 times the standard error. Columns represent different levels of connectance (labeled across the top) while rows represent the different parameters used to create the distributions of relative impacts. The rows are labeled according to *impact of the prey on the predator/impact of the predator on the prey* with each value being the maximum/minimum of the uniform distribution used. The code to create this figure can be found in Appendix A.

Post et al. (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. The 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 (Fig. 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 and 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

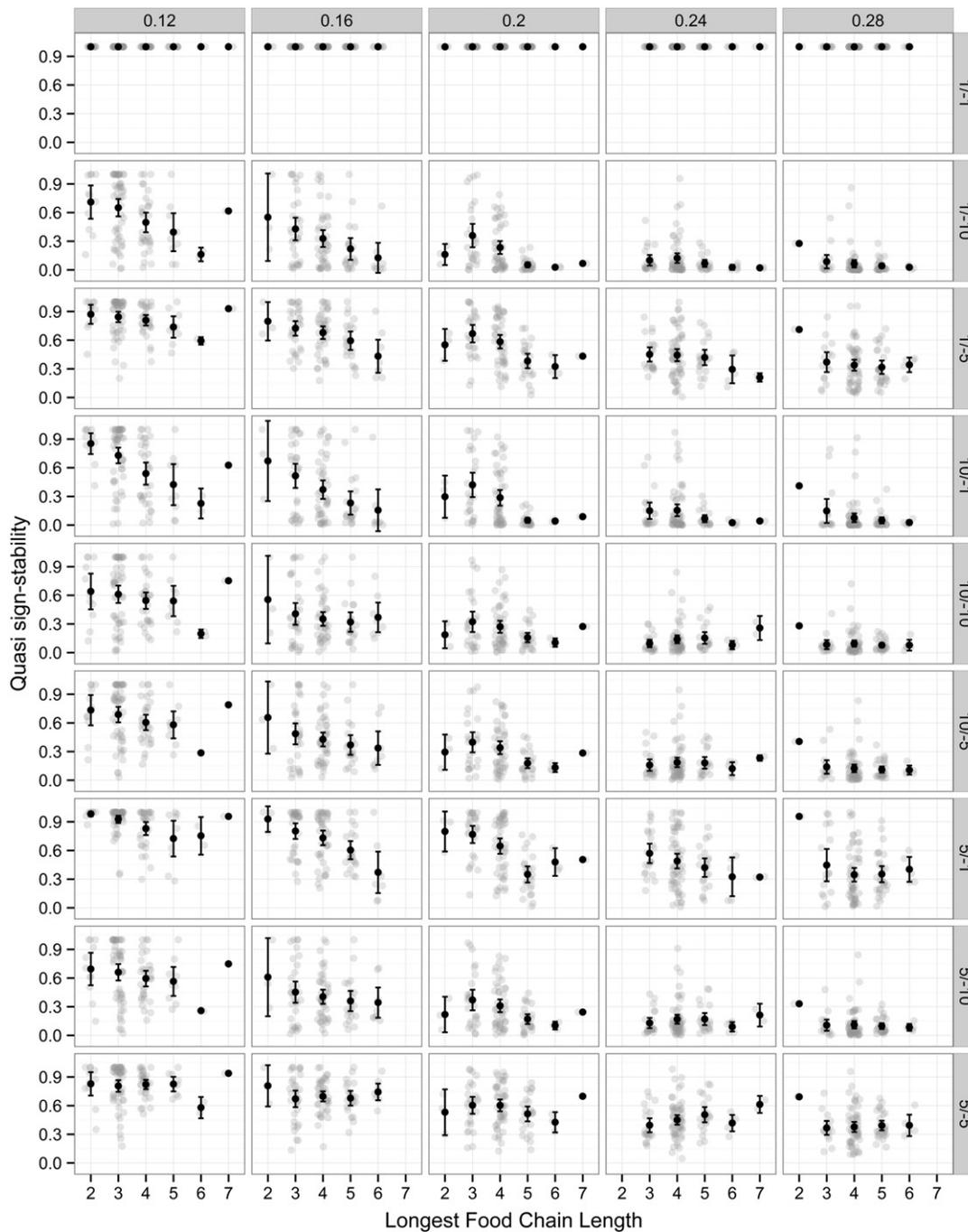


Fig. 5. Plot of quasi sign-stability against longest chain length in niche model food webs. Gray dots are individual data points (data has been jittered to avoid overlap) while black dots are the mean. Error bars are 95% confidence intervals calculated as the mean plus/minus 1.96 times the standard error. Columns represent different levels of connectance (labeled across the top) while rows represent the different parameters used to create the distributions of relative impacts. The rows are labeled according to *impact of the prey on the predator/impact of the predator on the prey* with each value being the maximum/minimum of the uniform distribution used. The code to create this figure can be found in Appendix A.

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. Alternatively ecosystems of greater size may offer a greater opportunity for patch dynamics where longer chains may exist in a spatial context (e.g., by top predators being present in some patches but not others; Holt, 1996, 2002; Polis et al., 1997). The contradictory patterns observed by Post et al. (2000) and Young et al. (2013) may therefore be explained by slight modification to the general hypothesis of dynamic constraints and systemic selection we have outlined above.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.fooweb.2014.11.002>.

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